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FALL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*), SAND ROLLER (*PERCOPSIS TRANSMONTANA*), AND SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) INTERACTIONS IN A SNAKE RIVER RESERVOIR: A TALE OF THREE SPECIES

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ABSTRACT—We studied some of the relationships between federally listed fall Chinook Salmon, *Oncorhynchus tshawytscha*, endemic Sand Roller, *Percopsis transmontana*, and non-native Smallmouth Bass, *Micropterus dolomieu*, in Lower Granite Reservoir on the Snake River. Because of its recent reappearance and population increase, the Sand Rollers could be filling the role of a “native invader” in the reservoir food web. We speculated that Sand Rollers could either negatively affect fall Chinook Salmon by potentially competing with them for resources in shoreline habitats or, alternatively, benefit the salmon by providing a buffer against Smallmouth Bass predation. Nighttime beach seining showed that habitat use by fall Chinook Salmon and Sand Rollers overlapped completely in spring when both species were present along shorelines. Diet data from stomach samples also showed high overlap, but data on stable isotopes of ^{13}C and ^{15}N suggested that each species could be obtaining much of their dietary energy from different reservoir locations. Although habitat and diet overlap are evidence of competition, diel and spatial partitioning of resource use between fall Chinook Salmon and Sand Rollers may act to reduce potential competition. Analyses of Smallmouth Bass diets showed that fall Chinook Salmon and Sand Rollers comprised the majority of prey fish consumed by bass. Across years, as Smallmouth Bass increased their consumption of Sand Rollers (range 0.219 to 0.392 fish smallmouth $^{-1}$ day $^{-1}$), they decreased their consumption of fall Chinook Salmon (range 0.114 to 0.050 fish smallmouth $^{-1}$ day $^{-1}$). The greatest effect Sand Rollers may have on fall Chinook Salmon in Lower Granite Reservoir is to serve as a buffer against Smallmouth Bass predation.

Key words: abundance, Chinook Salmon, diet, habitat, Lower Granite Reservoir, predation, Sand Roller, Smallmouth Bass

Introduced aquatic organisms can alter fish communities through both direct effects such as predation (Preston and others 2012; O'Connor and others 2013; Gallardo and others 2016) and competition for food or space (Mills and others 2004), and indirect effects such as food web alteration (Ellis and others 2011; Stewart and Sprules 2011). Although these types of interactions have been extensively documented for non-native species (Strayer 2010), similar effects are not as well documented for native species that are able to effectively exploit altered habitat (Rodriguez 2006). In some instances, native fish respond to habitat alterations, food webs, and ecosystem function in ways that are similar to non-native invasive species, and thus have been

characterized as “native invaders” (Carey and others 2012). The concept of the native invader is illustrated by the proliferation of the native Northern Pikeminnow (*Ptychocheilus oregonensis*) following impoundment of the lower Snake and Columbia rivers (Brown and Moyle 1981; Rieinan and others 1991; Beamesderfer and others 1996). The transformation of riverine habitat to low-velocity impoundments with abundant seaward migrating Pacific salmon (*Oncorhynchus* spp.) smolts was an opportunity that Northern Pikeminnow were well-adapted to exploit (Beamesderfer and others 1996). As their population expanded, the levels of their increased predation on juvenile salmonids were similar to those exerted by non-native piscivorous fish in other

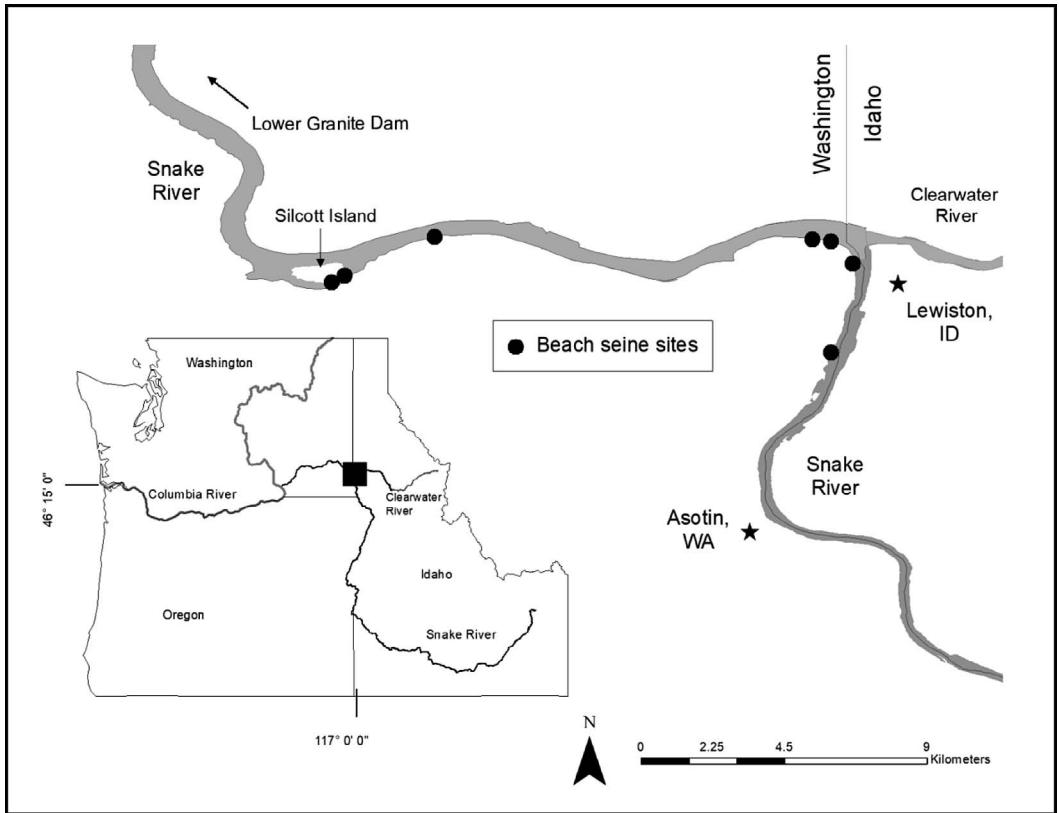


FIGURE 1. Lower Granite Reservoir with locations where Sand Rollers and fall Chinook Salmon were collected from late March to early July 2015.

systems (Beamesderfer and others 1996; Johnson and others 2008; Carey and others 2012).

More recently, the endemic Sand Roller (*Percopsis transmontana*), long absent (40+ years) in the Snake River, has greatly increased in abundance in Lower Granite Reservoir (Fig. 1; Tiffan and others 2017). Sand Rollers have the potential to act as native invaders in the sense that they may negatively affect Endangered Species Act (ESA)-listed fall Chinook Salmon (*O. tshawytscha*) juveniles. Many juvenile fall Chinook Salmon naturally produced in upstream spawning areas disperse downstream into Lower Granite Reservoir and rear for 2–4 months before becoming smolts and emigrating seaward (Connor and others 2003). Tiffan and others (2014a) found that growth of fall Chinook Salmon rearing in the reservoir was lower than in riverine habitats, and hypothesized that competition with other resident species could be partly responsible. The potential for compe-

tion for food and space between fall Chinook Salmon and Sand Rollers is not unreasonable, since both species are small (<115 mm fork length [FL]), opportunistic feeders that inhabit shallow shoreline areas for at least a portion of each day (Connor and others 2003; Tiffan and others 2014a; Tiffan and others 2017).

The potentially negative effects of competition between Sand Rollers and fall Chinook Salmon could be offset by differential predation on the 2 species. Non-native Smallmouth Bass (*Micropterus dolomieu*) are the primary predator in Lower Granite Reservoir (Anglea 1997; Naughton and others 2004; Erhardt and others 2018). Both Anglea (1997) and Naughton and others (2004) reported high consumption of salmonids by bass at some times, but made no mention of Sand Rollers in bass diets. More recently, Erhardt and others (2018) found that Sand Rollers and juvenile fall Chinook Salmon were the 2 most common prey fish consumed by bass in the

upper portion of the reservoir. Given that the Sand Roller is a relatively recent addition to the food web, Erhardt and others (2018) hypothesized that Sand Rollers may provide a predation buffer for fall Chinook Salmon and thus provide a positive benefit in terms of reducing predation losses of juvenile Pacific salmon.

In this paper, we examine some of the ecological relationships between Sand Rollers, acting as a native invader, native ESA-listed fall Chinook Salmon (NMFS 1992), and predatory non-native Smallmouth Bass. Our 1st objective was to assess the temporal overlap in habitat use and diet between fall Chinook Salmon and Sand Rollers. A high degree of overlap in these metrics could provide evidence of possible competition. Our 2nd objective was to describe annual trends in Smallmouth Bass predation to determine whether Sand Rollers could be acting as a predation buffer for fall Chinook Salmon.

METHODS

Study Area

Lower Granite Reservoir is located on the lower Snake River in southeastern Washington, and is impounded by Lower Granite Dam, which lies 173 river kilometers (rkm) upstream of the confluence of the Snake and Columbia rivers (Fig. 1). The impoundment of Lower Granite Reservoir extends 61 km upstream to Asotin, Washington. The Clearwater River enters the reservoir at Lewiston, Idaho (rkm 224). Lower Granite Reservoir is a run-of-the-river reservoir and is operated primarily for hydro-power and navigation. Flows can range from $>4200 \text{ m}^3\text{s}^{-1}$ in the spring to $450 \text{ m}^3\text{s}^{-1}$ during winter. The average channel width of Lower Granite Reservoir is about 630 m, and water depths average 17 m and range from shallow shoreline areas to a maximum of 42 m near the dam. Normal pool elevation fluctuates about 1.5 m annually. Reservoir water temperatures along shorelines range from about 8°C in early April to $>23^\circ\text{C}$ in August.

Sand Roller and Fall Chinook Salmon Sampling and Analysis

We collected Sand Rollers and fall Chinook Salmon in the upper portion of Lower Granite Reservoir in 2015. Most of the shallow-water habitat that supports rearing fall Chinook

Salmon and Sand Rollers is located in this area of the reservoir (Tiffan and others 2016). Although Sand Rollers occupy deep, offshore habitats during the day, they move into shoreline areas in the evening, presumably to feed (Tiffan and others 2017). We collected fish every 2 wk at 7 fixed sites (Fig. 1) from late March to early July, the time of peak presence of both species (Connor and others 2003; Tiffan and others 2017). We sampled sites at night (1 h after civil twilight to 02:00) using a 30-m long by 2-m deep beach seine with 6-mm nylon mesh. Using a boat, we set the seine parallel to and 15 m off shore and then pulled it straight into shore to sample an area of approximately 450 m^2 . We counted all collected Sand Rollers, and weighed (to the nearest 0.1 g) and measured (to the nearest 1 mm FL) a subsample. Likewise, we counted all fall Chinook Salmon, and collected a subsample for diet analysis (described below), which were weighed and measured for length. To assess mutual occupation of habitat over time, we pooled beach seine catches of both species across sites and compared them graphically.

On 4 occasions each (14 April, 28 April, 18 May, 10 June), we collected diet information from 21 to 35 Sand Rollers and 10 to 11 fall Chinook Salmon. Our sample sizes of fall Chinook Salmon were limited by ESA sampling restrictions. Using non-lethal gastric lavage, we collected stomach contents for diet analyses, which were then frozen in water on dry ice. Stomach contents were later sorted, and individual taxa were identified to the lowest practical taxon and blotted to remove excess water and then weighed (nearest 0.0001 g wet weight). We assessed the importance of different prey in fish diets using the Index of Relative Importance (IRI; Pinkas and others 1971), which was calculated as $\text{IRI} = (N + W) \times F$, where N = the numerical percentage of a prey item, W = the weight percentage of a prey item, and F = percent frequency of occurrence of a prey item. IRI values of predominant prey were summarized graphically by sample date. We used Morisita's overlap index (Morisita 1959) to quantify diet overlap by week based on counts of dominant prey items of Sand Rollers and Chinook Salmon. Because it is the most robust index if count data is available (Smith and Zaret 1982, cited in Chips and Garvey 2007), and because it is independent of sample size and

diversity (Wolda 1981), we used Morisita's original formula:

$$M = \frac{2 \sum_i^n p_{ij} p_{ik}}{\left[\sum_i^n p_{ij} [(n_{ij} - 1)/(N_j - 1)] + \sum_i^n p_{ik} [(n_{ik} - 1)/(N_k - 1)] \right]}$$

To obtain a more time-integrated examination of dietary energy source and trophic position, we analyzed Sand Roller and fall Chinook Salmon tissues for stable isotopes of nitrogen and carbon (Vander Zanden and others 1999; Post 2002). On 11 May, we collected 15 Sand Rollers and 10 fall Chinook Salmon, which we sacrificed and froze on dry ice. We later removed white muscle tissue from each fish to be dried at 60°C for 24 h, and ground to a fine powder with a mortar and pestle. A 0.5±0.1 mg sample of tissue was encapsulated in tin and analyzed for δ¹³C and δ¹⁵N signatures at Washington State University with a GV Instruments isotope ratio mass spectrometer (Manchester, UK) interfaced with a Costch Elemental Analyzer (Valencia, CA). The quantity measured in stable isotope analysis, δ, is the relative difference between isotope ratios of the sample and a standard, and is expressed in parts per thousand (‰) as δ = ((R_{sample} - R_{standard})/R_{standard}) × 1000, where R_{sample} is the isotopic ratio of the sample and R_{standard} is the isotopic ratio of the standard. As a standard reference material, we used protein hydrolysate powder calibrated to NIST standards. We considered samples "enriched" if they contained more of the heavy isotope relative to other collected samples and "depleted" if they contained less of the heavy isotope. Depleted δ¹³C values (more negative) would indicate that carbon came from benthic, offshore sources, whereas enriched values (less negative) would indicate carbon was obtained from littoral areas (France 1995; Hecky and Hesslein 1995). We inferred trophic position from δ¹⁵N values, where similar values for Sand Rollers and fall Chinook Salmon provide evidence of strong diet overlap.

Smallmouth Bass Sampling and Analysis

We used data collected by Erhardt and others (2018) to assess Smallmouth Bass predation on fall Chinook Salmon and Sand Rollers in the upper end of Lower Granite Reservoir. We selected this area because it was previously identified as an important rearing area for juvenile fall Chinook Salmon (Tiffan and others

2016), as well as being an area that may present a predation bottleneck (Erhardt and others 2017). This area also supports large numbers of Sand Rollers (Tiffan and others 2017).

We used biweekly estimates of total consumption of fall Chinook Salmon by Smallmouth Bass within our study area during 2013 to 2015 calculated by Erhardt and others (2018), along with similar data collected on bass consumption of Sand Rollers during that study (Erhardt, unpubl. data). We also used unpublished data from a similar 2012 study (Tiffan and others 2014b), in which Smallmouth Bass were collected by a mix of angling and electrofishing, as opposed to electrofishing alone (2013 to 2015 data). In brief, we used non-lethal gastric lavage to collect stomach contents from Smallmouth Bass captured by electrofishing or angling. We identified and weighed fall Chinook Salmon and Sand Rollers in samples. We often identified partially digested fish using diagnostic bones, and used bone length-weight regressions to estimate ingested weight (Hansel and others 1988; Parrish and others 2006; Erhardt and others 2014). We calculated the total proportions by number of fall Chinook Salmon and Sand Rollers in Smallmouth Bass stomachs by year, and graphically examined data for trends over time. Using correlation analysis, we then compared the relationships between prey proportions.

To determine consumption rate (C_{es} : number of each species eaten by Smallmouth Bass per day) of individual bass (Erhardt and others 2018), we used fall Chinook Salmon and Sand Rollers identified in stomach samples in evacuation rate models (Rogers and Burley 1991; Fritts and Pearsons 2004). We estimated mean consumption rates for each biweekly interval for different habitat strata (riprap or natural shorelines, and the reservoir above and below the confluence of the Snake and Clearwater rivers). We then multiplied the means by corresponding (strata-specific) temporal estimates of Smallmouth Bass abundance that were estimated with catchability models (electrofishing CPUE and mark-recapture abundance estimates) to derive total numbers of fall Chinook Salmon and Sand Rollers consumed within each biweekly interval. These interval totals were then summed across strata to estimate the total number of each species lost to Smallmouth Bass predation during each time interval. Smallmouth Bass

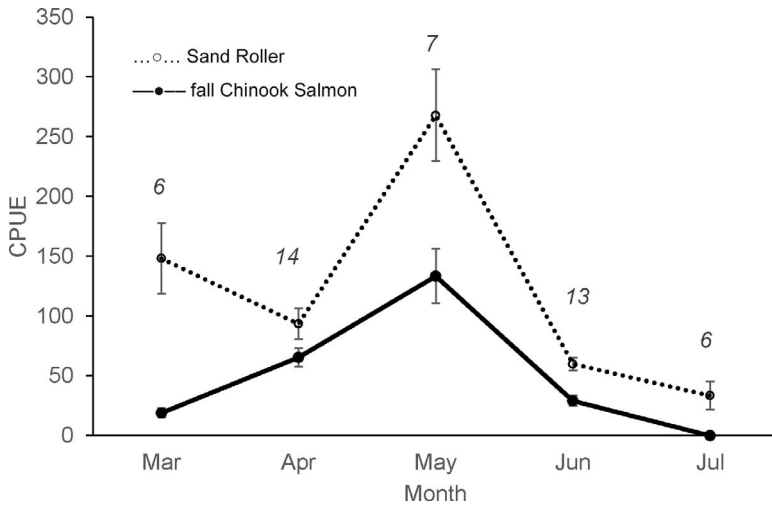


FIGURE 2. Mean \pm SE CPUE (# of fish per seine haul) of Sand Rollers (dotted line) and fall Chinook Salmon (solid line) in Lower Granite Reservoir from late March to early July 2015. Italicized numbers represent the number of hauls.

abundance data was summed similarly. We retained total loss and Smallmouth Bass abundance data from both sampling reaches from the Erhardt and others (2018) study that fell within our study area (SRTZ [above confluence] and CON [below confluence] reaches; Erhardt and others 2018) and sampling intervals for the months of May to June, when the peak distributions of fall Chinook Salmon and Sand Rollers overlapped. Next, we derived annual estimates of Smallmouth Bass consumption rate by dividing the total number of fall Chinook Salmon and Sand Rollers consumed by the total bass abundance for each biweekly sampling interval and calculating an annual mean from all intervals (4 per year). We examined annual trends graphically and compared the consumption rates for each species with correlation analysis.

RESULTS

We conducted 46 beach seine hauls from March through July 2015 and caught 5050 Sand Rollers and 2342 fall Chinook Salmon. Of 46 beach seine hauls, 34 contained both Sand Rollers and fall Chinook Salmon, and 3 hauls contained neither species. Catch of Sand Rollers ranged from 0 to 659 fish haul⁻¹, and catch of fall Chinook Salmon ranged from 0 to 457 fish haul⁻¹. Although total catch of Sand Rollers was higher than that of fall

Chinook Salmon, biweekly catches followed the same temporal trends that increased from March to May and then decreased from May to July (Fig. 2). Fall Chinook Salmon averaged 59.8 ± 8.6 (SD) mm ($n = 41$, range = 50–88 mm) and 2.1 ± 1.3 g ($n = 41$, range = 1.0–7.0 g). Sand Rollers averaged 57.9 ± 15.5 mm ($n = 498$, range = 29–107 mm) and 3.9 ± 3.7 g ($n = 498$, range = 0.4–23.4 g).

We examined the diets of 41 fall Chinook Salmon and 107 Sand Rollers. The most important taxa for both species were dipterans (Chironomidae) and *Neomysis mercedes* (Order Mysidacea, opossum shrimps). Dipterans were most important to the diets of both fish species, in terms of numbers and weight, followed by *Neomysis mercedis* (Table 1). These 2 taxa combined composed 79 to 97% of fall Chinook Salmon diets (by weight) and 91 to 97% of Sand Roller diets (by weight) from April through June. Diets of fall Chinook Salmon and Sand Rollers showed considerable overlap and similarity based on IRI percentages and Morisita's similarity index (Table 2).

Stable isotopes of carbon showed that fall Chinook Salmon were more enriched in $\delta^{13}\text{C}$ than Sand Rollers and had a mean \pm SE $\delta^{13}\text{C}$ of -22.7 ± 0.27 , evidence that most of their energy derived from littoral sources. In contrast, the mean \pm SE $\delta^{13}\text{C}$ value for Sand Rollers was -25.2 ± 0.27 , suggesting a greater dietary energy contribution from offshore, benthic sources.

TABLE 1. Number of prey (N), frequency of occurrence (F), and wet weight of prey (Wt, g) consumed by fall Chinook Salmon ($n = 41$) and Sand Rollers ($n = 107$) in Lower Granite Reservoir from April through June 2015. Main diet items were Diptera (primarily Chironomidae), the opossum shrimp *Neomysis mercedis*, and other invertebrates. * = weight <0.001 g.

| Date | Fall Chinook Salmon | | | | | | | | | Sand Roller | | | | | | | | |
|--------|---------------------|----|------|--------------------------|---|------|-------|----|------|-------------|----|------|--------------------------|----|------|-------|----|------|
| | Diptera | | | <i>Neomysis mercedis</i> | | | Other | | | Diptera | | | <i>Neomysis mercedis</i> | | | Other | | |
| | N | F | Wt | N | F | Wt | N | F | Wt | N | F | Wt | N | F | Wt | N | F | Wt |
| 14-Apr | 35 | 6 | 0.03 | 9 | 3 | 0.09 | 17 | 11 | 0.02 | 211 | 20 | 0.15 | 11 | 8 | 0.13 | 19 | 12 | 0.05 |
| 28-Apr | 56 | 10 | 0.10 | 27 | 8 | 0.29 | 58 | 23 | 0.14 | 100 | 21 | 0.36 | 72 | 20 | 0.45 | 32 | 20 | 0.19 |
| 18-May | 152 | 10 | 0.27 | 1 | 1 | 0* | 51 | 10 | 0.01 | 159 | 29 | 0.43 | 42 | 13 | 0.40 | 60 | 20 | 0.17 |
| 10-Jun | 234 | 10 | 0.59 | 0 | 0 | 0 | 26 | 9 | 0.02 | 198 | 23 | 0.19 | 17 | 11 | 0.07 | 19 | 12 | 0.06 |

Stable isotopes of nitrogen for fall Chinook Salmon had a mean \pm SE $\delta^{15}\text{N}$ value of 11.7 ± 0.18 , evidence that they fed at a higher trophic level than Sand Rollers, which had a mean \pm SE $\delta^{15}\text{N}$ value of 9.2 ± 0.29 .

Fall Chinook Salmon and Sand Rollers were the predominant prey fish in Smallmouth Bass diets. Of 3276 Smallmouth Bass sampled, fall Chinook Salmon were found in 296 bass stomachs, with mean annual proportions (by number) ranging from 0.09 to 0.15, and Sand Rollers were found in 975 stomachs, with proportions ranging from 0.24 to 0.50. There was a negative correlation between the proportions of fall Chinook Salmon and Sand Rollers found in bass diets from 2012 to 2015, but it was not significant ($r = -0.75, P = 0.25$). Generally, in years of high Sand Roller consumption, fewer fall Chinook Salmon were consumed by bass (Fig. 3).

Estimates of Smallmouth Bass consumption of fall Chinook Salmon and Sand Rollers showed similar patterns to the proportion of those prey in bass diets. There was a significant negative correlation between mean annual rates of consumption of fall Chinook Salmon and Sand Rollers ($r = -0.95, P = 0.045$). As bass consump-

tion of Sand Rollers increased, consumption of fall Chinook Salmon decreased (Fig. 4). Consumption rates were always higher for Sand Rollers, and ranged from a low of 0.219 fish smallmouth⁻¹ day⁻¹ in 2013 to a peak of 0.392 fish smallmouth⁻¹ day⁻¹ in 2015. The consumption rate of fall Chinook Salmon generally decreased from a high of 0.114 fish smallmouth⁻¹ day⁻¹ in 2012 to a low of 0.050 fish smallmouth⁻¹ day⁻¹ in 2014 (Fig. 4). We estimated that overall 167,358 fall Chinook Salmon and 673,365 Sand Rollers were lost to Smallmouth Bass predation in our study area from 2012 to 2015.

DISCUSSION

We found high overlap in both habitat use and diet between fall Chinook Salmon and Sand Rollers, but diel and spatial partitioning of resource use between the 2 species may act to reduce potential competition. Fall Chinook Salmon are shoreline oriented during rearing (Tiffan and others 2006, 2014b) and are most active during the day (Tiffan and others 2010). By contrast, Sand Rollers occupy deeper, off-shore habitat during the day in reservoir habitats, but move into shoreline habitat at night, presumably to feed and spawn (Tiffan

TABLE 2. Index of Relative Importance (IRI [%]) of diet items for 41 fall Chinook Salmon and 107 Sand Rollers captured with beach seines in Lower Granite Reservoir from April through June 2015. Diet items are abbreviated as Dip = Diptera (primarily Chironomidae); Neo = *Neomysis mercedis*; and Other = other invertebrates. *M* is Morisita's overlap index values by week.

| Date | Fall Chinook Salmon | | | Sand Roller | | | <i>M</i> |
|--------|---------------------|-----|-------|-------------|-----|-------|----------|
| | Dip | Neo | Other | Dip | Neo | Other | |
| 14-Apr | 64 | 29 | 7 | 86 | 11 | 3 | 1.05 |
| 28-Apr | 39 | 40 | 21 | 50 | 44 | 6 | 0.41 |
| 18-May | 93 | 0 | 7 | 77 | 20 | 3 | 0.52 |
| 10-Jun | 97 | 0 | 3 | 86 | 6 | 8 | 0.80 |

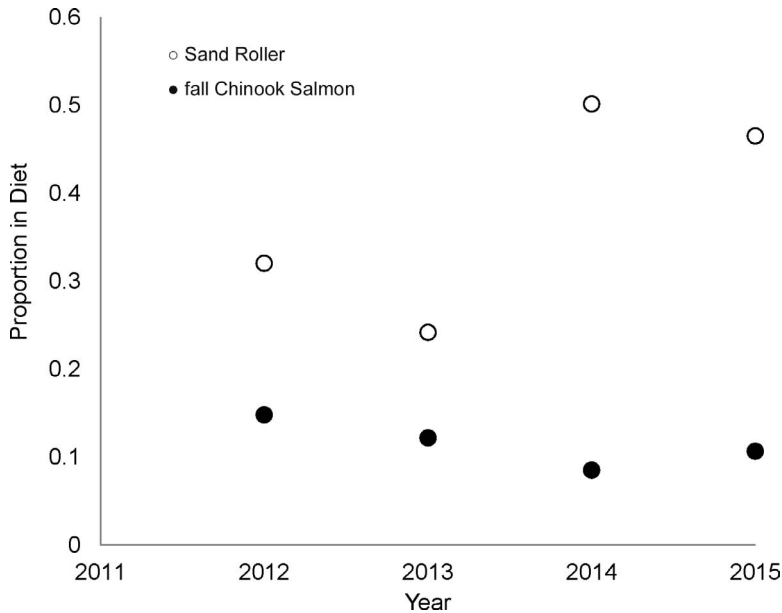


FIGURE 3. Annual proportion (by number) of Sand Rollers (open circles) and fall Chinook Salmon (solid circles) in Smallmouth Bass diets in Lower Granite Reservoir from April through June, 2012 to 2015.

and others 2017). This diel habitat segregation means that both species occupy the same habitat only at night. It is unknown how nighttime use of shoreline areas by Sand Rollers affects fall Chinook Salmon, but the effect may be minimal, since rearing fall Chinook Salmon are largely inactive at night (Tiffan and others 2010). The greatest impacts may occur during crepuscular periods, when both species may be feeding, but our diet data provide conflicting results.

Both fall Chinook Salmon and Sand Rollers mainly consumed chironomids and *Neomysis mercedis*, which is not surprising since both fish are opportunistic feeders and these invertebrates make up the majority of the prey biomass (Tiffan and others 2014a). Although stomach sampling demonstrated high dietary overlap, the limited stable isotope data showed that most dietary carbon was assimilated from different sources. Fall Chinook Salmon were more enriched in $\delta^{13}\text{C}$ than Sand Rollers, evidence that their energy provenance was from littoral sources (for example Vander Zanden and Vadeboncouer 2002). In contrast, Sand Rollers were more depleted in $\delta^{13}\text{C}$, indicating that they derived much of their energy from offshore benthic habitats where carbon is typically more depleted (for example Vander Zanden and Vadeboncouer

2002). Regardless, Sand Rollers may be feeding to some extent in shoreline habitats, which may reduce prey resources for fall Chinook Salmon given the high abundance of Sand Rollers we encountered. The $\delta^{15}\text{N}$ values differed substantially between fall Chinook Salmon and Sand Rollers, suggesting that they did not occupy the same trophic position, which provides further evidence that competition may be reduced between the 2 species. In addition, a high abundance of prey could also reduce competition during overlapping periods of habitat use. It is important to recognize, however, that stable isotope data were limited, so only very general inferences can be drawn from them. Further study of the abundance and isotopic signatures of invertebrate prey from both shoreline and offshore habitats would help clarify the energy provenance for both fall Chinook Salmon and Sand Rollers.

The greatest effect that Sand Rollers may have on fall Chinook Salmon is to serve as a buffer against Smallmouth Bass predation. Smallmouth Bass are opportunistic predators (Coble 1975), and Sand Rollers now compose the greatest prey fish portion (by weight) of bass diets in Lower Granite Reservoir (Erhardt and others 2018). In contrast, Anglea (1997) found no Sand Rollers in

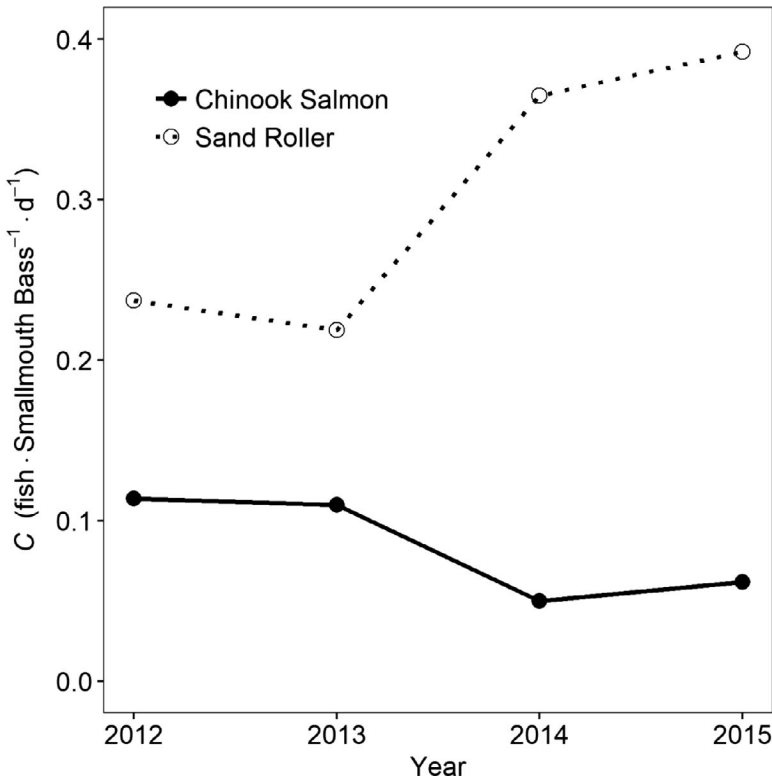


FIGURE 4. Estimated Smallmouth Bass consumption rate of Sand Rollers and fall Chinook Salmon during May and June in Lower Granite Reservoir from 2012 to 2015.

the diets of more than 4200 Smallmouth Bass sampled from Lower Granite Reservoir in 1994–1995. Similarly, Naughton and others (2004) did not identify the species of “non-salmonid” fish consumed in their study, but extensive sampling by University of Idaho personnel in the 1990s suggests they were not Sand Rollers (Bennett and others 1995a, 1995b). The consequence of the resurgence of the Sand Roller population in the reservoir was that as their proportion in Smallmouth Bass diets increased, the proportion of fall Chinook Salmon in bass diets generally decreased. This generally translated to lower consumption and loss of fall Chinook Salmon in years when Sand Roller consumption and loss was high. It is likely that if Sand Rollers had not increased in abundance in recent years, consumption and loss of fall Chinook Salmon would have been higher than we observed in this study. This is supported by higher Smallmouth Bass consumption and loss of fall Chinook Salmon in upstream reaches of the unpounded Snake

River where Sand Rollers are absent, compared to downstream reaches where they are present and compose a large portion of Smallmouth Bass diets (Connor and others 2017).

The negative impact of predation by Smallmouth Bass on fall Chinook Salmon is similar to typical responses observed when non-native predators are introduced and become established in new systems (Mooney and Cleland 2001). The resurgence of the Sand Roller population in the Snake River, although encouraging and interesting in its own right, adds a new dimension to the ecological interaction among all 3 species. Although this study was limited in scope, it provided evidence that Sand Rollers, acting as a native invader, may be providing a predation buffer for fall Chinook Salmon. The relationship between Sand Rollers and fall Chinook Salmon may be facilitative (Stachowicz 2001), wherein Sand Rollers functionally replace fall Chinook Salmon in Smallmouth Bass diets, thus providing fall Chinook Salmon with some protection from

predation. Although this may be beneficial for fall Chinook Salmon in the short term, long-term consequences are unpredictable, particularly if environmental conditions change (Bronstein 1994; Stachowicz 2001). Alternatively, it is possible that Sand Roller availability could increase predation risk if it augments Smallmouth Bass growth or survival, which may increase bass abundance and hence predation. Continued monitoring of Sand Rollers, fall Chinook Salmon, and Smallmouth Bass is necessary to track changes in diets and interactions among them and other species in the aquatic community in Lower Granite Reservoir.

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