

RESEARCH ARTICLE

And the Dams Came Down: Deconstructing dams and myxozoan disease following Klamath River Dam Removals

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Four large dams were removed from the Klamath River in Oregon and California, USA in 2023-24. This was the largest dam removal and restoration project in U.S. history, with a primary aim to restore critical habitat for threatened and endangered salmon populations that the dams had constrained to the lower half of the river basin for over a century. The dam removals resulted in profound physical changes to the river that are expected to alter host-pathogen dynamics in significant ways. Reconnecting the lower and upper portions of the river basin has increased habitat available to salmon, and adult salmon have already begun to return to streams upstream from the former dams where they were historically present. These fish now have longer migration routes, altering the distribution and abundance of both hosts and pathogens. To develop a management plan for the reconnected river, our workgroup drew from a combination of Western Science and Traditional Ecological Knowledge to inform disease risk predictions. While our initial synthesis included multiple pathogens for which there was evidence of disease related impacts, in this forum we focus on *Ceratonova shasta*, which is considered the primary pathogen limiting salmon recovery in this river system. For juvenile salmon, we predict a reduction in disease risk resulting from the decrease in overlap between infected salmonid and annelid hosts, attributable to the restoration habitats that favor salmonids but are less suitable for annelids. For both juvenile and adult salmon that utilize the newly accessible upper river habitats, we predict increased risk of infection and disease resulting from extended migration routes. For adults, the increased risk is expected to be associated with prespawn mortality, previously not observed in salmon in this river system. Long term, we expect the combination of increased diversity in salmonid life histories in combination with the availability of more and diverse habitat will temper disease risk and restore some balance to this host-parasite cycle.

Background

The removal of four dams on the Klamath River in 2023-24 reconnected a river divided since 1917, and opened over 600 river kilometers of habitat for salmon. This reconnection is expected to permit reestablishment of ecologically and culturally important populations of Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*O. kisutch*) and Steelhead (anadromous *O. mykiss*) into the upper river and its tributaries, and create the

opportunity for re-expression of diverse salmon life-history types. Previous dam removals in other systems have changed river sediment transport and geomorphology, flow and temperature regimes and water quality that are expected to benefit ecosystem function, and restore resiliency to salmon populations (reviewed in Bellmore et al. 2019). However, these physical environmental changes will also alter fish-pathogen interactions and disease risk. To provide river managers with insights on how disease risks will be affected by dam removal, we formed a broad working group with different expertises and knowledge of the Klamath River to analyze existing data and disease models, and to develop conceptual models for future disease risks (Bartholomew et al. 2023).

Immediately following dam removal there have been impacts that we consider to be short-term in their effects, primarily from the removal of physical structures and the release of sediment from the reservoirs. These effects include high turbidity, low dissolved oxygen and marginally higher water temperatures. Removal of the lowermost dam also resulted in closure of a salmon mitigation hatchery, whose operations were moved into an upriver tributary until salmon runs reestablish naturally. Our analysis primarily focused on the long-term changes in connectivity, flow dynamics, thermal regimen, water quality and sediment transport that are expected to occur.

Framework for Predictions

Our initial analysis considered pathogens present historically in the Klamath River that have a documented effect on salmon health. However, the myxozoan *Ceratonova shasta* is considered the dominant pathogen of juvenile salmon populations and a primary factor limiting their recovery (Bartholomew et al. 2022; Fujiwara et al. 2011). Since 2002, a collaborative monitoring program has been in place allowing collection of data for modeling disease risk under changing environmental conditions, and thus, this parasite was selected to structure our predictions for future salmon disease risk. We focus on risk of disease rather than risk of exposure or infection because infection with *C. shasta* does not necessarily result in disease, and the latter has a population-level impact.

- *Ceratonova shasta* specifically infects species of Pacific Northwest salmonids, and can cause severe intestinal necrosis. In rivers where the parasite is endemic the native fishes have developed resistance to severe disease. However, resistance can be overwhelmed and infections result in high mortality when water temperatures are warm (which increase parasite proliferation and salmonid stress) and flows are low (which enhance transmission, increase water temperature, and impede salmonid migration). As a parasite with a two-host life cycle, disease risk is also a function of the extent of overlap with two different host species. Thus, predicting *C.*

shasta disease risk not only requires data on the susceptibility and distribution of its salmonid host, but also knowledge of distribution, population densities and infection prevalence of its annelid host, *Manaynukia occidentalis*.

Another consideration in assessing disease risk due to *C. shasta* is that the parasite is a species complex, with three distinct genotypes with differences in host specificity and virulence. Chinook Salmon and Coho Salmon become infected by genotypes I and II, respectively, and can suffer severe disease when they encounter high parasite densities. Although genotype I has high fidelity for its host, genotype II appears able to infect a broader range of species, including Rainbow Trout that are not endemic to the Klamath. Steelhead (and native Redband Rainbow Trout) become infected with genotype 0 and rarely show overt signs of disease despite exhibiting extensive histopathology and shedding mature parasite stages (Estensoro et al. 2025). For this reason, we focus on genotypes I and II, although all three genotypes are present below the dams. Upstream of the dams genotype I has been absent because migration of Chinook Salmon was blocked, genotype II has persisted, likely as a result of stocking of non-endemic Rainbow Trout, and genotype 0 is present, in native Redband Rainbow Trout.

Predicted physical changes in the Klamath River

C. shasta disease risk prior to dam removal varied among river sections as a result of both physical and biological factors. Predictions for disease risk post-dam removal took this into account and stratified the river into four sections (Figure 1) to allow comparison:

- S1: estuary to river kilometer (RKM) 228 – This lower river section includes several major tributaries. Dam removal is expected to cause lower flows and higher water temperatures at base flow (during summer), with no other major long-term physical changes.
- S2: RKM 228 to Iron Gate Dam – Prior to dam removals the flows in this section were controlled by releases from Iron Gate Dam, resulting in low-velocity, stable habitats. Following dam removal there will be a significant increase in turbidity immediately in the short-term. In the long-term, without dams the flow regime will become more dynamic, with episodic high flows. Water temperatures will increase earlier in the spring and cool earlier in the fall.
- S3: Iron Gate Dam to Keno Dam - Formerly the hydroelectric reach, this section included the four dams that were removed. Changes in this section have been dramatic as reservoirs were

converted to free-flowing riverine habitat, natural temperature regimes were restored, and habitats were reconnected.

- S4: Keno Dam to headwaters – Two smaller dams will remain in place; both are low head dams with fish passage facilities. This section includes Upper Klamath Lake and several major tributaries. No physical changes will occur here as a result of dam removal but changes will occur in fish diversity and distribution as salmon populations re-establish.

Predicted changes in *Ceratonova shasta* disease risk for salmonids

Disease risk factors include presence of stable habitats that support annelid hosts, overlap of fish and annelid hosts in time and space, and water temperatures that favor parasite proliferation and surpass thresholds for development of disease in fish.

Predicted changes in disease risk for each of the river sections:

- S1: Prior to dam removal, both exposure and disease risk were relatively low in this river section during most years as a result of restricted annelid populations, low parasite densities and the short migration route to the ocean for juvenile fish. Post dam removal we expect annelid distribution will remain restricted, and may decline as a result of lower summer/fall baseflows that restrict available habitat. Exposure, and in turn, disease risk for both juvenile and adult salmon will continue to be low relative to other river sections, and over time should decrease as myxospore inputs from fish infected upriver decrease.
- S2: Prior to dam removals this river section was characterized by the highest disease risk for *C. shasta* infection as a result of high myxospore input from adult salmon congregating in the vicinity of the lowermost dam barrier and returning to Iron Gate Hatchery and dense annelid host populations located downstream. Immediately following dam removal, sediment deposition has reduced annelid densities. Although populations that persist are expected to re-colonize rapidly, over the long-term we expect annelid habitat will decrease as a result of the more dynamic flow and sediment regimes, and that the increased bed mobility will restrict population expansion and persistence seasonally (Alexander et al., in press). Thus, while annelids will persist, their populations will become patchier and densities will be lower overall, in turn reducing disease risk for migrating juvenile fish. We also

expect the overlap between periods of parasite release and juvenile fish migration during spring will be reduced. This previous overlap was, in part, a result of hatchery release timing, which will no longer be controlled but volitional (salmon-driven). Although earlier warming of water temperatures in spring will result in both earlier fry emergence and parasite release (Chiaramonte 2013), naturally produced juvenile fish are likely to migrate before the peak of parasite release. Changes in both hatchery and natural production will also result in more fish migrating during fall, when disease risk is low.

- S3: Prior to dam removal there were no migratory salmon in this section of river, and re-establishment has been rapid following removal, exceeding expectations. In the first fall (first returns) after removal was complete, fish spawned in tributaries in this reach, and in the second fall migrated above the remaining dams. Disease risk is difficult to predict as there are changes that both benefit and deter re-establishing salmonids and annelid populations. Former reservoirs comprised ~60% of this section and were inhospitable habitats for annelid hosts except at their inflows, which supported high annelid densities (Stocking and Bartholomew 2007). Their restoration to riverine habitats has eliminated the productive inflow habitats but may create additional suitable annelid habitat. Similarly, cessation of hydropeaking operations eliminated the highly dynamic flow and temperature fluctuations that occurred in ~25% of this section, returning it to a more stable riverine habitat that could support both salmonid and annelid hosts. Thus while we predict changes in invertebrate host distribution, there may be no net change in annelid abundance. This section also has significant groundwater spring inputs that will create cold-water refugia and result in variable water temperatures in this section that will benefit migrating salmon.

Prior to dam removal only genotypes 0 and II were present in this river section; with the reestablishment of Chinook Salmon we predict genotype I will also become established. However, we anticipate that a high proportion of adult salmon will spawn in tributaries, and thus many of the myxospores released upon their death will not reach the mainstem populations of the annelid host.

S4: Similar to S3, migratory salmon had been extirpated from this river section prior to dam removal, but as of fall 2025 adult Chinook Salmon have been observed migrating above the two remaining dams and through Upper Klamath Lake into the headwater tributaries, demonstrating rapid reestablishment. As physical changes have not occurred in this section of the river, changes in disease risk will be a result of these new arrivals. Genotype I will likely establish in areas where genotype II is already present. If juvenile salmon become infected in this reach they will continue to be exposed throughout their migration, and infection outcome will be more dependent on environmental conditions than for fish originating from downstream sections. Similarly, although *C. shasta*-associated prespawn mortality has not been documented in Klamath River populations, the longer migration of adult salmon presents a disease risk.

Synopsis of Disease Risk Predictions

Timing of fish migrations after dam removals is generally expected to decrease overlap between out-migrating, infected juvenile salmon and peak annelid population densities, resulting in lower annelid infection prevalence and reduced infection risk for juvenile salmon. Removal of these migration barriers will also provide access to adult spawning and juvenile rearing habitat in tributaries where the parasite cannot establish. Restoration of flow and sediment regimes in the mainstem Klamath River are expected to decrease disease risk by disrupting complex parasite life cycles, and increases in the frequency of unimpeded flows and riverbed mobilizing events should result in patchier distribution and lower densities of the annelid host. Myxospore deposition will also be patchier as salmon disperse throughout the upper basin and previously inaccessible tributaries, resulting in reduced rates of annelid encounter. Actinospore release is expected to shift earlier in response to increased water temperatures in spring and cooler water temperatures predicted for fall. A greater diversity of salmon life histories will eventually have the opportunity to be expressed, a subset of which will likely have reduced overlap with the parasite by migrating earlier or overwintering in tributaries and migrating in the fall. At the same time, *C. shasta* genotypes will become redistributed as their hosts reestablish. For upriver populations of juvenile and adult salmon, extended migration times may increase exposure and associated disease risks. Alterations to the river temperature regime are also expected to change migration patterns of juvenile salmon, decreasing their temporal overlap with peaks of parasite release from annelids. However, challenges in allocation of water for agriculture and endangered fishes will continue to exist, and changing climate conditions are introducing new stressors.

Fish Disease Management Options

Prior to dam removal, flow manipulation was the primary tool for reducing parasite density (dilution), reducing annelid habitat (disturbance) and encouraging fish migration (migration speed). Without the larger dams in place, options for manipulating river flows to reduce disease risk will be limited and will continue to be challenged by water availability and demands of agriculture in the upper basin. In the future, flow releases will need to be tied to natural precipitation events such as rain or snow melt to achieve volumes previously associated with beneficial responses. A second management strategy was timing of juvenile hatchery salmon release to reduce overlap with peak parasite abundance. The release of millions of fish from Iron Gate Hatchery normally occurred following migration of naturally produced fish, in late spring. However, with the relocation of hatchery operations upriver (to Fall Creek Hatchery), it may be more productive to allow volitional release of fish both earlier in the spring, and in the fall, thus encouraging a diversity of life histories better adapted to endemic pathogens.



Art Images: These two images depict the predictions made for salmon migration in the years immediately following dam removal. In Year 2 following dam removal fish had migrated into the hydroelectric reach, and by Year 3 are expected to fully occupy upper river tributaries of Klamath Lake. Fish in these pieces are cast glass, with white fish representing the extirpated salmon runs. Sculpture size approximately 2.5 x 2.0 m.

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REFERENCES

- Alexander, J. D., T. T. Daley, D. H. Goodman, J. L. Bartholomew, H. L. Robinson, and N. A. Som. In press. "Discharge Magnitude Drives Inter-Annual Variation in Distribution of the Invertebrate Host (*Manayunkia occidentalis*) of a Salmon Parasite (*Ceratonova shasta*)."
Transactions of the American Fisheries Society.
- Bartholomew, J. L., J. D. Alexander, J. Alvarez, et al. 2023. "Deconstructing Dams and Disease: Predictions for Salmon Disease Risk Following Klamath River Dam Removals." *Frontiers in Ecology and Evolution* 11: 1245967. <https://doi.org/10.3389/fevo.2023.1245967>.
- Bartholomew, J. L., J. D. Alexander, S. L. Hallett, G. Alama-Bermejo, and S. D. Atkinson. 2022. "*Ceratonova shasta*: A Cnidarian Parasite of Annelids and Salmonids." *Journal of Parasitology* 149: 1862–75.
- Bellmore, J. B., G. R. Pess, J. J. Duda, J. E. O'Connor, A. E. East, and Folley, et al. 2019. "Conceptualizing Ecological Responses to Dam Removal: If You Remove, What's to Come?" *BioScience* 69: 26–39. <https://doi.org/10.1093/biosci/biy152>.
- Chiaramonte, L. V. 2013. "Climate Warming Effects on the Life Cycle of the Parasite *Ceratomyxa shasta* in Salmon of the Pacific Northwest." Master's Thesis, Department of Fisheries and Wildlife, Corvallis, Oregon.
- Estensoro, I., B. López-Gurillo, C. Tafalla, et al. 2025. "Better the Devil You Know: Sympatric Fish Host Copes Better than Allopatric with a Myxozoan Parasite." *Frontiers in Cellular and Infection Microbiology* 15. <https://doi.org/10.3389/fcimb.2025.1576014>.
- Fujiwara, M., M. S. Mohr, A. Greenberg, J. S. Foott, and J. L. Bartholomew. 2011. "Effects of Ceratomyxosis on Population Dynamics of Klamath Fall-Run Chinook Salmon." *Transactions of the American Fisheries Society* 140: 1380–91. <https://doi.org/10.1080/00028487.2011.621811>.
- Stocking, R. W., and J. L. Bartholomew. 2007. "Distribution and Habitat Characteristics of *Manayunkia speciosa* and Infection Prevalence with the Parasite *Ceratomyxa shasta* in the Klamath River, Oregon-California." *Journal of Parasitology* 93: 78–89. <https://doi.org/10.1645/GE-939R.1>.