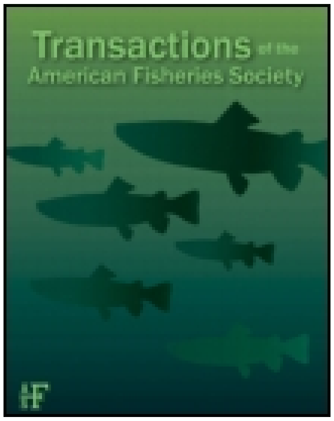




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# Infection of Juvenile Salmonids by Salmincola californiensis (Copepoda: Lernaeopodidae) in Reservoirs and Streams of the Willamette River Basin, Oregon

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ARTICLE

# Infection of Juvenile Salmonids by *Salmincola californiensis* (Copepoda: Lernaeopodidae) in Reservoirs and Streams of the Willamette River Basin, Oregon

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***Abstract***
**We assessed infection prevalence and intensity by the ectoparasitic copepod *Salmincola californiensis* among salmonid species rearing in reservoirs and streams upstream of reservoirs in the Willamette River basin, Oregon, during 2012 and 2013. Infection levels of juvenile Chinook Salmon *Oncorhynchus tshawytscha*, Rainbow Trout *O. mykiss*, and Cutthroat Trout *O. clarkii* were greater in reservoirs than in streams and increased with the age and size of fish. Copepods were more likely to be attached within the brachial cavity of reservoir fish (79%), whereas fins were the most common attachment site on stream fish (71%). Chinook Salmon in reservoirs were more vulnerable to infection than other species. Age-0 Chinook Salmon in reservoirs showed increasing infection prevalence throughout the year, reaching 84% by fall (compared with 11% in streams). Infection intensity was greater for age-0 Chinook Salmon in reservoirs than for those in streams. Infection prevalence for reservoir-rearing Rainbow Trout was < 1% at age 0, 22% at age 1, 36% at age 2, and 38% at age 3. Intensity was low for age-1 Rainbow Trout and increased for age-2 and age-3 fish. Infection prevalence for reservoir-rearing Cutthroat Trout collected in spring (39%) was greater than for those rearing in streams (4.5%). Juvenile kokanee *O. nerka* were only present in reservoirs and were rarely infected with copepods. The lack of water current in reservoirs may increase the likelihood of infection in the brachial cavity. Greater infection levels observed for juvenile Chinook Salmon compared with the other species in reservoirs may be a function of behavioral, physiological, and habitat differences. We concluded that copepod infection in reservoirs reached levels that could decrease the fitness and survival of Chinook Salmon smolts, potentially hampering conservation and recovery efforts.**

The freshwater copepod *Salmincola californiensis* parasitizes Pacific salmon and trout of the genus *Oncorhynchus* (Kabata 1969). The ectoparasite attaches to a solid subdermal support of a host fish, such as fin rays, rods of a gill filament, or bone (Kabata and Cousens 1973). Low-level infections are generally not believed to be lethal to host fish, especially if the parasites are not attached within the brachial cavity. However, high-intensity infections on or near the gills can cause gill tissue destruction (Kabata and Cousens 1977; Sutherland and Wittrock 1985), resulting in anemia and mortality for smolts during saltwater transition (Pawaputanon 1980; Sutherland and Wittrock 1985). Copepods attached along the brachial cavity rim or inner operculum can indirectly cause the distal portion of gill lamellae to atrophy due to the pressure they exert by the movement of the operculum (Kabata and Cousens 1977).

The life cycle of *S. californiensis* consists of several stages involving a single host fish. The adult female has two large egg sacs that require approximately 1 month to hatch, and the free-swimming infectious copepodid (~0.69 mm in length) can survive for about 2 d after hatching, during which time it attempts to find a host (Kabata and Cousens 1973). Passing shadows and water disturbances caused by a potential host fish increase the swimming activity of copepodids and the

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probability of finding a suitable host (Kabata and Cousens 1977; Poulin et al. 1990). After the initial attachment to a host, the copepod undergoes several chalimus stages in which it reattaches to a suitable subdermal support, ending with the adult stage within weeks after hatching.

The level of *S. californiensis* infection increases with host body length, with larger individuals of a species within a water body having a greater parasite load (Nagasawa and Urawa 2002; Barndt and Stone 2003). Larger fish are likely more susceptible to infection due to their greater surface area and the increased water volume circulated over their gills (Poulin et al. 1991). In natural systems, larger fish are older and may be more susceptible because of a longer exposure time. Attachment location is also dependent on host size, with copepods most often on the fin bases of smaller fish and the gills of larger fish (Kabata and Cousens 1977).

Here, we report parasite–host relationships of juvenile Chinook Salmon *O. tshawytscha*, kokanee *O. nerka* (lacustrine Sockeye Salmon), Rainbow Trout *O. mykiss*, and Cutthroat Trout *O. clarkii* rearing in reservoirs and streams in the Willamette River basin of western Oregon. These data were collected as part of a larger study evaluating the juvenile Chinook Salmon use of reservoir habitat to aid in the recovery of the population (Monzyk et al. 2012, 2013). Chinook Salmon in the upper Willamette River basin were listed as threatened in 1999 under the Endangered Species Act (NMFS 1999). Anecdotal information and our field observations suggested that juvenile Chinook Salmon rearing in reservoirs were more susceptible to infection than other species in reservoirs and juvenile Chinook Salmon in streams. Few studies have examined host–parasite relationships of *S. californiensis* and salmonids in lentic systems (Bailey and Margolis 1987; Chigbu 2001; Hargis et al. 2014), and all have focused on *O. nerka* (anadromous or nonanadromous morphs).

Recent management and recovery efforts in the Willamette River basin include transporting adult Chinook Salmon around dams into historic spawning habitat above reservoirs (NMFS 2008). The majority of their progeny enter reservoirs soon after hatching in the spring as small subyearlings (<40 mm fork length), where they rear for several months before passing the dam during the fall when the reservoirs are drawn down (Keefer et al. 2012; Romer et al. 2012). Reservoirs are a novel rearing habitat for this otherwise stream-type salmonid. Juvenile Chinook Salmon rearing in reservoirs grow significantly faster than those in streams upstream of the reservoirs (Korn and Smith 1971; Monzyk et al. 2013), and their larger size may contribute to increased infection risk. An understanding of the infection levels experienced by juveniles rearing in or above reservoirs is needed because mortality associated with high-intensity infection could ultimately hinder their recovery.

In this study we evaluated levels of parasitic copepod infection throughout the year for each salmonid species rearing in streams and reservoirs. Our primary objective was to compare infection levels among species and between rearing locations (reservoir or stream). We investigated the relationship between the host size and the duration of exposure by comparing infection levels between age-classes within species. We also investigated whether host size accounted for the differences in infection levels between rearing locations.



## STUDY AREA

We assessed *S. californiensis* infection levels among salmonids rearing in four Willamette River basin reservoirs: Detroit, Cougar, Fall Creek, and Lookout Point (Figure 1). The high-head dams and reservoirs are operated by the U.S. Army Corps of Engineers primarily for flood control and range in size from 518 to 1,766 ha when at full pool. Generally, reservoirs are drawn down > 30 m in elevation in the fall to increase flood control capacity and are refilled in the spring. During drawdown, most reservoirs retain a large residual pool > 40 m deep. However, Fall Creek Reservoir is drawn down > 55 m to the streambed by late fall and held at this level for approximately 2 weeks. This reservoir is also the smallest and is located at the lowest elevation (256-m elevation at full pool).

All four reservoirs support native juvenile Chinook Salmon, Rainbow Trout, and Cutthroat Trout. Detroit Reservoir also has introduced kokanee, which reproduce naturally in the rivers upstream of the reservoir and are supplemented each May with unmarked hatchery fingerlings (50–75 mm fork length). In addition, unmarked hatchery Rainbow Trout were released in Detroit Reservoir in late June of each year and could not be distinguished from naturally produced fish. Marked hatchery Chinook Salmon and Rainbow Trout (identified by the presence of a clipped adipose fin) were present in Lookout Point and Detroit reservoirs.

We also assessed the infection levels among salmonids rearing in the streams upstream of the reservoirs, except for Fall Creek upstream of Fall Creek Reservoir. The North Santiam River is a fourth-order stream that enters Detroit Reservoir at an elevation of 481 m above sea level when the reservoir is at full pool. The South Fork McKenzie River above Cougar Reservoir is a fourth-order stream that enters the reservoir at 518 m elevation. The Middle Fork Willamette River is a fifth-order stream that enters Lookout Point Reservoir at an elevation of 287 m. We also sampled fish in the North Fork Middle Fork Willamette River, a fourth-order stream that enters the Middle Fork Willamette River 7.6 km upstream of Lookout Point Reservoir (Figure 1). The watersheds of the rivers are predominately forest land cover types.

## METHODS

We used various sampling techniques to collect fish rearing in reservoirs in 2012–2013. In Detroit, Cougar, and Lookout Point reservoirs, small salmonids were sampled from March–June with floating box traps set along the shoreline. Traps

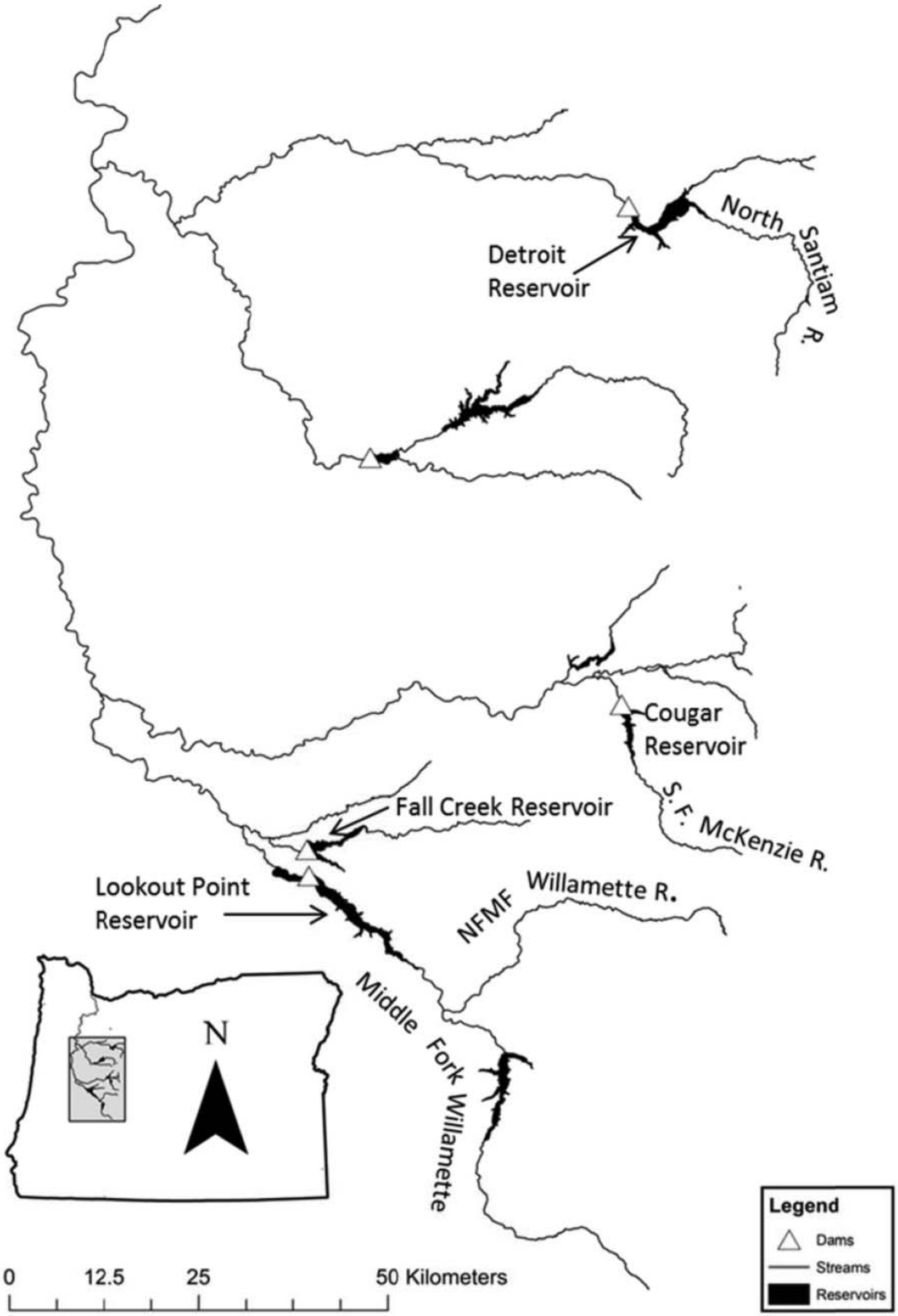


FIGURE 1. Map of the Willamette River basin, Oregon. Fish from the labeled water bodies were sampled for copepods in 2012 and 2013. Abbreviations are as follows: NFMF = North Fork Middle Fork, S. F. = South Fork, and R. = River.

consisted of a 0.61-m × 0.61-m × 0.91-m (width × height × length) PVC frame wrapped with 0.42-cm delta mesh with a 51-mm throat opening. Traps were placed perpendicular to shore with a 5-m lead net (0.91 m deep) extending from the shore to the trap opening. Oneida Lake traps were larger and deployed farther from shore in the spring (April–June). Floating Oneida Lake traps had a 0.64-cm delta mesh holding box (2.4 m × 2.4 m × 2.4 m) and were placed 34 m from shore with a 3.0-m-deep lead net. All traps sites were randomly selected. In addition, gill nets were set in the forebay of Detroit and Lookout Point reservoirs from July through December. Gill nets were 24.4 m long by 4.6 m deep, consisting of four 6.1-m panels with square mesh sizes of 9.5, 12.7, 19.1, and 25.4 mm. Gill nets were set at 4.6-m depth intervals from the surface to a maximum depth of 27.6 m (six nets total) and checked daily. Finally, rotary screw traps placed directly below the tailrace of dams were used to collect fish exiting all the reservoirs. Rotary screw traps were designed to capture fish moving downstream and were equipped with live boxes that safely held juvenile salmonids until the trap could be checked. A 2.4-m-diameter screw trap below Fall Creek Reservoir was the only source of fish collection below this reservoir in 2012. In 2013, an additional fish trap was deployed in the tailrace that screened a portion of the dam discharge and collected fish in a holding well.

Salmonids rearing in the streams above the reservoirs were collected in 2012–2013 with rotary screw traps and seining. Screw traps were 1.5 m in diameter and operated from March to November. We chose trap sites that were as close to the reservoir as possible. The trap on the South Fork McKenzie River was 2 km upstream from the head of Cougar Reservoir. Traps on the North Santiam and Middle Fork Willamette rivers were 7 and 9 km upstream of the reservoir, respectively. Seining was conducted at various sites upstream of screw traps from August–September each year in reaches with known Chinook Salmon spawning and rearing habitat. Seines were approximately 3 m wide and 1.2 m deep, constructed with 0.64-cm delta mesh. Snorkelers were deployed to initially locate fish. The seine was placed downstream and the snorkelers then reentered the river upstream and slowly herded fish into the seine.

We categorized fish as stream or reservoir rearing based on collection location and assumed rearing occurred in that habitat for the majority of its life prior to capture. Although upstream and downstream movements of fish between rearing locations (stream and reservoir) was possible, the distance between stream sampling sites and reservoirs would likely limit any bias this movement would cause.

All fish captured were anesthetized (50 mg/L MS-222 [tricaine methanesulfonate]), examined for an adipose fin clip, and measured (mm) to fork length (FL). Each fish was macroscopically examined for the presence of gravid adult female copepods attached to the fins or branchial cavity. To limit fish handling, we did not attempt to determine specific attachment location within the branchial cavity. We counted copepods at each attachment location from a randomly selected subset of the fish collected each day (minimum of 5 fish/species/d/gear type). Only gravid adult female copepods were counted to determine prevalence and intensity since this life stage was easily visible during field examinations. We estimated the age of each fish using length-frequency analysis. For each location and year, we plotted individual fish size by date and assigned age.

Copepod infection was described in terms of prevalence (percentage of individuals infected) and intensity (number of parasites per infected fish) following the conventions established by Margolis et al. (1982). The prevalence and intensity of copepod infection were assessed each month for each species, age-class, and rearing location (reservoir and stream). We compared prevalence between rearing locations ($z$-test; $\alpha = 0.05$) for each species and for each age-class. Prevalence comparisons were made within seasons to account for the disproportionate temporal sampling effort between rearing locations and the possibility that infection levels differ among seasons due to exposure time. We defined seasons as winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Data from both years was pooled for monthly and seasonal analyses unless otherwise stated. We also compared prevalence among age-classes within species and between rearing locations. To investigate whether infection differences between rearing locations were due to fish size, we categorized age-0 Chinook Salmon into 5-mm-FL size-groups (e.g., 65–69 mm) and compared infection levels between rearing locations for each group. Copepod intensity data failed tests of normality and constant variance; we used the nonparametric Kruskal–Wallis one-way analysis of variance (ANOVA) ($\alpha = 0.05$) for comparisons between rearing locations for each species and age-class.

## RESULTS

We examined 13,082 reservoir-rearing and 3,329 stream-rearing salmonids for infection by *S. californiensis*. Juvenile Chinook Salmon comprised the majority of the fish collected in both rearing locations (Table 1). Within each species, Chinook Salmon, kokanee, and Rainbow Trout generally maintained distinct size differences between cohorts that aided our ability to assign age (Figure 2). Cutthroat Trout were rare and we were unable to estimate their age based on limited length-frequency data. No Cutthroat Trout were collected in the North Santiam River or Detroit Reservoir. Only age-0 and age-1 Chinook Salmon and kokanee were collected, with kokanee collected almost exclusively in reservoirs. Rainbow Trout ranged from age 0 to age 3. Copepod infection levels for each species and rearing location were similar between years.

Overall, copepods were more often attached within the branchial cavity of reservoir fish compared to stream fish. Seventy-nine percent of the 19,156 copepods counted on reservoir

TABLE 1. Comparison of the prevalence of *Salmincola californiensis* infection for Pacific salmonid species by season and age-class in reservoirs and streams, 2012–2013. Prevalence is the proportion of fish infected.

| | Reservoir | | | Stream | | | |
|---|---|---|---|---|---|---|---|
| Season | *n* | Mean fish length (mm) | Copepod prevalence | *n* | Mean fish length (mm) | Copepod prevalence | *P*-value |
| | | | **Chinook Salmon, age 0** | | | | |
| Winter | 18 | 51 | 0.000 | 1 | 57 | 0.000 | |
| Spring | 2,245 | 61 | 0.041 | 280 | 60 | 0.000 | 0.001 |
| Summer | 1,457 | 134 | 0.308 | 2,511 | 66 | 0.032 | < 0.001 |
| Fall | 5,725 | 144 | 0.849 | 217 | 86 | 0.106 | < 0.001 |
| | | | **Chinook Salmon, age 1** | | | | |
| Winter | 227 | 128 | 0.991 | 68 | 88 | 0.103 | < 0.001 |
| Spring | 325 | 145 | 0.809 | 11 | 104 | 0.091 | < 0.001 |
| Summer | | | | 12 | 132 | 0.333 | |
| Fall | 102 | 220 | 0.941 | 3 | 161 | 1.000 | 0.408 |
| | | | **Cutthroat Trout** | | | | |
| Winter | 2 | 115 | 0.000 | | | | |
| Spring | 91 | 195 | 0.385 | 22 | 148 | 0.045 | 0.005 |
| Summer | 10 | 157 | 0.000 | 11 | 171 | 0.273 | 0.246 |
| Fall | 7 | 171 | 0.143 | 5 | 170 | 0.200 | 0.600 |
| | | | **Kokanee, age 0** | | | | |
| Spring | 34 | 80 | 0.000 | | | | |
| Summer | 417 | 114 | 0.005 | | | | |
| Fall | 782 | 143 | 0.003 | 1 | 100 | 0.000 | |
| | | | **Kokanee, age 1** | | | | |
| Winter | 50 | 149 | 0.000 | | | | |
| Spring | 14 | 153 | 0.286 | | | | |
| Summer | 146 | 244 | 0.000 | | | | |
| Fall | 101 | 260 | 0.000 | | | | |
| | | | **Rainbow Trout, age 0** | | | | |
| Spring | | | | 2 | 54 | 0.000 | |
| Summer | 12 | 62 | 0.000 | 74 | 52 | 0.000 | |
| Fall | 4 | 110 | 0.250 | 32 | 65 | 0.000 | 0.209 |
| | | | **Rainbow Trout, age 1** | | | | |
| Winter | 8 | 95 | 0.000 | | | | |
| Spring | 66 | 98 | 0.015 | 40 | 103 | 0.050 | 0.653 |
| Summer | 484 | 161 | 0.217 | 16 | 109 | 0.063 | 0.241 |
| Fall | 494 | 195 | 0.263 | 4 | 104 | 0.250 | 0.609 |
| | | | **Rainbow Trout, age 2** | | | | |
| Winter | 19 | 194 | 0.263 | 3 | 187 | 0.000 | 0.788 |
| Spring | 74 | 206 | 0.324 | | | | |
| Summer | 84 | 235 | 0.417 | 9 | 227 | 0.333 | 0.896 |
| Fall | 34 | 289 | 0.382 | | | | |
| | | | **Rainbow Trout, age 3** | | | | |
| Winter | 10 | 250 | 0.300 | | | | |
| Spring | 15 | 336 | 0.533 | 2 | 280 | 0.500 | 0.505 |
| Summer | 23 | 318 | 0.304 | 4 | 286 | 0.250 | 0.708 |
| Fall | 2 | 326 | 0.500 | 1 | 340 | 0.000 | |

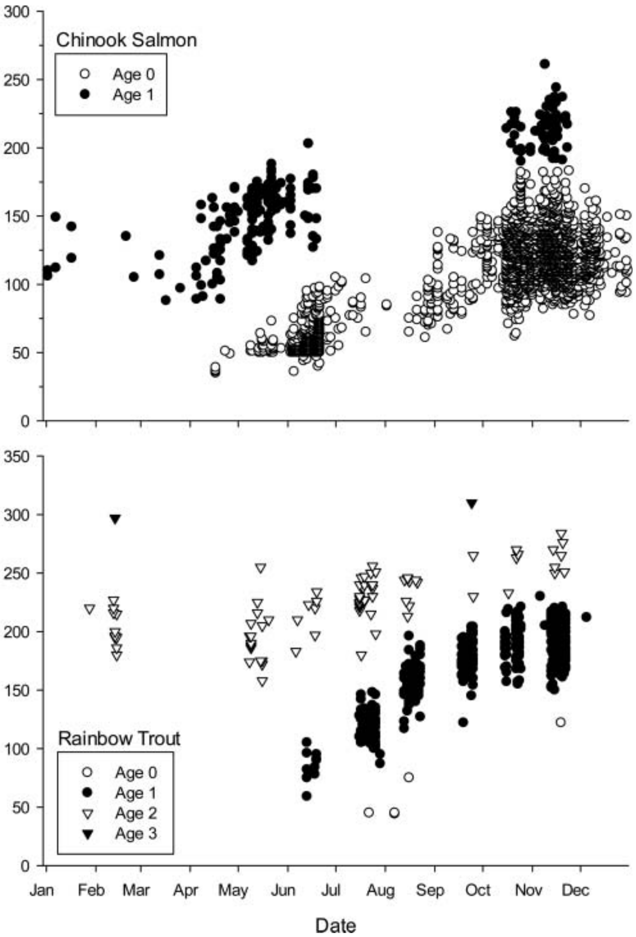


FIGURE 2. Size and age by month for juvenile Chinook Salmon collected in Cougar Reservoir (top panel) and for Rainbow Trout collected in Detroit Reservoir (bottom panel) in 2013.

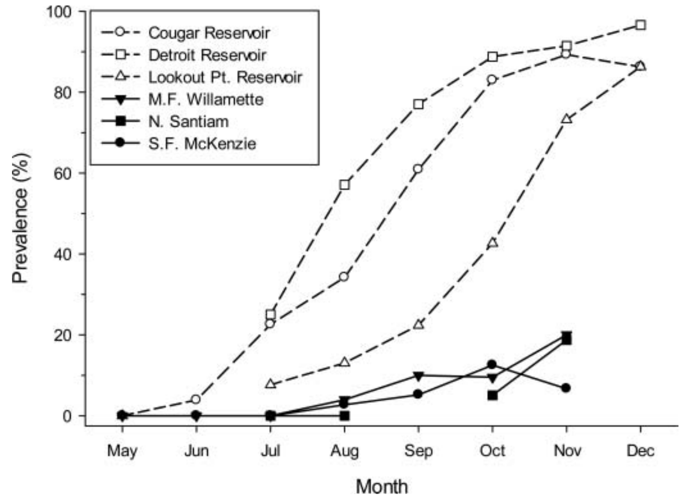


FIGURE 3. Prevalence (percentage of individuals infected) of *Salmincola californiensis* infection for age-0 Chinook Salmon in reservoirs (open symbols) and streams (closed symbols), 2012–2013. Abbreviations are as follows: M.F. = Middle Fork, N. = North, and S.F. = South Fork.

fish were attached within the branchial cavity compared with 29% of the 200 copepods counted on stream fish ($z$-test; $P =$ 0.001). Most copepods were attached within the brachial cavity of reservoir Chinook Salmon (79% of 18,230) and Rainbow Trout (73% of 758) but not Cutthroat Trout (32% of 150). In streams, brachial cavity attachment accounted for only 27% of copepods ($n = 156$) on Chinook Salmon and 37% ($n = 38$) on Rainbow Trout. Only six copepods were counted on Cutthroat Trout in streams, with 33% attached within the brachial cavity.

## Chinook Salmon

The infection prevalence for both age-classes of Chinook Salmon was significantly greater in reservoirs than in streams ($z$-test: $P < 0.001$) (Table 1). An increasing prevalence through time was evident for age-0 Chinook Salmon from both rearing locations but was more rapid for reservoir-rearing fish, with > 75% infected by November compared with < 15% of stream-rearing fish infected in that same timeframe (Figure 3). The intensity of infection was also greater for reservoir fish (Table 2). In both years, the first copepods were observed on age-0, reservoir-rearing Chinook Salmon in June ($n = 91$ infected Chinook Salmon; mean length = 79.3 mm FL; range = 40–154 mm), with increasing intensity from June to December (Figure 4). In streams we did not observe copepods until August each year ($n = 30$ infected Chinook Salmon; mean length = 67.8 mm FL; range = 47–88 mm), and the maximum intensity never exceeded two copepods per fish for the entire year. By fall copepod intensity was significantly greater for reservoir-rearing fish than for those in streams (Figure 5). Chinook Salmon that remained in reservoirs an additional year (age 1) had consistently high monthly prevalence levels, ranging from 78% to 97% (Figure 6). Intensity continued to increase each month, reaching a median of 13 copepods/fish (range 2–28) by the fall. Overall, the intensity in age-1 fish was significantly greater than in age-0 fish (Kruskal–Wallis one-way ANOVA on ranks: $P < 0.001$).

Juvenile Chinook Salmon in reservoirs were significantly larger on average than those in streams (Table 1), possibly contributing to their greater infection prevalence and intensity. However, when controlling for size, age-0 Chinook Salmon still had greater copepod prevalence in reservoirs than in streams (Table 3), suggesting greater exposure risks in reservoirs. For each size-group, fish in Cougar Reservoir had a higher prevalence despite being collected earlier in the year than South Fork McKenzie River fish and therefore exposed to infection for less time. In addition, fish of similar size were more likely to have copepods attached within their brachial cavity if they reared in a reservoir (Table 3). Although sample sizes were smaller in other reservoir–stream systems, a similar pattern was evident. Age-0 Chinook Salmon between 100 and 120 mm FL in Detroit Reservoir

TABLE 2. Intensity (number of parasites per infected fish) of *Salmincola californiensis* infection for Pacific salmonid species by age-class in reservoirs and streams (all locations combined), 2012–2013.

| | | | | Copepod intensity | | |
|---|---|---|---|---|---|---|
| Species | Age | *n* | Mean FL, mm (SD) | Mean | Median | Range |
| | | | **Reservoir** | | | |
| Chinook Salmon | 0 | 4,803 | 142 (38) | 3.3 | 3 | 1–37 |
| | 1 | 333 | 171 (42) | 6.6 | 4 | 1–34 |
| Kokanee | 0 | 4 | 140 (29) | 1.3 | 1 | 1–2 |
| | 1 | 4 | 170 (39) | 3.3 | 3 | 1–5 |
| Rainbow Trout | 0 | 1 | 122 | 3.0 | 3 | 3 |
| | 1 | 236 | 181 (23) | 1.9 | 1 | 1–8 |
| | 2 | 76 | 236 (39) | 3.2 | 2 | 1–26 |
| | 3 | 19 | 333 (57) | 3.5 | 2 | 1–15 |
| Cutthroat Trout | | 32 | 241 (68) | 4.7 | 3 | 1–13 |
| | | | **Stream** | | | |
| Chinook Salmon | 0 | 104 | 74 (14) | 1.1 | 1 | 1–2 |
| | 1 | 15 | 122 (52) | 3.0 | 1 | 1–10 |
| Rainbow Trout | 1 | 4 | 86 (12) | 1.8 | 1.5 | 1–3 |
| | 2 | 3 | 247 (6) | 5.7 | 1 | 1–15 |
| | 3 | 2 | 243 (67) | 7.0 | 7 | 1–11 |
| Cutthroat Trout | | 5 | 283 (46) | 1.2 | 1 | 1–2 |



($n$ = 33; mean = 112 mm FL) had an infection prevalence of 59%, while fish in the same size-group in the North Santiam River ($n$ = 29; mean = 109 mm FL) had a prevalence of 3%. The exposure risk for age-0 Chinook Salmon varied by reservoir. Infection prevalence and intensity levels were lowest in Lookout Point Reservoir and greatest in Fall Creek Reservoir in both years (Figure 7).

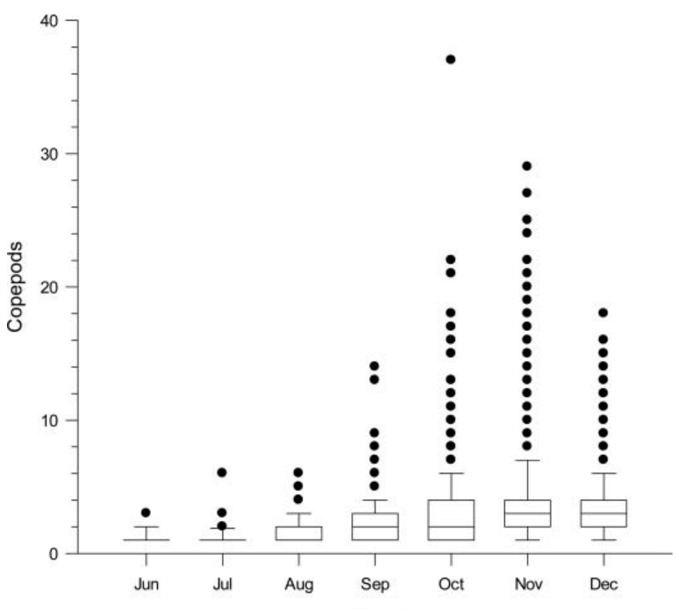


FIGURE 4. Intensity (number of parasites per infected fish) of *Salmincola californiensis* infection for age-0 Chinook Salmon rearing in Lookout Point, Detroit, Cougar, and Fall Creek reservoirs (combined) by month, 2012–2013. The horizontal lines in the boxes denote the medians, the box dimensions represent the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the solid circles are outliers.

## Rainbow Trout

The prevalence of copepod infection among age-0 Rainbow Trout was low in both reservoirs and streams, possibly due to their later emergence timing compared with Chinook Salmon. Age-0 Rainbow Trout were not collected in either rearing location until summer and were small (mean length = 53 mm FL). No copepods were observed on age-0 stream fish in any season ($n$ = 108). Of the 16 age-0 Rainbow Trout collected in reservoirs, only 1 was infected, a 122-mm fish with three copepods collected in Detroit Reservoir in November 2013.

Age-1 Rainbow Trout had an overall infection prevalence of 22% ($n$ = 1,052). Most age-1 Rainbow Trout collected in reservoirs were from Detroit Reservoir ($n$ = 952) and were likely unmarked hatchery fish that were released in June of each year. Rainbow Trout in Detroit Reservoir had an infection prevalence of 5% by July ($n$ = 73) that increased to 27% by August ($n$ = 173), with little change in subsequent months (range = 16–29%). By fall, prevalence was 26% and the intensity of infection was low (median = 1; range = 1–8). In Lookout Point and Cougar reservoirs, the infection prevalence for natural-origin age-1 Rainbow Trout was 2% in spring ($n$ = 54), 5% in summer ($n$ = 20), and 22% in fall ($n$ = 18), with a low intensity

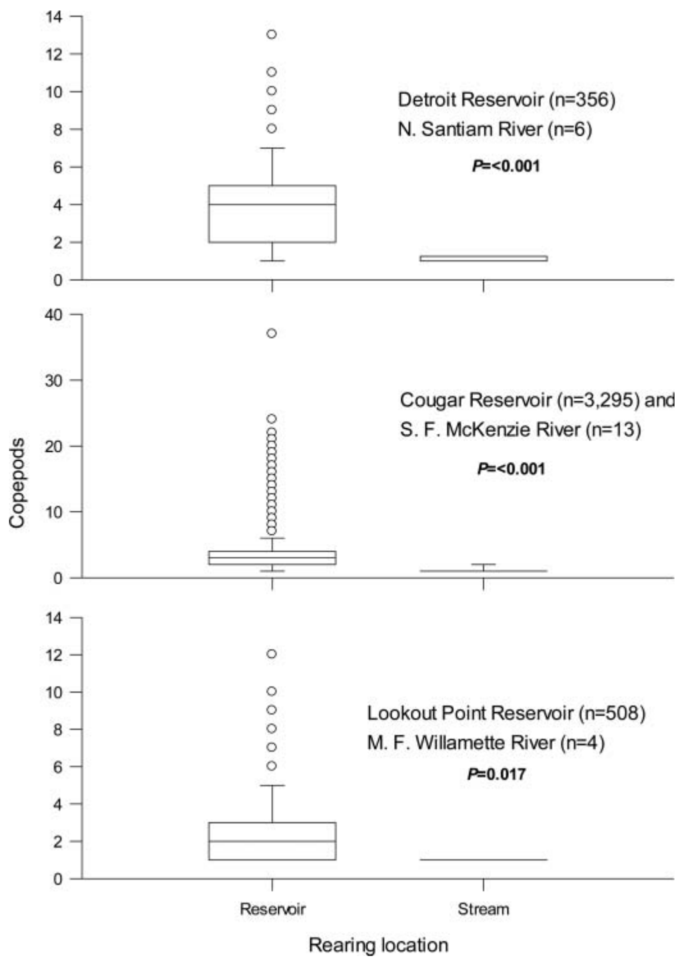


FIGURE 5. Intensity (number of parasites per infected fish) of *Salmincola californiensis* infection for age-0 Chinook Salmon rearing in reservoirs and streams, fall 2012–2013. The horizontal lines in the boxes denote the medians, the box dimensions represent the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the circles are outliers. The given *P*-values are from Mann–Whitney rank sum tests.

(median = 1; range = 1–3). In the North Santiam River upstream of Detroit Reservoir, overall infection prevalence for age-1 Rainbow Trout was 11% ($n$ = 9), with all but one fish captured from mid-August to October. Among the other streams (South Fork McKenzie and Middle Fork Willamette), prevalence was 5% in spring ($n$ = 39) and 8% in summer ($n$ = 12). There were no significant differences in prevalence between reservoir and stream fish in any season, although sample sizes were small, resulting in low test power (<0.1). However, when data across seasons for all reservoirs were pooled and compared with all stream data, prevalence was significantly higher in reservoirs for age-1 Rainbow Trout ($z$-test: $P$ = 0.007).

Prevalence increased slightly for older age-classes of Rainbow Trout in reservoirs (Table 1). Sample sizes were small for older age-classes of Rainbow Trout in streams, and there were no significant differences in infection prevalence between rearing locations in any season, although a trend of greater prevalence for reservoir fish was evident (Table 1). Pooled across seasons, prevalence in reservoirs was 36% for age-2 ($n$ = 211) and 38% for age-3 ($n$ = 50) Rainbow Trout, whereas in streams prevalence was 25% for age-2 ($n$ = 12) and 28% for age-3 ($n$ = 7) Rainbow Trout. The median infection intensity was two copepods per fish for both age-2 (range = 1–26) and age-3 (range = 1–15) Rainbow Trout.

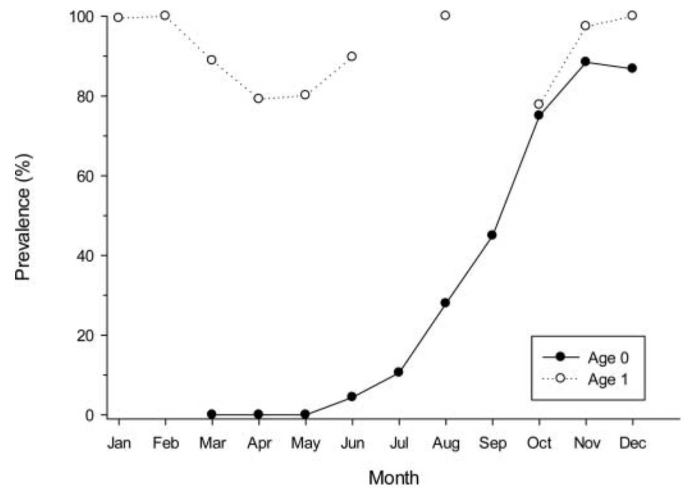


FIGURE 6. Copepod infection prevalence (percentage of individuals infected) for age-0 and age-1 Chinook Salmon in Lookout Point, Detroit, Cougar, and Fall Creek reservoirs (combined), 2012–2013.

## Cutthroat Trout

Cutthroat Trout were relatively rare in our collections and most were caught in spring (Table 1). Cutthroat Trout in reservoirs had significantly higher infection prevalence (39%) than those in streams (5%) during the spring (Table 1). We could not detect differences in the summer or fall, but the power of the tests was low (≤0.18). Infection intensity was also greater in reservoirs (Table 4). Although we were unable to determine the age of Cutthroat Trout, larger individuals had higher prevalence in both rearing locations (Table 4).

## Kokanee

Kokanee in Detroit Reservoir were rarely infected with parasitic copepods. Although age-0 kokanee were similar in size to age-0 Chinook Salmon and age-1 Rainbow Trout, the infection prevalence for kokanee was generally <1% in all months sampled (Figure 7). Only four of the 1,233 age-0 kokanee examined for copepods were infected, with intensity ranging from 1 to 2 copepods/fish (Table 2). Age-1 kokanee had an overall infection prevalence of 1% ($n$ = 311), with an intensity ranging from 2 to 5 copepods/fish. All copepods were attached within the brachial cavity.

TABLE 3. Prevalence of *Salmincola californiensis* infection by size-group of age-0 Chinook Salmon in Cougar Reservoir and the South Fork McKenzie River, 2012–2013. Prevalence is given as the proportion of fish infected.

| | Cougar Reservoir | | | | South Fork McKenzie River | | | |
|---|---|---|---|---|---|---|---|---|
| Size-group (mm) | *n* | Prevalence | Brachial attached (%) | Median date of capture | *n* | Prevalence | Brachial attached (%) | Median date of capture |
| 50–54 | 650 | 0.014 | 0 | Jun 14 | 279 | 0.004 | 0 | Jul 15 |
| 55–59 | 523 | 0.017 | 10 | Jun 17 | 342 | 0.015 | 0 | Jul 29 |
| 60–64 | 288 | 0.049 | 7 | Jun 18 | 373 | 0.027 | 0 | Aug 23 |
| 65–69 | 212 | 0.038 | 13 | Jun 20 | 443 | 0.038 | 0 | Aug 30 |
| 70–74 | 221 | 0.081 | 4 | Jun 17 | 372 | 0.051 | 0 | Sep 07 |
| 75–79 | 142 | 0.155 | 11 | Jun 21 | 248 | 0.040 | 0 | Sep 07 |
| 80–84 | 156 | 0.276 | 28 | Aug 14 | 163 | 0.049 | 0 | Sep 08 |
| 85–89 | 143 | 0.448 | 34 | Aug 28 | 85 | 0.094 | 22 | Sep 13 |
| 90–94 | 159 | 0.503 | 43 | Oct 17 | 24 | 0.083 | 33 | Sep 16 |
| 95–99 | 192 | 0.661 | 49 | Oct 30 | 6 | 0.167 | 0 | Sep 12 |



## Species Comparisons in Reservoirs

Juvenile Chinook Salmon in reservoirs were more vulnerable to infection than other reservoir-rearing salmonids. This was most evident in Detroit Reservoir, where age-0 Chinook Salmon had a significantly greater infection prevalence than did similarly sized age-0 kokanee and age-1 Rainbow Trout ($z$-test: $P = 0.001$; Figure 8). Among these groups of fish, age-0 Chinook Salmon also had a significantly greater infection intensity (Kruskal–Wallis one-way ANOVA on ranks: $P < 0.001$). Across all reservoirs, the infection prevalence for juvenile Chinook Salmon ranged from 75% to 100% by the fall, whereas Rainbow Trout infection prevalence was generally $< 50\%$ for all age-classes.

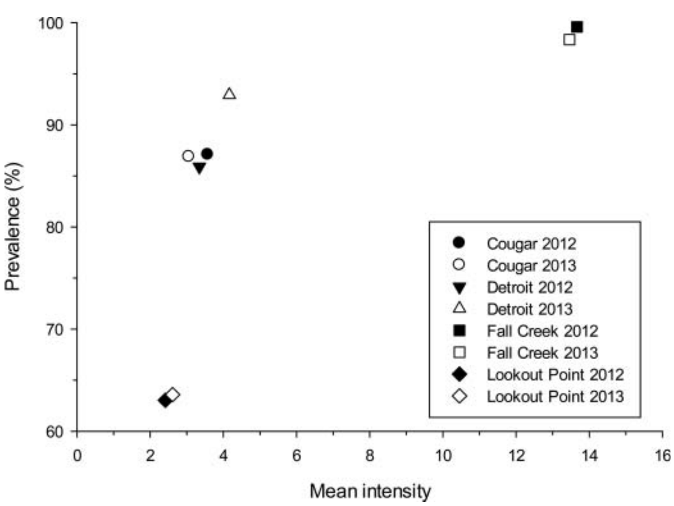


FIGURE 7. Intensity and prevalence of *Salmincola californiensis* infection for age-0 Chinook Salmon rearing in Cougar, Detroit, Fall Creek, and Lookout Point reservoirs in fall 2012 (closed symbols) and 2013 (open symbols).

## DISCUSSION

Our results provide evidence that salmonids rearing in Willamette River basin reservoirs had greater copepod infection prevalence and intensity than stream-rearing fish, with the infection more likely to occur in the brachial cavity. The difference in infection between rearing locations may be partly attributed to the larger size of reservoir fish. Several studies have attributed increased infection prevalence of *Salmincola* spp. to larger host size (Amundsen et al. 1997; Nagasawa and Urawa 2002; Barndt and Stone 2003). Poulin et al. (1991) demonstrated in a laboratory study that a closely related copepod species, *Salmincola edwardsii*, was more likely to infect larger Brook Trout *Salvelinus fontinalis* due to the greater host surface area and longer period of exposure. Kabata and Cousens (1977) reported that the brachial cavity was the preferred attachment location on larger juvenile fish. Our results agree with these studies. We consistently observed greater levels of infection with larger, older fish for each species and rearing location. However, we also found evidence of greater infection in reservoirs than streams regardless of fish size, suggesting reservoirs impart a greater exposure risk to fish than streams. This was evident from our results, which demonstrated that age-0 Chinook Salmon in any given size-group were more likely to be infected if in reservoirs and it was more likely for the infection to occur within the brachial cavity of the host fish.

There were clear differences in the infection rate among fish species in the reservoirs. Juvenile Chinook Salmon demonstrated the greatest infection vulnerability, kokanee were rarely infected, and Rainbow Trout showed intermediate infection rates. The infection prevalence we observed in kokanee was much less than that reported by Hargis et al. (2014) for age-0 (12%) and age-1 (60%) kokanee in a Colorado reservoir. The prevalence we observed in Rainbow Trout was similar to

TABLE 4. Prevalence and intensity of *Salmincola californiensis* infection for Cutthroat Trout by size range in reservoirs and streams, 2012–2013. Prevalence is the proportion of fish infected.

| | Reservoir | | | Stream | | |
|---|---|---|---|---|---|---|
| Size range (mm) | *n* | Prevalence | Median intensity (maximum) | *n* | Prevalence | Median intensity (maximum) |
| <100 | 18 | 0.056 | 1 (1) | 4 | 0.000 | |
| 100–299 | 84 | 0.333 | 3 (13) | 31 | 0.097 | 1 (1) |
| ≥300 | 8 | 0.875 | 1 (11) | 3 | 0.667 | 1 (2) |



the 25–36% reported by Barndt and Stone (2003) for juvenile steelhead (anadromous Rainbow Trout) in a small Columbia River tributary stream. This is the first study to report copepod infection levels for Chinook Salmon rearing in reservoirs. Anecdotal information suggests that infection levels may be high in other reservoirs in the Pacific Northwest.

There are several possible factors that influence the infection vulnerability of a species, such as the following: habitat overlap between parasite and host, feeding behavior (i.e., the host targets copepodids as a food source), schooling behavior of a particular host (lateral transmission), morphological differences among host species, or a combination of these. Chinook Salmon move from shallow nearshore habitat in the spring to deeper pelagic habitat by early summer (Monzyk et al. 2013). Although all three species occupied the pelagic zone of reservoirs by early summer, only Chinook Salmon showed increasing infection levels, suggesting that infection continued to occur in this zone.

Differential feeding behaviors among species may explain the differences we observed in the summer. Rondorf et al. (1990) observed that subyearling Chinook Salmon occasionally consumed small prey items (daphnia *Daphnia* spp.) that were approximately 0.7 mm in length, similar to the mean copepodid length (0.69 mm). If juvenile Chinook Salmon actively feed on copepodids, this could explain the increasing infection rate through time. In contrast, Budy et al. (2005) demonstrated that Rainbow Trout in reservoirs select prey items ≥ 1 mm in length, suggesting they may not target copepodids as a food source. Kokanee differ morphologically, with more narrowly spaced gill rakers than Chinook Salmon and Rainbow Trout (Townsend 1944; Foote et al. 1999), which may prevent ingested copepodids from attaching within the brachial cavity.

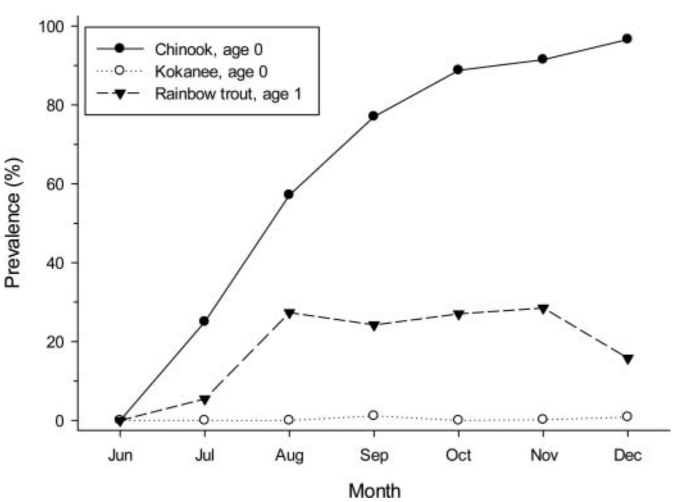


FIGURE 8. Prevalence of *Salmincola californiensis* infection for age-0 Chinook Salmon, age-0 kokanee, and age-1 Rainbow Trout in Detroit Reservoir, 2012–2013.

Chinook Salmon may be exposed to copepodids in the pelagic zone of reservoirs based on their vertical position and behavior. Habitat segregation based on depth was evident in the summer among the three salmonid species in Detroit Reservoir. Rainbow Trout occupied the surface habitat (0–9 m), Chinook Salmon were generally 14–23 m deep, and Kokanee were the deepest (Monzyk et al. 2013). Also, Chinook Salmon were observed in small schools (usually < 100 fish) while rearing in reservoirs and are known to congregate in the forebay of reservoirs (Beeman et al. 2013). Kabata and Cousens (1973) reported that newly hatched copepodids are nearly motionless for approximately 30 min before actively swimming, and Poulin et al. (1990) reported that inactive copepodids sink at a rate of 0.12 cm/s. This means that a copepodid descends about 2.2 m in the water column after hatching before actively searching for a host. Given the wide depth range Chinook Salmon occupied in the reservoirs and their schooling behavior, there could be considerable overlap between parasite and host, with potential for lateral transmission of copepod infection.

The propensity of reservoir fish to be infected in the brachial cavity regardless of size may be related to the lack of current in reservoirs. McGladdery and Johnston (1988) suggested that copepodids may be retained in the brachial cavity if water flow rates in hatcheries are insufficient to flush copepodids out of the cavity, thereby allowing copepodids to reinfect the same host. The relationship between higher transmission rates and low-flow environments has also been noted in wild salmonids (Friend 1941). During the copepodid stage, the copepod crawls along the host's body in search of a suitable attachment location (Kabata and Cousens 1973). The lack of water currents around the host's body in reservoirs may provide optimum conditions for copepods to seek out preferred attachment locations within the brachial cavity.

In both years of this study, we observed the highest levels of infection prevalence and intensity for Chinook Salmon in Fall Creek Reservoir and the lowest levels in Lookout Point Reservoir. The lengths of Chinook Salmon in the two reservoirs were similar and would not explain the infection differences observed. Prior to sampling, Fall Creek Reservoir was drawn down to run-of-river conditions in late winter to provide downstream passage for juvenile Chinook Salmon. It appears that copepods are able to “reseed” the reservoir after winter drawdowns flush out most of the reservoir water. Infected fish may remain in the stream or isolated pools above the dam and infect the subyearling Chinook Salmon cohort that enters the reservoir the following spring. Another possibility is that infected adult steelhead and Chinook Salmon that are transported above the dam in the spring and summer are the main vector for reseeding the reservoir with copepodids while holding in the stream above the reservoir. Adult Chinook Salmon and steelhead can be infected with several hundred copepods per fish (Fasten 1921) and therefore could be an important source of copepodids in the reservoirs. Adult Chinook Salmon and steelhead are released at the head of Fall Creek Reservoir or in the stream a few kilometers upstream and copepodids could easily drift into the reservoir. However, adult Chinook Salmon in the Middle Fork Willamette River are released $>$ 30 km upstream of Lookout Point Reservoir. If copepodids from these adults are unable to drift to the reservoir within their 2-d life span, this could explain the lower infection levels observed in this reservoir.

In 2012 and 2013, 18% of the infected age-0 Chinook Salmon from Fall Creek Reservoir had an intensity of $\geq$ 20 copepods/fish within the brachial cavity. About 6% of fall-migrating yearlings in Cougar Reservoir had a similar high-intensity infection. Pawaputanon (1980) demonstrated that juvenile Sockeye Salmon with a mean intensity of 23 copepods/fish experienced 90% mortality during salinity tolerance tests compared with 10% mortality for noninfected control fish (an 80% mortality rate). No studies to date have been conducted on smolt mortality rates during saltwater transition for other species or at lower infection levels. The effects of infection at different levels of intensity on juvenile Chinook Salmon survival during saltwater transition are not currently known but merit further investigation. If high infection intensity is shown to cause mortality to Chinook Salmon smolts, then measures can be taken to reduce infection. One possible management action would be the treatment of infected adults before transporting them above dams to reduce the potential for juvenile infection, if adults are proven to be a major vector. Transporting adult salmonids around dams in the Pacific Northwest is now a common practice, with juvenile progeny occupying reservoir habitat at some point in their life. Reservoirs represent novel habitats for these normally riverine species and offer greater growth opportunities but also a greater likelihood of parasitic copepod infection. High levels of infection by parasitic copepods in juvenile salmonids may be a common phenomenon in many reservoirs of the Pacific Northwest. As efforts continue to reintroduce salmonids above barriers in the Willamette River basin and throughout the Pacific Northwest, juvenile salmonids will likely continue to spend a portion of their lives rearing in lentic environments. While we have described here the contemporary levels of infection intensity and frequency and the differences among species and rearing habitats, a more complete understanding of the specific effects of parasitic copepods is needed, especially with respect to salmonid survival and fitness.

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