

Smallmouth Bass in the Pacific Northwest: A Threat to Native Species; a Benefit for Anglers

MICHAEL P. CAREY,¹ BETH L. SANDERSON,¹ THOMAS A. FRIESEN,²
KATIE A. BARNAS,¹ and JULIAN D. OLDEN³

¹NOAA Fisheries, Northwest Fisheries Science Center, Seattle, Washington, USA

²Oregon Department of Fish and Wildlife, Corvallis, Oregon, USA

³University of Washington, School of Aquatic and Fishery Sciences, Seattle, Washington, USA

*As a popular sportfish, smallmouth bass (*Micropterus dolomieu*) generates considerable angling opportunities with benefits to local economies even outside of their native range. Smallmouth bass was first introduced to the Pacific Northwest region of North America as a sportfish over 80 years ago, and this species is now widely distributed. More recently, smallmouth bass have become a large component of the fish community in many streams, rivers, and lakes. Smallmouth bass thrive in the Pacific Northwest largely due to the habitat created by human modifications of the landscape. While a desired sportfish, smallmouth bass may also negatively affect native fishes. Of greatest concern is predation on threatened and endangered Pacific salmon; however, the current level of knowledge is inadequate to make informed management decisions for smallmouth bass. Management options for smallmouth bass are complicated further because fisheries agencies are simultaneously charged with enhancing fishing opportunities and controlling predators of threatened and endangered salmon. To advance conservation science, there is a need to determine the utility of different management approaches, and testing options in key areas of overlap between smallmouth bass and salmon is suggested.*

Keywords smallmouth bass, predation, sportfish, invasive species, threatened and endangered salmon

INTRODUCTION

Smallmouth bass (*Micropterus dolomieu*) supports popular recreational fisheries and has been intentionally stocked in over 20 countries, as far from their native range as Japan and South Africa (Iguchi et al., 2004; Woodford et al., 2005; Aday et al., 2009). A freshwater fish native to central and eastern North America, the native range of smallmouth bass extends from the Great Lakes and St. Lawrence River south through the Mississippi River and tributaries (Figure 1). In the Pacific Northwest (PNW) of the United States, large numbers of anglers target the black basses, which include smallmouth bass and largemouth bass (*M. salmoides*). The black bass fishery supports millions of angler fishing days per year and contributes significantly to local economies (Table 1). As in other regions, fishing has

declined over the last decade (Sutton et al., 2009), although the proportion of anglers targeting both species of bass relative to the total number of freshwater anglers has remained fairly stable (Table 1). Differences in angler trends among states and through time are not well understood. While an important sportfish in the PNW, smallmouth bass is a species with considerable potential to impact native species, communities, and freshwater ecosystems in the region (Vander Zanden et al., 1999, 2004; Cucherousset and Olden, 2011).

The juxtaposition between smallmouth bass, the popular sportfish, and smallmouth bass, the potentially harmful non-native species, creates an unfortunate and intense conflict. Smallmouth bass have been identified as a factor contributing to the decline of wild populations of Pacific salmon (*Oncorhynchus* spp.), now listed under the U.S. Endangered Species Act (ESA; Lackey et al., 2006; Sanderson et al., 2009). Thus, although recreational opportunities created by smallmouth bass represent significant societal value, the extent to which this species may hinder the recovery of Pacific salmon requires attention.

Address correspondence to Dr. Michael P. Carey, NOAA Fisheries, Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA 98112, USA. E-mail: Michael.P.Carey@noaa.gov

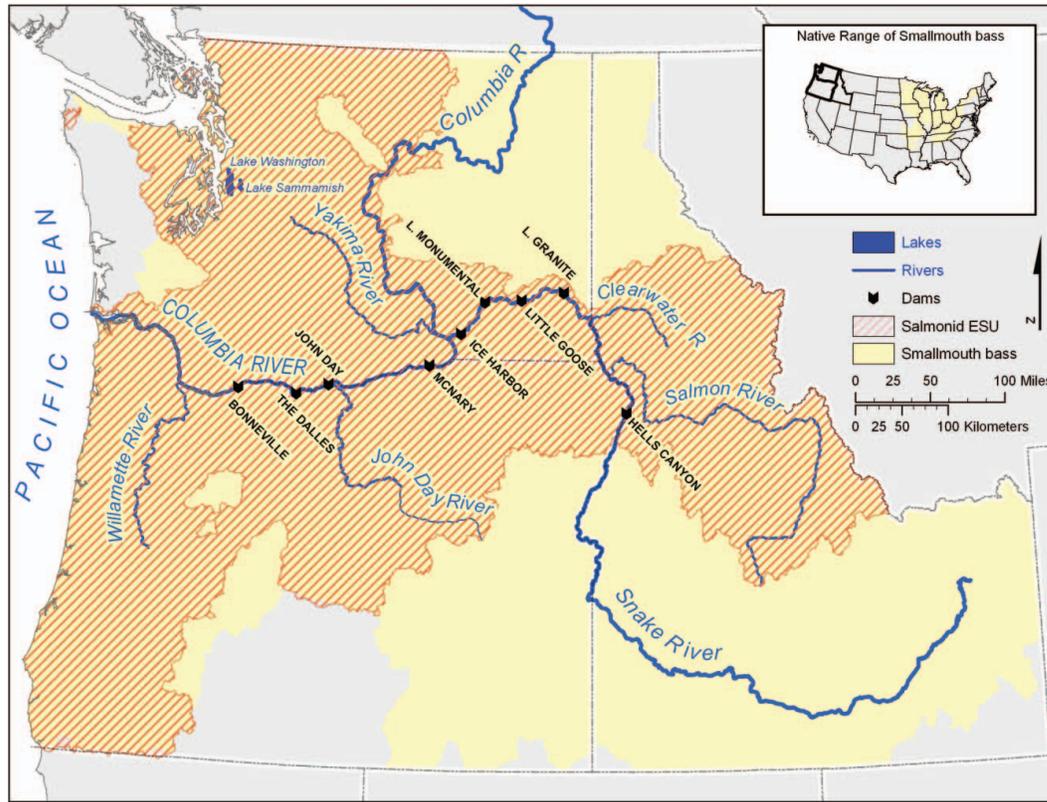


Figure 1 Smallmouth bass (*Micropterus dolomieu*) distribution in their native range (NatureServe, 2009) and in the PNW by fourth field HUC (hydrologic unit code). Locations indicate areas where diet data is available on smallmouth bass populations. The combined distribution of the evolutionary significant units (ESU) of threatened and endangered salmon is overlaid for the PNW (color figure available online).

Herein, the focus is on smallmouth bass in the PNW to explore the apparent conflict created by a species that is both a popular sportfish and a threat to ESA-listed species. A com-

Table 1 Number of anglers, percentage of anglers out of total freshwater anglers, and number of days fishing for black bass (smallmouth bass and largemouth bass) in the PNW (U.S. Fish and Wildlife Service [USFWS], 1996, 2001, 2006)

State	Year	Number of bass anglers	Percent of bass anglers out of total	Number of days fishing	Economic value (\$)
Idaho	2006	54,000	15	329,000	9,870,000
	2001	53,000	13	526,000	15,780,000
	1996	73,000	15	498,000	14,940,000
Oregon	2006	70,000	14	778,000	23,340,000
	2001	63,000	10	541,000	16,230,000
	1996	73,000	16	1,212,000	36,360,000
Washington	2006	75,000	14	1,087,000	32,610,000
	2001	102,000	16	1,393,000	41,790,000
	1996	150,000	21	2,122,000	63,660,000

Note: Smallmouth bass and largemouth bass are collectively referred to as black bass and are often reported in combination for management purposes. The net economic value (the value anglers place on sport fishing over and above their expenditures, in dollars) for black bass is estimated by the number of days fishing and an estimate of \$30/day economic value of fishing for warmwater species (TCW Economics 2008).

prehensive summary of the history and ecology of smallmouth bass in the PNW is provided, and research exploring the impact of smallmouth bass on salmon is reviewed. Next, management strategies are explored for smallmouth bass and the implications of management actions for smallmouth bass, threatened and endangered salmon, and recreational anglers. Generalities about the conflicts involving smallmouth bass are applicable to other game species that require management of competing demands for natural resources.

HISTORY AND ECOLOGY OF SMALLMOUTH BASS IN THE PNW

Humans have been transplanting smallmouth bass outside its native range for over 135 years. In the western United States, smallmouth bass were first introduced to California in 1874 (Lampman, 1946). This was followed by the 1923 introduction by the Oregon master game warden of 425 smallmouth bass into the Willamette River, Oregon (Lampman, 1946; LaVigne et al., 2008), and the intentional stocking of approximately 5,000 smallmouth bass into the Yakima River, Washington, in 1925. Throughout the PNW, smallmouth bass were stocked for sport fishing by state fisheries commissions and local citizens who did not anticipate the potential negative implications for

native species, particularly salmon. Judge S. H. Greene, described as a fishing authority of the early 1900s, stated in *The Oregonian* that (the bass would) “prove himself, if given the opportunity, the best friend of our salmon and trout” (Lampman, 1946, p. 103).

Smallmouth bass is now among the most widespread non-native species of fish in the PNW (Boersma et al., 2006; Sanderson et al., 2009; Figure 1), occupying both lentic systems, such as Lake Washington and Lake Sammamish, Washington (Pflug and Pauley, 1984; Fayram and Sibley, 2000), and lotic systems, such as the Columbia River and Snake Rivers (Tabor et al., 1993; Zimmerman and Parker, 1995; Naughton et al., 2004). Smallmouth bass inhabit many systems considered critical to the lifecycle of ESA-listed Pacific salmon (Figure 1). Volitional movement of smallmouth bass from original stocking sites, such as the documented exchange of fish between the Yakima and Columbia Rivers (Fritts and Pearsons, 2004), as well as extensive stocking by the Idaho, Oregon, and Washington state agencies, has led to its wide distribution over the last 50 years. In addition, Rahel (2004) and Johnson et al. (2009) suggested that unauthorized stocking has occurred in other regions of North America, and it is believed that it has occurred prevalently in the PNW. Private hatcheries throughout the PNW also sell and produce bass for stocking private ponds. In 2010, two private hatcheries were licensed to sell hatchery largemouth bass in Oregon for stocking (www.dfw.state.or.us/resources/fishing/fish_propagation.asp). Stocking by state, federal, and private hatcheries, along with illegal public translocations, may collectively supplement and expand current smallmouth bass populations and further hinder efforts to conserve native species.

Initially, smallmouth bass were a minor component of the resident fish communities. For instance, while stocked in the Willamette River in 1923, it was not until 1944 that smallmouth bass collections were reported. Subsequently, only four individuals were found in a survey in 1951, and smallmouth bass was not commonly collected during sampling by the Oregon Department of Fish and Wildlife (ODFW) in the 1980s (LaVigne et al., 2008). More recently, the percentage of smallmouth bass has increased in many communities, and its range has likely expanded. In the last 20 years, smallmouth bass has become a major component of the food web for the Willamette River. Smallmouth bass was the dominant non-native species during surveys conducted in 1998, 1999, and 2006, and its distribution and abundance in the Willamette River has increased substantially over time (LaVigne et al., 2008). Other systems also show expanding trends, such as in the John Day Reservoir (Columbia River), where recent electrofishing catches of smallmouth bass were higher than surveys in 1990s (Figure 2). In the lower John Day River, an initial stocking of only 80 individual smallmouth bass in 1971 has led to a population that supports a recreational fishery (Shrader and Gray, 1999) and has expanded to the upper-reaches of the basin (D. J. Lawrence and J. D. Olden, unpublished data). This demonstrates that a small number of individuals can establish a large population of smallmouth bass in some PNW

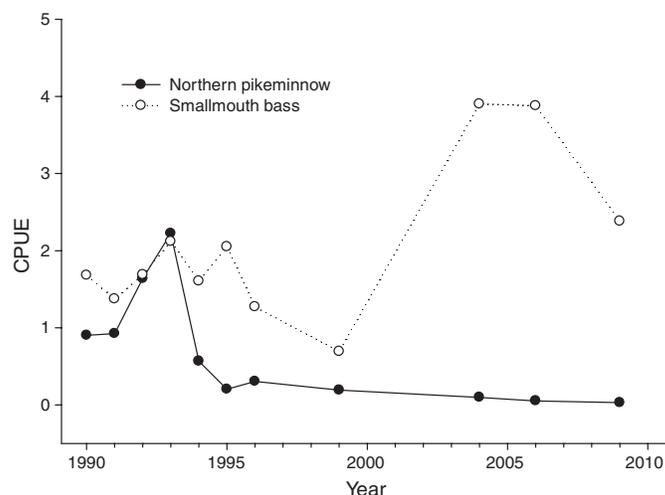


Figure 2 Catch per unit effort (CPUE; fish per 900 s of continuous boat electrofishing) of northern pikeminnow and smallmouth bass in John Day Reservoir, 1990–2009 (Oregon Department of Fish and Wildlife, unpublished data). Data were collected for fish capable of consuming juvenile salmon: northern pikeminnow ≥ 250 -mm fork length and smallmouth bass ≥ 200 -mm fork length (Vigg et al., 1991; Zimmerman, 1999). Removal fisheries for northern pikeminnow ≥ 250 -mm fork length were implemented throughout the lower Columbia River basin in 1991 (Friesen and Ward, 1999).

systems and suggests that impacts may not become apparent for decades.

Smallmouth bass have spread and thrived in the Columbia and Snake Rivers largely due to habitat created by human activities. Specifically, the reservoir habitat formed by dams creates slow backwaters and warmer temperatures throughout the river, benefiting smallmouth bass populations and disfavoring natives (Zimmerman and Parker, 1995; Naughton et al., 2004; LaVigne et al., 2008). Preferences of smallmouth bass are evident at finer spatial scales within the habitats created by dams. Smallmouth bass abundances are higher in forebay and mid-reservoir areas, where the lowest flows, warmest water, and highest water clarity occur (Zimmerman and Parker, 1995). Conditions created by dam construction are similar to the habitats occupied by smallmouth bass in their native region. Elsewhere, reservoirs facilitate expansion by providing suitable habitat and act as stepping-stones for movement across the landscape (Johnson et al., 2008). Smallmouth bass also thrives below dams and in undammed systems with suitable environmental conditions. Climate change is predicted to expand the amount of suitable habitat for smallmouth bass (Vander Zanden et al., 1999, 2004; Sharma et al., 2009) as well as extend the warm-water periods in impoundments, leading to more temporal overlap between juvenile salmon and smallmouth bass (Petersen and Kitchell, 2001). Thus, the impact of smallmouth bass is expected to increase in the PNW with rising temperatures (Beamesderfer and North, 1995; Tabor et al. 2007). A full understanding of smallmouth bass expansion also requires the consideration of other mechanisms, such as displacement of native predators through competition or intentional removal by humans.

POTENTIAL IMPACTS OF SMALLMOUTH BASS ON ENDANGERED SALMON

Predation

Smallmouth bass consumes vertebrates (primarily fish) and invertebrates (such as crayfish) in their native range (Warren, 2009). In the PNW, smallmouth bass consumes similar prey items. For example, native crayfish (*Pacifastacus leniusculus*) and sculpin (*Cottus* spp.) were the primary diet items of smallmouth bass in Lake Sammamish, Washington (Pflug and Pauley, 1984). In the John Day Reservoir, Washington is also the primary diet item for smallmouth bass, with crayfish increasing in importance further downstream toward the John Day Dam (Poe et al., 1991). Smallmouth bass is a non-selective, opportunistic feeder (Pflug and Pauley, 1984; Weidel et al., 2000; Warren, 2009). In the PNW, this means smallmouth bass may consume juvenile Pacific salmon when the two species overlap in time and space. For example, in Lake Washington, predation by smallmouth bass increases in spring (50% salmon by weight of diet items) when juvenile sockeye salmon utilizes littoral areas occupied by smallmouth bass during outmigration (Fayram and Sibley, 2000; Tabor et al., 2007). No salmon were found in smallmouth bass diets between July and September (Fayram and Sibley, 2000), suggesting limited spatial overlap during most of the year in

Lake Washington. Not all of these studies (e.g., Lake Washington) pertain to salmon that are threatened or endangered; however, they do provide information about overall feeding and potential impacts on salmon from smallmouth bass.

In areas inhabited by threatened or endangered salmon, specifically in the Columbia and Snake River basins, the percent of smallmouth bass diets containing salmon ranges from 0 to 65% by frequency and 0 to 89% by weight (Table 2). Smallmouth bass predation on salmon differs through time and across regions, leading to the large range in diet composition. For example, percent salmon in smallmouth bass diets was 12.4% (9.8% Chinook, 2.6% unspecified salmon) below Bonneville Dam, 14.2% (7.7% Chinook, 6.5% unspecified salmon) in lower Columbia River reservoirs, and 25.8% (12.6% Chinook, 2.5% steelhead; 10.7% unspecified) in the lower Snake River annually from 1990 to 1996 (Zimmerman, 1999; Table 2). Major tributaries of the Columbia River show similar variation in the percentage of salmon in smallmouth bass diets (Table 2). When identified, Chinook salmon is the most frequently consumed salmon species. At dams on the lower Snake River, salmon composed a higher proportion of the fish consumed by smallmouth bass at Lower Granite Dam than at Lower Monumental Dam or Little Goose Dam in 2007 (Table 3). In the few locations with standardized sampling in multiple years (Bonneville Reservoir, The Dalles Reservoir, and John Day Reservoir), the percent of

Table 2 Summary of smallmouth bass diets reported in the range of anadromous salmon in the Columbia and Snake River basins by body of water and year

Body of water	Year(s)	Percent of diet		Reference
		Frequency ^a	Weight ^a	
Columbia River basin				
Below Bonneville Dam	1990–96	2.6 U, 9.8 C		Zimmerman (1999)
John Day Reservoir	1983–85	4 U	4.2 U	Poe et al. (1991)
	1983–86	1–7 U	4 U	Vigg et al. 1991
Hanford Reach–McNary Reservoir	1990	65 U	59 U	Tabor et al. (1993)
Bonneville, Dalles, John Day, McNary Reservoirs	1990		31.1 U	Poe et al. (1994)
Bonneville, Dalles, John Day Reservoirs	1990–96	6.5 U, 7.7 C		Zimmerman (1999)
Snake River basin				
Lower Granite Reservoir	1994		89 U	Bennett et al. (1999)
	1995		56 U	Bennett et al. (1999)
	1996	< 1.0 C, < 1.0 S, < 1.0 U		Bennett and Naughton (1999)
	1997	< 1.0 C, < 1.0 S, < 1.0 U		Bennett and Naughton (1999)
Ice Harbor, L. Monumental, Little Goose, L. Granite Reservoirs	1991		12.4 U	Poe et al. (1994)
L. Monumental, Little Goose, L. Granite Reservoirs	1991, 1994–96	12.6 C, 2.5 S, 10.7 U		Zimmerman (1999)
Snake River arm	1996	< 1.0 C, < 1.0 S, < 1.0 U		Bennett and Naughton (1999)
	1997	< 1.0 C, < 1.0 S, < 1.0 U		Bennett and Naughton (1999)
Clearwater River arm, Snake River	1996	< 1.0 C, < 1.0 U		Bennett and Naughton (1999)
	1997	< 1.0 C, < 1.0 S, < 1.04 U		Bennett and Naughton (1999)
Snake River—above Salmon River	1996		1.9 C	Nelle (1999)
	1997		< 1.0 C	Nelle (1999)
Snake River—below Salmon River	1996		< 1.0 C	Nelle (1999)
	1997		0	Nelle (1999)
Major tributaries				
John Day River	1977	0 U		Shrader and Gray (1999)
	1978	0 U		Shrader and Gray (1999)
Willamette River	2000	< 1.0 U		Summers and Daily (2001)
Yakima River	1998–2001	47 U		Fritts and Pearsons (2004)

^aSalmon species are indicated for each study: C—Chinook (*Oncorhynchus tshawytscha*), S—steelhead (*Oncorhynchus mykiss*), and U—unspecified.

Table 3 Percent of fish consumed by smallmouth bass that are salmon reported in the range of anadromous salmon in the Columbia and Snake River basins by body of water and year

Body of water	Year(s)	Percent salmon	Reference
Columbia River basin			
Bonneville, Dalles, John Day	1999	17.7	Zimmerman et al. (2000)
Bonneville (below dam)	2008	34	Weaver et al. (2009)
Bonneville	1999	8.7	Zimmerman et al. (2000)
	2008	19	Weaver et al. (2009)
The Dalles	2006	5.4	Takata et al. (2007)
	2009	6	Weaver et al. (2009)
John Day	2006	13.6	Takata et al. (2007)
	2009	17	Weaver et al. (2009)
Snake River Basin			
L. Monumental, Little Goose, L. Granite	1999	22.2	Zimmerman et al. (2000)
Lower Granite	2007	50	Weaver et al. (2008)
Ice Harbor	2007	10	Weaver et al. (2008)
Lower Monumental	2007	14	Weaver et al. (2008)
Little Goose	2007	16	Weaver et al. (2008)

fish consumed by smallmouth bass that is salmon increased in the more recent sample (Table 3). Understanding what determines regional differences in predation rates and incorporating temporal and spatial habitat use is necessary to predict the interaction between smallmouth bass and salmon. Unfortunately, there is a geographic and temporal bias as large efforts to monitor the effects of smallmouth bass have occurred in only a few locations and times.

The impact of smallmouth bass in some river systems is evident from consumption rates that range from 0 to 3.89 salmon consumed per predator each day (Table 4). More salmon are consumed by an individual smallmouth bass in the Yakima River than in locations along the lower Columbia River (Table 4). Relative to the mainstem and major tributaries, fewer salmon are consumed by an individual smallmouth bass in the Snake River basin. Similarly, Fritts and Pearsons (2004) estimated that over 335,000 juvenile salmon were consumed annually (March–June) in the Yakima River, a higher annual value relative to other locations. With few studies available across the PNW, data suggests that between 0 and 35% of wild salmon are consumed during outmigration by smallmouth bass (Table 4). Again, the largest impact of smallmouth bass on the percentage of the outmigrating salmon consumed appears in the Yakima River relative to the lower Columbia and Snake River locations, although the paucity of data from other locations limits the generality of this statement. Comparing between regions is tenuous due to the low amount of data, differences in the number and timing of outmigrating salmon, abiotic conditions, system size, and sampling technique to name a few complications. Testing the interaction between temperature and outmigration timing is an important next step to understand the regional differences in smallmouth bass predation on salmon. Overall, smallmouth bass predation reduces juvenile salmon populations under certain conditions, and this effect will only increase as smallmouth bass

populations continue to expand in range or number. Even low predation rates by smallmouth bass at individual locations could accumulate into a substantial impact over an entire salmon run.

Abiotic Conditions

Abiotic factors, such as changes in flow, water clarity, and temperature, are capable of altering the number of salmon consumed by smallmouth bass (Naughton et al., 2004). Low flow conditions due to dams augment predation by increasing salmon residence time, while simultaneously reducing energetic costs for smallmouth bass (Tabor et al., 1993). Reservoirs also reduce water clarity, making salmon more susceptible to visual predators. Flow and water clarity highly influence predation, thus requiring location-specific estimates even between seemingly similar near-dam and mid-reservoir habitats (Vigg et al., 1991; Petersen, 1994). In the PNW, temperatures greater than 15°C have been shown to increase smallmouth bass consumption rates and predation on juvenile salmon (Fayram and Sibley, 2000; Tabor et al., 2007). For instance, juvenile salmon have a thermal refuge from smallmouth bass in the pelagic zone of Lake Washington until they pass the littoral zone during outmigration, when and where temperatures are warmer (Tabor et al., 2007).

Salmon Size and Origin

The ratio of predator to prey size helps determine prey susceptibility and capture success. Smallmouth bass preferentially prey on smolts due to their high abundance and small size in the Columbia and Yakima rivers (Tabor et al., 1993; Fritts and Pearsons, 2006). In the lower Columbia River, most individuals consumed were less than 130 mm Fork Length (FL) (Zimmerman, 1999). Smallmouth bass also selects for salmon weakened by bacterial kidney disease as compared to healthy individuals (Mesa et al., 1998).

Smallmouth bass consumes salmon of both wild and hatchery origin. Self-sustaining populations of wild or naturally produced salmon are the goal of conservation efforts, and the role of hatchery-origin salmon in the recovery of salmon populations is complex. Whether smallmouth bass consume hatchery or naturally produced salmon is dependent on availability and characteristics of the juvenile salmon. In Lake Sammamish (Washington), juvenile salmon from the Issaquah Hatchery dominated smallmouth bass diets (Pflug and Pauley, 1984). By contrast, up to 85% of salmon consumed by smallmouth bass in the mainstem Columbia and Yakima rivers were naturally produced fish (Tabor et al., 1993, Fritts and Pearsons, 2004). In both systems, the naturally produced salmon consumed by smallmouth bass were Chinook salmon, which are smaller than their hatchery counterparts and available over a longer period than the short pulses of hatchery released salmon. In other systems, hatchery fish are typically considered more susceptible to predation due to maladaptive defenses (Maynard et al., 1995; White et al., 1995; Fritts and Pearsons, 2004).

Table 4 Summary of smallmouth bass impacts on salmon in the Columbia and Snake River basins: estimates of the number of salmon consumed per day by individual predators, number of salmon consumed per year by the resident smallmouth bass population, and percent of juvenile salmon run consumed are reported for bodies of water by year

Body of water	Year (s)	Number per day	Number per year	Percent run	Reference
Columbia River basin					
Bonneville, The Dalles, John Day	1995–96	1.4 U			Zimmerman (1999)
	1995–96	0.01 U			Zimmerman (1999)
Bonneville Dam	1995–96	1.1 U			Zimmerman (1999)
John Day Reservoir	1983–86		243,000 U		Rieman et al. (1991)
	1983–86			1 U	Beamesderfer and Ward (1994)
	1995–96	0.3–0.5 U			Ward and Zimmerman (1999)
John Day Reservoir, McNary Dam	1983–86	0.04 U			Vigg et al. (1991)
Hanford Reach–McNary Reservoir	1990	1.4 fCw(May), 1.0fCw(June)			Tabor et al. (1993)
Snake River basin					
Snake River	1991	0.01 U			Shively et al. (1996)
Hells Canyon	1996	0–0.0277 fCh	1,139 fCh		Nelle (1999)
	1997	0–0.019 fCh	7,14 fCh		Nelle (1999)
	1996	0–0.003 fCw	1,326 fCw		Nelle (1999)
	1997	0 fCw			Nelle (1999)
Little Goose, Lower Granite	1995–96	0.1 U			Zimmerman (1999)
Lower Granite Reservoir	1992	0.06 sC	31,512 sC	4.01 sC	Curet (1993)
	1994	0–0.375 U	76,584 C, 5, 892S		Anglea (1997)
	1995	0–0.018 U	51,937 C, 12, 083S	7 sC, < 0.02 yC, S	Anglea (1997)
	1996	0–0.012 U	1,200 C, 5, 528S		Naughton et al. (2004)
	1997	0–0.048 U	6,343 C, 4, 466S		Naughton et al. (2004)
Major tributary					
Yakima-Benton	1998	3.89 fC(April), 2.59fC(May)			McMichael et al. (1999)
Yakima-Vangie	1998	2.80 fC(April), 1.69fC(May)			McMichael et al. (1999)
Yakima	1998			27 fCw	McMichael et al. (1999)
	1998		335,626 U		Fritts and Pearsons (2004)
	1999		120,922 U	35 fCw, 2 fCh, 1 sC, sOw	Fritts and Pearsons (2004)
	2000		166,544 U	26 fCw, 1 fCh, 2C, sOw	Fritts and Pearsons (2004)
	2001		178,526 U	4 fCw, 4 fCh, 3 sC, sOw, O, 2 sC, O h	Fritts and Pearsons (2004)

Note: The following are indicated when available: run times (f—fall, s—spring), salmon species (O—coho [*Oncorhynchus kisutch*], C—Chinook, S—steelhead, U—unspecified), and origin (h—hatchery, w—wild).

Community Interactions

Understanding the effect of smallmouth bass predation on the entire PNW community of fish is necessary to understand their impact and determine appropriate management responses. Of primary concern is how smallmouth bass interact with other piscivorous species, as competitive interactions may occur among species that also consume salmon. Northern pikeminnow (*Ptychocheilus oregonensis*) is the primary native fish predator of juvenile salmon, and it occupies a similar niche as smallmouth bass in the Columbia River basin. An intensive removal program for northern pikeminnow has been operating since 1991 in areas of the Columbia River basin to reduce the number of salmon lost to predation (Beamesderfer et al., 1996; Friesen and Ward, 1999). Of concern is the possibility that reductions in northern pikeminnow may increase resources available to

smallmouth bass (Beamesderfer et al., 1996). Initially, the northern pikeminnow removal program did not result in increases in smallmouth bass density (Ward and Zimmerman, 1999). More recently, smallmouth bass and northern pikeminnow abundance are going in opposite directions in the John Day Reservoir (Figure 2). A model of the upper Columbia River food web suggests that smallmouth bass interacts with northern pikeminnow by foraging on similar resources (Harvey and Kareiva, 2005). This model predicts that a reduction in smallmouth bass will lead to more resources and a larger population of northern pikeminnow. Understanding the potential interactions of smallmouth bass with native predators in the community is necessary to predict the outcome of management actions.

In addition to smallmouth bass, other non-native predators are present throughout the PNW (Sanderson et al., 2009). For example, walleye (*Stizostedion vitreum*) is a non-native

predator of salmon and a popular sportfish of anglers in the PNW. Walleye is a more significant predator per capita; Poe et al. (1991) reported that walleye had a higher percentage of salmon in their diet (14%) compared to smallmouth bass (4%) in the John Day Reservoir. Furthermore, salmon losses to predation were higher for walleye (13% of total annual salmon consumed) than smallmouth bass (9%) in the John Day Reservoir (Rieman et al., 1991). Presently, walleye is not as prevalent throughout the PNW as smallmouth bass. Because these non-native species share similar resources, monitoring indirect responses of non-target species (e.g., walleye) is necessary to evaluate the outcome of management actions, such as changing fishing regulations on smallmouth bass. There is also a need to evaluate the cumulative effects of all of these predators, including the native northern pikeminnow, on salmon smolts through their entire outmigration. For instance, northern pikeminnow, smallmouth bass, and walleye combined were estimated to consume 7–17% of all salmon that annually migrate through the John Day Reservoir (Petersen and Kitchell, 2001).

Competitive Effects

Smallmouth bass is foremost considered a top predator; however, an ontogenetic niche shift from insects and zooplankton to crayfish and fish occurs as it grows (Olson and Young, 2003; Warren, 2009). Due to the breadth of resources consumed by smallmouth bass, there is the potential for competitive interactions with many other species of fish including salmon. Other predators that go through an ontogenetic niche shift interact with their prey by both predation and competition, depending on the life stage of the predator (Garvey et al., 1998; Persson and Bronmark, 2002). Thus, in addition to interacting as predators, smallmouth bass may also compete with salmon. In the Willamette River, diet similarities between juvenile Chinook salmon and juvenile smallmouth bass suggested that resource limitations could result in the potential for competition (Table 5).

Table 5 Diet comparisons by number (*n*) and wet weight (*g*) of stomach contents for Chinook salmon and smallmouth bass < 200 mm FL in the lower Willamette River, 2002–2003 (prey diversity is Shannon's *H* (values increase with diversity), diet evenness is Shannon's equitability [1.0 = complete evenness], and similarity is Schoener's index of diet overlap [values > 0.60 indicate biologically significant overlap]); adapted from Vile et al. (2004).

Diet metric	Chinook salmon	Smallmouth bass
Sample size	346	48
Number of prey items	42,603	277
Preferred prey (<i>n</i>)	Daphnia 91%	Daphnia 46%
Preferred prey (<i>g</i>)	Daphnia 43%	Crayfish 62%
Prey taxa richness	41	17
Prey diversity	0.51	1.94
Diet evenness	0.12	0.64
Similarity (<i>n</i>)		0.54
Similarity (<i>g</i>)		0.23

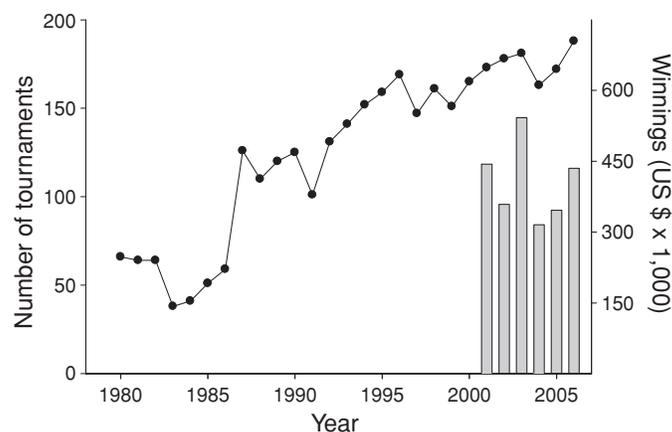


Figure 3 The number (●) and prize money (▣) of tournaments for black bass (smallmouth bass and largemouth bass) held in Washington state (Baker, 2003a,b, 2004, 2005, 2006, 2007)

OPTIONS AND IMPLICATIONS FOR SMALLMOUTH BASS MANAGEMENT

As a non-native sportfish, smallmouth bass confound policy considerations for state and federal agencies charged with both the conservation of native, sensitive, or ESA-listed species and support of freshwater angling opportunities (a situation similar to native–non-native fish management in the southwestern United States; Rinne et al., 2004). The number of anglers and fishing days for both bass species create a huge economic incentive to devote resources to maintaining the fishery (Table 1). The popularity of the bass fishery is evident in the increasing number of tournaments now held in Washington each year, with nearly \$500,000 in prize money awarded annually (Figure 3). The presence of numerous official bass-angling clubs for adult and youth anglers supports the societal importance of the bass fishery (e.g., The Bass Federation clubs with 12 in Idaho, 3 in Oregon, 12 in Washington; B.A.S.S. clubs with 7 in Idaho, 23 in Oregon, in 10 Washington). Similarly, state agencies must accommodate wild fish protection groups (e.g. The Native Fish Society, Wild Fish Conservancy). Preservation groups favor actions to protect native species, whereas angling groups are primarily interested in maintaining, if not promoting, the sport fishery. Both groups influence public perception of smallmouth bass. To move forward, several avenues of research are proposed to inform management and dialogue with the recreational fishing community is suggested and imperative (Smith, 2004).

Reducing Predation

Management strategies must be developed and tested to reduce the predatory impacts of smallmouth on salmon. Management options to reduce predation on ESA-listed salmon include altering dam operations and limiting smallmouth bass to water bodies where their presence is considered less harmful. Higher flow through reservoirs decreases temperature and water

clarity, both of which can reduce smallmouth bass predation (Vigg et al., 1991; Petersen, 1994; Fayram and Sibley, 2000; Naughton et al., 2004; Tabor et al., 2007) and influence smallmouth bass nesting success (Henderson and Foster, 1957; Lukas and Orth, 1995; Peterson and Kwak, 1999). Managing discharge and thermal regimes to disfavor smallmouth bass was successful at the Flaming Gorge Dam on the Green River in Wyoming (Bestgen et al., 2007). Serendipitously, conditions for reduced predation by smallmouth bass are similar to those for more efficient outmigration of salmon smolts (Naughton et al., 2004). Specifically, increased spill from dams facilitates outmigration by reducing reservoir delays and duration of exposure to predators (Zimmerman and Ward, 1999). Fisheries managers will need to develop and test management tools to allocate flow and optimize temperature to promote native species and reduce smallmouth bass predation. However, allocating discharge to spill more water over the dams decreases the capacity to generate power through the turbines. Conflicts between reducing smallmouth bass predation and producing power make altering the distribution of water between turbines and spill a challenge to accomplish.

Controlling Populations

Management options for controlling smallmouth bass populations through fishing regulations include liberalizing harvest to increase bag limits for number and/or sizes of smallmouth bass, removing any limits to angler catch, and mandatory kill policies. Presently, the general statewide angler harvest restrictions for black bass in Oregon and Washington specify no minimum size, five fish per day, and no more than three fish greater than 15 inches. As an aside, managing smallmouth bass and largemouth bass separately may be beneficial as these species have different physiologies, morphologies, and microhabitat preferences. Differences between species of bass likely lead to varying impacts on salmon and may require unique management actions. Liberalizing harvest is a possible means to reduce population size (Barfoot et al., 2002); however, this management action may not have a large effect on populations, because most smallmouth bass anglers practice catch and release (Aday et al., 2009), and hooking mortality is low (Clapp and Clark, 1989).

Most bass anglers are opposed to destroying individuals; thus, extreme regulations, such as mandatory retention (Johnson et al., 2009), are not viable. Regulation changes, such as altering size limits, have altered largemouth bass populations in Minnesota, despite catch-and-release practices (Carlson and Isermann, 2010). However, predation rates on salmon are greater among smallmouth bass less than 250 mm (Fritts and Pearson, 2006), and bass anglers do not target these smaller individuals. Research is needed to explore active control measures that will influence smallmouth bass populations in the PNW, both by determining the effect of removing larger individuals on the overall population and by considering management options to target smaller fish.

To address the conflicting management challenges of smallmouth bass, site-specific regulations are a likely first step. Different regulations could be applied to areas containing smallmouth bass if sites were characterized by their potential impact on salmon and importance to the recreational fishery. In areas of high potential impact to salmon, regulations could try to eliminate smallmouth bass populations. In areas that are important to the recreational fishery but do not have a large impact on salmon, regulations can maintain the fishery. The benefit of limiting smallmouth bass sites for fishing is that it may ameliorate angler concerns of destroying the fishery throughout the PNW. The downside is the difficulty in identifying appropriate water bodies and the potential for these areas to provide a source population to unintended locations, thereby establishing a new population or supplementing an unwanted population.

Outreach to Stakeholders

Any management action requires efforts in education and enforcement (Jackson et al., 2004). This is certainly true for management actions in which regulations are not uniform across the landscape. Deterrents are needed for violating regulations and transplanting species. For example, illegal transportation and stocking is being increasingly discouraged throughout North America (Rahel, 2004; Johnson et al., 2009). The state of Oregon recently made transplanting fish a felony. Oregon Senate Bill 571 (2010) states “. . .releasing or attempting to release any live fish into a body of water that was not taken from that body of water without a permit is a Class C felony, if the violation is committed intentionally or knowingly, or a Class A misdemeanor, if the violation is committed recklessly or with criminal negligence.”

Successful management actions require that the recreational community is a major part of the resolution process. Accessing the knowledge of recreational groups, outfitters, professional guides, and individuals will be helpful in identifying large and small populations of smallmouth bass and determining locations of the principal fisheries. Engaging the recreational community in solving the smallmouth bass conflict also provides an opportunity for education and outreach. Education on the harmful impacts of smallmouth bass is imperative, as a successful dialogue requires all constituent groups be similarly educated (Rahel, 2004). The economic incentives of the smallmouth bass fishery must also be acknowledged in the resolution process. Likewise, the economic value of the recreational fishery for native species is substantial. For example, the net economic value for recreational fishing of steelhead (*O. mykiss*) in freshwater alone was estimated to exceed \$51 million in Washington in 2006 (TCW Economics, 2008). By broadening the dialogue among constituent groups, a resolution is more likely to accommodate the varied human interests revolving around smallmouth bass fishery in the PNW.

SUMMARY

Overall, there is lack of basic information on system-wide abundances and ecology of smallmouth bass to make informed management decisions for the recreational fishery and to determine the best strategies for preventing, controlling, or eradicating smallmouth bass impacts on salmon. Continued monitoring of smallmouth bass is needed, as effects might not be detectable until years after populations stabilize in an area and range expansion ceases. Management actions directed at smallmouth bass are likely to have direct, indirect, and non-linear effects that reverberate through the food web, implying a need to shift from a single-species to multi-species perspective for management strategies directed at conserving native species. We recommend that processes beyond direct predation (e.g., competition) be considered when evaluating the effect of smallmouth bass on native species and that changes in smallmouth bass populations may influence other non-native species. Moreover, the measured responses of native species should include non-consumptive effects, such as lower spawning success. For all management options, management experiments should be begun and continued to build information and advance conservation science. The suggested strategy would be to test management options in key areas of overlap between smallmouth bass and salmon. Lessons explored for smallmouth bass can be applied to other sportfish entangled in similar management conflicts.

ACKNOWLEDGMENTS

The authors thank M. Vanlandeghem for insight into bass clubs and tournaments, M. Weaver of ODFW for the electrofishing data presented in Figure 2, and D. Holzer for assistance with the map in Figure 1. NOAA Fisheries, ODFW, and the University of Washington supported this work. Additional support for M.P.C. was provided through an National Research Council (NRC) Postdoctoral Associateship at the Northwest Fisheries Science Center. J.D.O. acknowledges funding support from the U.S. Environmental Protection Agency Science To Achieve Results (STAR) Program (Grant 833834). Reviews by L. Kuehne, J. Williams, W. Dickoff, J. Butzerin, and M. McClure substantially improved the manuscript.

REFERENCES

- Aday, D. D., J. J. Parkos III, and D. H. Wahl. Population and community ecology of Centrarchidae, pp. 134–164. In: *Centrarchid Fishes: Diversity, Biology, and Conservation* (Cooke, S., and D.P. Philipp, Eds.). Chichester, United Kingdom: Wiley–Blackwell (2009).
- Anglea, S. M. *Abundance and food habits of smallmouth bass and distribution of crayfish in Lower Granite Reservoir, Idaho-Washington*. Master's Thesis, University of Idaho, Moscow, ID (1997).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 03-09. Washington Department of Fish and Wildlife 2002 Annual Report (2003a).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 01-03. Washington Department of Fish and Wildlife 2001 Annual Report (2003b).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 04-08. Washington Department of Fish and Wildlife 2003 Annual Report (2004).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 05-10. Washington Department of Fish and Wildlife 2004 Annual Report (2005).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 06-04. Washington Department of Fish and Wildlife 2006 Annual Report (2006).
- Baker, B. M. *Summary report of results of bass and walleye fishing held in Washington*. FPA 07-01. Washington Department of Fish and Wildlife 2006 Annual Report (2007).
- Barfoot, C. A., D. M. Gadowski, and J. H. Petersen. Resident fish assemblages in shallow shorelines of a Columbia River impoundment. *NW Sci.*, **76**: 103–117 (2002).
- Beamesderfer, R. C., and North. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. *N. Amer. J. Fisheries Manag.*, **15**: 688–704 (1995).
- Beamesderfer, R. C., and D. L. Ward. *Review of the status, biology, and alternatives for management of smallmouth bass in John Day Reservoir*. Informational Report 94-4. Clackamas, OR: Oregon Department of Fish and Wildlife (1994).
- Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. Evaluation of the biological basis for a predator control program on northern squawfish in the Columbia and Snake rivers. *Canadian J. Fisheries Aquatic Sci.*, **53**: 2898–2908 (1996).
- Bennett, D. H., J. A. Chandler, and L. K. Dunsmoor. Smallmouth bass in the Pacific Northwest: Benefit or liability, pp. 126–135. In: *Proceedings of the First International Smallmouth Bass Symposium* (Jackson, D. C., Ed.). Mississippi Agricultural and Forestry Experimental Station, Mississippi State University, MS (1999).
- Bennett, D. H., and G. P. Naughton. *Predator abundance and salmonid prey consumption in tailrace and forebay of Lower Granite Dam*. Completion Report to U.S. Army Corps of Engineers, Walla Walla District, Project 14-45-0009-1579. Moscow, ID: College of Fish and Wildlife, University of Idaho (1999).
- Bestgen, K. R., K. A. Zelasko, and C. T. Wilcox. *Non-native fish removal in the Green River, Lodore and Whirlpool canyons, 2002–2006, and fish community response to altered flow and temperature regimes, and non-native fish expansion*. Final Report, Colorado River Recovery Implementation Program Project Number 115, Larval Fish Laboratory Contribution 149 (2007).
- Boersma, P. D., S. H. Reichard, and A. N. Van Buren. *Invasive Species in the Pacific Northwest*. Seattle: University of Washington Press, 150–151 (2006).
- Carlson, A. J., and D. A. Isermann. Mandatory catch and release and maximum length limits for largemouth bass in Minnesota: Is exploitation still a relevant concern? *N. Amer. J. Fisheries Manag.*, **30**: 209–220 (2010).
- Clapp, D. F., and R. D. Clark, Jr. Hooking mortality of smallmouth bass caught on live minnows and artificial spinners. *N. Amer. J. Fisheries Manag.*, **9**: 81–85 (1989).
- Cucherousset, J., and J. D. Olden. Ecological impacts of non-native freshwater fishes. *Fisheries*, **36**: 215–230 (2011).
- Curet, T. S. *Habitat use, food habitats, and the influence of predation on subyearling chinook salmon in Lower Granite and Little*

- Goose reservoirs. *Master's Thesis*, University of Idaho, Moscow, ID (1993).
- Fayram, A. H., and T. H. Sibley. Impact of predation by smallmouth bass on sockeye salmon in Lake Washington, Washington. *N. Amer. J. Fisheries Manag.*, **20**: 81–89 (2000).
- Friesen, T. A., and D. L. Ward. Management of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. *N. Amer. J. Fisheries Manag.*, **19**: 406–420 (1999).
- Fritts, A. L., and T. N. Pearsons. Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. *Trans. Amer. Fisheries Soc.*, **133**: 880–895 (2004).
- Fritts, A. L., and T. N. Pearsons. Effects of predation by nonnative smallmouth bass on native salmonid prey: The role of predator and prey size. *Trans. Amer. Fisheries Soc.*, **135**: 853–860 (2006).
- Garvey, J. E., N. A. Dingleline, N. S. Donovan, and R. A. Stein. Exploring spatial and temporal variation within reservoir food webs: Predictions for fish assemblages. *Ecol. Appl.*, **8**: 104–120 (1998).
- Harvey, C. J., and P. M. Kareiva. Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. *Biol. Invas.*, **7**: 651–663 (2005).
- Henderson, C., and R. F. Foster. Studies of smallmouth black bass (*Micropterus dolomieu*) in the Columbia River near Richland, Washington. *Trans. Amer. Fisheries Soc.*, **86**: 112–127 (1957).
- Iguchi, K. I., K. Matsuura, K. M. McNyset, A. T. Peterson, R. Scachetti-Pereira, K. A. Powers, D. A. Vieglais, E. O. Wiley, and T. Yodo. Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Trans. Amer. Fisheries Soc.*, **133**: 845–854 (2004).
- Jackson, J. R., J. C. Boxrucker, and D. W. Willis. Trends in agency use of propagated fishes as a management tool in inland fisheries, pp. 121–138. In: *Propagated Fishes in Resource Management, American Fisheries Society Symposium 44* (Nickum, M. J., P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, Eds.). Bethesda, MD: American Fisheries Society (2004).
- Johnson, B. M., R. Arlinghaus, and P. J. Martinez. Introduced species—are we doing all we can to stem the tide of illegal fish stocking? *Fisheries*, **34**: 389–394 (2009).
- Johnson, P. T. J., J. D. Olden, and M. J. Vander Zanden. Dam invaders: impoundments facilitate biological invasions in freshwaters. *Front. Ecol. Environ.*, **6**: 357–363 (2008).
- Lackey, R. T., D. H. Lach, and S. L. Duncan. Policy options to reverse the decline of wild Pacific salmon. *Fisheries*, **31**: 344–351 (2006).
- Lampman, B. H. *The Coming of the Pond Fishes*. Portland, OR: Metropolitan Press, 101–111 (1946).
- LaVigne, H. R., R. M. Hughes, R. C. Wildman, S. V. Gregory, and A. T. Herlihy. Summer distribution and species richness of non-native fishes in the mainstem Willamette River, 1944–2006. *NW Sci.*, **82**: 83–93 (2008).
- Lukas, J. A., and D. J. Orth. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Trans. Amer. Fisheries Soc.*, **124**: 726–735 (1995).
- Maynard, D. J., T. A. Flagg, and C. V. W. Mahnken. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids, pp. 307–314. In: *American Fisheries Society Symposium 15* (Schramm, Jr., H. L., and R. G. Piper, Eds.). Bethesda, MD (1995).
- McMichael, G. A., A. L. Fritts, T. N. Pearsons, and J. L. Dunnigan. Lower Yakima River predatory fish monitoring: progress report 1998, pp. 93–124. In: *Proceedings of the Workshop on Management Implications of Co-Occurring Native and Introduced Fishes*. Portland, OR: ODFW and NMFS (1999).
- Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. Vulnerability to predation and physiological stress responses in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. *Canadian J. Fisheries Aquatic Sci.*, **55**: 1599–1606 (1998).
- NatureServe Explorer: An online encyclopedia of life. Version 7.1. Available from NatureServe, Arlington, VA, <http://www.natureserve.org/explorer> (2009).
- Naughton, G. P., D. H. Bennett, and K. B. Newman. Predation on juvenile salmonids by smallmouth bass in the Lower Granite Reservoir System, Snake River. *N. Amer. J. Fisheries Manag.*, **24**: 534–544 (2004).
- Nelle, R. D. *Smallmouth bass predation on juvenile fall Chinook salmon in the Hells Canyon Reach of the Snake River, ID. Master's Thesis*, University of Idaho, Moscow, ID (1999).
- Olson, M. H., and B. P. Young. Patterns of diet and growth in co-occurring populations of largemouth bass and smallmouth bass. *Trans. Amer. Fisheries Soc.*, **132**: 1207–1213 (2003).
- Oregon Senate Bill 571 - Introduction of fish into bodies of water*. Legislative Session, Chapter 243, Effective date: January 1, 2010 (2009).
- Persson, A., and C. Bronmark. Foraging capacity and resource synchronization in an ontogenetic diet switcher, pikeperch (*Stizostedion lucioperca*). *Ecology*, **83**: 3014–3022 (2002).
- Petersen, J. H. Importance of spatial pattern in estimating predation on juvenile salmonids in the Columbia River. *Trans. Amer. Fisheries Soc.*, **123**: 924–930 (1994).
- Petersen, J. H., and J. F. Kitchell. Climate regimes and water temperature changes in the Columbia River: Bioenergetic implications for predators of juvenile salmon. *Canadian J. Fisheries Aquatic Sci.*, **58**: 1831–1841 (2001).
- Peterson, J. T., and T. J. Kwak. Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecol. Appl.*, **9**: 1391–1404 (1999).
- Pflug, D. E., and G. B. Pauley. Biology of smallmouth bass (*Micropterus dolomieu*) in Lake Sammamish, Washington. *NW Sci.*, **58**: 118–130 (1984).
- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. Feeding of predaceous fishes on outmigrating juvenile salmonids in John Day Reservoir, Columbia River. *Trans. Amer. Fisheries Soc.*, **120**: 405–420 (1991).
- Poe, T. P., R. S. Shively, and R. A. Tabor. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake rivers, pp. 347–360. In: *Theory and Application in Fish Feeding Ecology* (Stouder, D. J., K. L. Fresh, and R. J. Feller, Eds.). Columbia, SC: University of South Carolina Press (1994).
- Rahel, F. J. Unauthorized fish introductions: Fisheries management of the people, for the people, or by the people? pp. 431–444. In: *Propagated Fishes in Resource Management, American Fisheries Society Symposium 44* (Nickum, M. J., P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, Eds.). Bethesda, MD: American Fisheries Society (2004).
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Trans. Amer. Fisheries Soc.*, **120**: 448–458 (1991).
- Rinne, J. N., L. Riley, R. Bettaso, R. Sorenson, and K. Young. Managing Southwestern native and nonnative fishes: Can we mix oil and water

- and expect a favorable solution? pp. 445–466. In: *Propagated Fishes in Resource Management, American Fisheries Society Symposium 44* (Nickum, M. J., P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, Eds.). Bethesda, MD: American Fisheries Society (2004).
- Sanderson, B. L., K. A. Barnas, and A. M. W. Rub. Nonindigenous species of the Pacific Northwest: An overlooked risk to endangered salmon? *Bioscience*, **59**: 245–256 (2009).
- Sharma, S., M.-L. Herborg, and T. T. Therriault. Predicting smallmouth bass invasion and their potential impact on native salmonid and cyprinid populations. *Diversity Distribut.*, **15**: 831–840 (2009).
- Shively, R. S., T. P. Poe, and S. T. Sauter. Feeding response by northern squawfish to a hatchery release of juvenile salmonids in the Clearwater River, ID. *Trans. Amer. Fisheries Soc.*, **125**: 230–236 (1996).
- Shrader, T., and M. E. Gray. *Biology and management of John Day river smallmouth bass*. Information Report 99-1. Portland, OR: Oregon Department of Fish and Wildlife (1999).
- Smith, M. L. Perceptions about science and scientism in fisheries management: An angler's view, pp. 145–150. In: *Propagated Fishes in Resource Management, American Fisheries Society Symposium 44* (Nickum, M. J., P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, Eds.). Bethesda, MD: American Fisheries Society (2004).
- Summers, J., and K. Daily. *Willamette river bass diet study: Spring 2000*. Information Report 2001-04. Portland, OR: Oregon Department of Fish and Wildlife (2001).
- Sutton, S. G., K. Dew, and J. Higgs. Why do people drop out of recreational fishing? A study of lapsed fishers from Queensland, Australia. *Fisheries*, **34**: 443–452 (2009).
- Tabor, R. A., B. A. Footen, K. L. Fresh, M. T. Celedonia, F. Mejia, D. L. Low, and L. Park. Smallmouth bass and largemouth bass predation on juvenile Chinook salmon and other salmonids in the Lake Washington basin. *N. Amer. J. Fisheries Manag.*, **27**: 1174–1188 (2007).
- Tabor, R. A., R. S. Shively, and T. P. Poe. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *N. Amer. J. Fisheries Manag.*, **13**: 831–838 (1993).
- Takata, H. K., M. J. Reesman, G. E. Reed, L. D. Layng, and T. A. Jones. *Development of a system-wide predator control program: Indexing and fisheries evaluation*. 2006 Annual Report to the Bonneville Power Administration. Portland, OR: Oregon Department of Fish and Wildlife, Contract Number DEB1719-94BI24514 (2007).
- TCW Economics. *Economic analysis of the non-treaty commercial and recreational fisheries in Washington State*. December 2008, Sacramento, CA, with technical assistance from The Research Group, Corvallis, OR (2008).
- USFWS (U.S. Fish and Wildlife Service). National survey of fishing, hunting, and wildlife-associated recreation (1996).
- USFWS (U.S. Fish and Wildlife Service). National survey of fishing, hunting, and wildlife-associated recreation (2001).
- USFWS (U.S. Fish and Wildlife Service). National survey of fishing, hunting, and wildlife-associated recreation (2006).
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, **401**: 464–467 (1999).
- Vander Zanden, M. J., J. D. Olden, J. H. Thorne, and N. E. Mandrak. Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecol. Appl.*, **14**: 132–148 (2004).
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Trans. Amer. Fisheries Soc.*, **120**: 421–438 (1991).
- Vile, J. S., T. A. Friesen, and M. J. Reesman. Diets of juvenile salmonids and introduced fishes of the lower Willamette River, pp. 185–221. In: *Biology, behavior, and resources of resident and anadromous fish in the lower Willamette River*. Salem: ODFW Information Report 2007-03 (2004).
- Ward, D. L., and M. P. Zimmerman. Response of smallmouth bass to sustained removals of northern pikeminnow in the lower Columbia and Snake rivers. *Trans. Amer. Fisheries Soc.*, **128**: 1020–1035 (1999).
- Warren, M. L. Centrarchid identification and natural history, pp. 375–534. In: *Centrarchid Fishes: Diversity, Biology, and Conservation* (Cooke, S., and D. P. Philipp, Eds.). Chichester, United Kingdom: Wiley–Blackwell (2009).
- Weaver, M. H., H. K. Takata, M. J. Reesman, L. D. Layng, G. E. Reed, and T. A. Jones. *Development of a system-wide predator control program: fisheries evaluation*. 2007 Annual Report to the Bonneville Power Administration. Portland, OR: Oregon Department of Fish and Wildlife, Contract Number DE-B1719-94BI24514 (2008).
- Weaver, M. H., H. K. Takata, M. J. Reesman, and E. S. Van Dyke. *Development of a system-wide predator control program: Fisheries evaluation*. 2008 Annual Report to the Bonneville Power Administration. Portland, OR: Oregon Department of Fish and Wildlife, Contract Number DE-B1719-94BI24514 (2009).
- Weidel, B. C., D. C. Josephson, and C. C. Krueger. Diet and prey selection of naturalized smallmouth bass in an oligotrophic Adirondack lake. *J. Freshwater Ecol.*, **15**: 411–420 (2000).
- White, R. J., J. R. Karr, and W. Nehlsen. Better roles for fish stocking in aquatic resource management, pp. 527–547. In: *American Fisheries Society, Symposium 15* (Schramm, Jr., H. L., and R. G. Piper, Eds.). Bethesda, MD (1995).
- Woodford, D. J., N. D. Impson, J. A. Day, and I. R. Bills. The predatory impact of invasive alien smallmouth bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African J. Aqua. Sci.*, **30**: 167–173 (2005).
- Zimmerman, M. P. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia and Snake rivers. *Trans. Amer. Fisheries Soc.*, **128**: 1036–1054 (1999).
- Zimmerman, M. P., T. A. Friesen, D. L. Ward, and H. K. Takata. *Development of a system-wide predator control program: Indexing and fisheries evaluation*. 1999 Annual Report to the Bonneville Power Administration. Portland, OR: Oregon Department of Fish and Wildlife, Contract Number DE-B1719-94BI24514 (2000).
- Zimmerman, M. P., and R. M. Parker. Relative density and distribution of smallmouth bass, channel catfish, and walleye in the lower Columbia and Snake rivers. *NW Sci.*, **69**: 19–28 (1995).
- Zimmerman, M. P., and D. L. Ward. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River Basin, 1994–1996. *Trans. Amer. Fisheries Soc.*, **128**: 995–1007 (1999).