



# United States Department of the Interior



## FISH AND WILDLIFE SERVICE

1655 Heindon Road  
Arcata, California, 95521  
Phone: (707) 822-7201 FAX: (707) 822-8411

In Reply Refer To:  
AFWO

### Technical Memorandum

**TO:** Dave Hillemeier, Yurok Tribal Fisheries, and

Craig Tucker, Karuk Department of Natural Resources

**FROM:** Nicholas A. Som and Nicholas J. Hetrick, Arcata Fish and Wildlife Office, and

Julie Alexander, Oregon State University

**SUBJECT:** Response to Request for Technical Assistance – Polychaete Distribution and Infections

**DATE:** September 20, 2016

**Purpose.** The Arcata Fish and Wildlife Office (AFWO) Fisheries Program is working with its scientific co-investigators to develop a series of four technical memorandums that summarize recent findings of studies that contribute to our current understanding of *Ceratanova shasta* (syn *Ceratomyxa shasta*) infections in the Klamath River, in response to requests for technical assistance from the Yurok and Karuk tribes. Each of the topics addressed in the four technical memorandums: 1) geomorphic channel conditions and flow, 2) polychaete distribution and infections, 3) actinospore and myxospore concentrations, and 4) prevalence of *C. shasta* infections in juvenile and adult salmonids, are identified in a conceptual model diagram (Figure 1) taken from Foott et al. (2011), and as discussed with the requesting tribes. The intent of the technical memorandums is to provide managers with a contemporary understanding of the state of the science with regard to the *C. shasta* in the Klamath River, and to provide a scientific basis to inform and support resource management decisions. In this technical memorandum, we summarize the state of the science regarding the infection and mortality experience of salmonids exposed to *C. shasta* in the Klamath River.

**Background.** High infection rates by the myxozoan parasite *C. shasta* have been documented in emigrating juvenile salmon populations during spring and early summer in the Klamath River (Foott et al. 1999; Nichols and Foott 2006; True et al. 2016; among others), which have been linked to population declines in fall Chinook Salmon (Fujiwara et al. 2011, True et al. 2013). While native salmonids exposed to low doses of the parasite exhibit some degree of resistance (Ching and Munday 1984; Bartholomew et al. 2001), they can become overwhelmed by high infectious doses that result in a diseased state and cause mortality (Ratliff 1981; Ching and Munday 1984; Bartholomew 1998; Stone et al. 2008). Fish that display clinical signs of *C. shasta* infection are also likely to be more prone to mortality because of increased susceptibility to other pathogens such as *Parvicapsula minibicornis* (Figure 2), to predation, and as a result of a compromised osmoregulatory system that is essential for successful ocean entry (S. Foott personal communication).

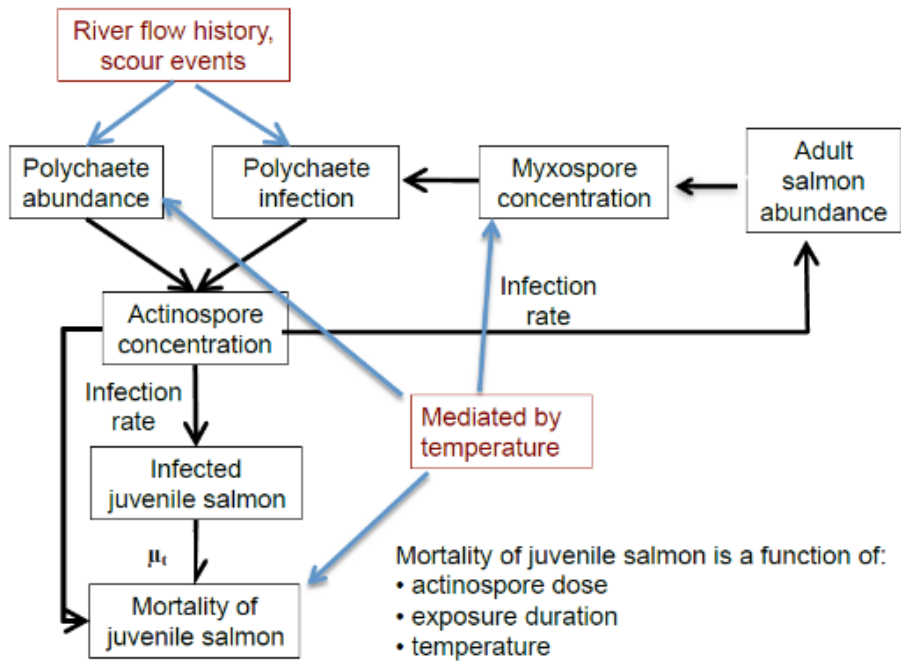


Figure 1. Conceptual model for variables that influence infection and mortality of juvenile Chinook Salmon, with  $\mu_t$  being the mortality rate of infected juvenile salmon, estimated from weekly actinospore concentrations in water samples. (taken from Foot et al. 2011).

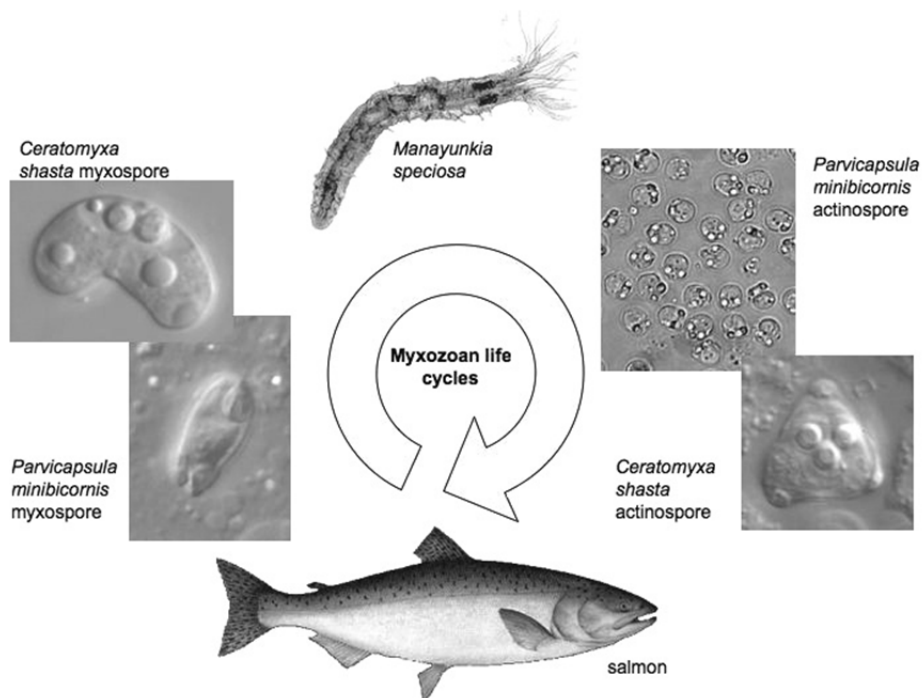


Figure 2. The life cycle of *Ceratomyxa shasta* and *Parvicapsula minibicornis* (graphic provided with permission from J. Bartholomew, Oregon State University). *Manayunkia speciosa* is a small freshwater polychaete worm (3-5 mm in length) and intermediate host of both parasites.

The parasite *C. shasta* is endemic to the Klamath Basin and is assumed to have co-evolved with the different species of salmonids it infects. Coevolution results in parasites that are in dynamic equilibrium with their hosts and low virulence, assuming continued environmental variation under which this equilibrium evolved (Toft and Aeschlimann 1991; Esch and Fernandez 1993). When environmental conditions are significantly altered, however, the change will most often favor the parasite because of its shorter generation time and greater genetic variation as compared to the host (Webster et al. 2007). In general, the parasite adapts more quickly to environmental change than the host, causing the parasite-host equilibrium to shift out of balance (Thompson 1994). This imbalance can be expressed as an elevated prevalence of host infections over naturally-occurring background or equilibrium levels, which is consistent with the abnormally high infection levels observed in juvenile salmon in the Klamath River during some years.

The life cycle of *C. shasta* is complicated and involves salmonids and a freshwater polychaete *Manayunkia speciosa* as alternate hosts, and two microscopic waterborne spore stages (Bartholomew et al. 1997, Meaders and Hendrickson 2009, Figure 2). Actinospores develop within infected polychaete worms that are later released into the water column where they may encounter and infect adult and juvenile salmonids. Clinical signs of the disease state exhibited by infected salmonids include necrosis of intestinal tissue that can be accompanied by a severe inflammatory reaction (enteronecrosis) and subsequent death (Bartholomew et al. 1989). The polychaete invertebrate host is necessary for completion of the life cycle and neither horizontal (fish to fish), or vertical (fish to egg) transmissions have been documented under laboratory conditions. Myxospores develop within infected salmonids and are released into the environment. After release, myxospores may be consumed by and infect polychaete worms, thus completing the life cycle.

The complexity of the *C. shasta* life cycle may lend itself to a variety of management approaches because actions can be tailored to target the different hosts or parasite spore stages, thus arresting the life cycle. Of particular interest, are aspects of the *C. shasta* life cycle that are susceptible to alteration via management alternatives (Figure 1). Given the nature of the parasite's life cycle, disruption of even a single element of the cycle could have profound impacts on survival of juvenile salmonids in the Klamath River.

***Polychaete Ecology.*** Morphological (e.g., body shape, structures for attachment), physiological and behavioral adaptations enable aquatic invertebrates to feed, grow, reproduce, and maintain productive populations in a constantly moving environment (Vogel, 1996). The polychaete worm *M. speciosa* is specifically adapted to life as a semi-sessile benthic invertebrate. Morphology consists of three body regions including the anterior end composed of the branchial crown, prostomium and peristomium, the thoracic region composed of 8 serially-repeated segments, and the posterior end composed of the pygidium (Thorp and Rogers 2015). *Manayunkia speciosa* inhabit flexible tubes which they construct from mucus, sand, and silt. The tubes are attached to substrate, allowing *M. speciosa* to suspension feed in the flowing water column by extending its branchial crown structure (“tentacles”) out of the tube in order to contact and ingest food particles. A series of hooks on the posterior end of the organism facilitates attachment of the worm to the inside of the tube.

Three types of feeding behavior have been reported for the genera *Manayunkia*: deposit feeding, suspension feeding, and secondary suspension feeding (Lewis 1968). *M. speciosa* has been reported in the literature as being suspension-type feeders (Stocking and Bartholomew 2007). Additionally, Stocking and Bartholomew (2007) observed populations of *M. speciosa* “freely roaming the sediment” at the mouth of the Williamson River in the Upper Klamath River Basin. This diversity in habitat use and flexibility in feeding behaviors contribute to *M. speciosa* being

able survive under various environmental and nutrient availability conditions (Hendrickson et al. 2008), found in still-water depositional habitats, slow flowing habitats such as lake reservoir inflows and outflows, and lotic habitats including pools, eddies, riffles, and runs).

Knowledge of the reproduction and development of *M. speciosa* is fairly limited. The sexes are separate (dioecious) and non-feeding larvae are brooded in the maternal tube with the adult worm (Leidy 1883). Males have a dorsal sperm duct and females have a sperm storage structure located in the radiolar crown (Holmquist 1973, Rouse 1995). Eggs develop in females asynchronously in the coelem (Eckelbarger 2005) and reproduction typically peaks in spring to early summer as temperatures increase (Hendrickson et al. 2008, Willson et al. 2010, Alexander et al., personal communication). *Ceratonova shasta* infections are not commonly observed in sexually mature individuals (male or female) and infection is not thought to be transmitted either vertically or horizontally among polychaetes. Progeny are reared in the maternal tube until they reach approximately 1 mm (Willson et al. 2010, Schloesser et al. 2016), which suggests they are not feeding independently (and thus not susceptible to infection by *C. shasta*) until they abandon the maternal tube (Alexander et al., personal communication).

***Distribution and Habitat.*** Though previous work suggested that the distribution of *M. speciosa* is influenced by substrate (Stocking and Bartholomew 2007, Malakauskas and Wilzbach 2012) and a limited range of flow conditions (Jordan 2012), several recent studies have attempted to isolate how hydraulics and substrate may interact to influence the distribution of *M. speciosa*. Malakauskas et al. (2013) performed a series of laboratory flume experiments in which the stability and texture of substrates were varied across flume water velocities. They observed that dislodgement of *M. speciosa* increased with increasing water velocities and decreasing substrate stability, and concluded that higher flows could directly influence the distribution of polychaetes by restricting habitat use to stable substrates. They also concluded that altered flows targeting mobile substrates could effectively dislodge *M. speciosa* from readily entrained substrates, but noted that the polychaetes exhibited attachment abilities similar to taxa found in higher-gradient, rapidly-flowing environments, and that *M. speciosa* could potentially move to lower velocity sections of stable substrates (e.g., behind rock outcroppings) during high flow events. The ability of some polychaetes to persist after high flow events (Alexander et al. 2014) complicates our ability to predict the effectiveness of pulse flow events that may be targeted to scour polychaetes.

Alexander et al. (2016) implemented a designed study to assess how hydraulic conditions interact with substrate and relate to the distribution of *M. speciosa* in the Klamath River. This work coupled field sampling (measurements taken during summer base-flow periods when sampling was feasible) with the development of 2-dimensional hydrodynamic models (2DHMs, Wright et al. 2014) that allowed predictions of depth and velocity at discrete riverine locations over a range of discharges. Results of this study showed that the distribution of polychaetes is correlated with hydraulic variables occurring during the water year's winter or spring peak discharge event. Applications of the 2DHM to peak flows occurring each in 2012, 2013, 2014, and 2016 all show a consistent pattern: increasing peak discharge is associated with decreases in predicted weighted-useable area (WUA) as shown in Table 1. We note, however, that 2DHM predictions at the peak discharges of 2016 should be taken cautiously as the 2DHMs were calibrated and validated to discharges near 8,500 cfs (Wright et al. 2014). Predictions made under discharges above 12,000 cfs represent a considerable extrapolation beyond the calibration bounds of the model.

Table 1. Weighted-usable-area (WUA) for *M. speciosa* habitat at 3 sites in the Klamath River as predicted by coupling the peak discharge (Q) model of Alexander et al. (2016) with depth and velocity predictions from the 2DHM of Wright et al (2014). “T” represents the Tree of Heaven site (river kilometer (rkm) 281; 350 m in length), “B” represents the site just upstream of Beaver Creek (rkm 264; 550 m in length), and “C” represents the site near the Community Center grange (rkm 259; 850 m in length). Discharge values are in cubic feet per second, and WUA values are units of probability-weighted square-meters.

Site	Year	Peak Q (cfs)	WUA
T	2014	2154	2867
	2013	2755	2797
	2012	4520	2543
	2016	12,148	1979
B	2014	2225	6717
	2013	2825	6551
	2012	4697	5975
	2016	12,395	4552
C	2014	2331	6277
	2013	2931	6009
	2012	5015	5491
	2016	12,960	3633

The sampling design utilized by Alexander et al. (2016) also lent to the investigation of polychaete distribution dynamics by re-sampling specific geo-referenced locations in subsequent years. The main data for fitting the predictive statistical model was collected in 2012. In 2013, a largely independent (i.e., compared to the 2012 locations) data set was collected to evaluate the predictive performance of the statistical model, and so very few locations were resampled. However, many of the 2013 sample locations were resampled in 2014 and again in 2016. Of specific the locations sampled in 2013, 208 were again sampled in 2014. Of the locations sampled in 2014, 286 were again sampled in 2016. These repeated sampling locations allow us to look at changes in the density of polychaetes over time, and potentially relate changes to hydraulic conditions. Although the repeat sampling data are currently under analysis and write-up, we provide a summary of their results here. Between the 2013 and 2014 sampling period the peak discharge out of Iron Gate Dam (IGD) was 1,890 cfs, and annual peaks in 2015 and 2016 were 3,580 cfs and 11,200 cfs, respectively.

At each sampling location, a relative measure of polychaete density was assessed and recorded, with ordinal values of 0 (no polychaetes), 25, 50, 75, and 100 representing percent polychaete cover. To evaluate potential changes over each time period, we took the difference between the percent cover values recorded at the beginning and end of the period such that a larger percent cover at the end of the time period would indicate an increase. We note that our sampling was initially designed to capture the full range of hydraulic conditions at the Klamath River sites where data was collected. As such, there were a large number of samples taken and replicated at locations learned to be well outside the bounds of suitability for *M. speciosa*. Therefore, many sampling locations that were initially observed as having zero percent cover remained void of

polychaete cover across the sample periods, resulting in no change in percent cover (Table 2). Between the 2013 and 2014 samples, with an IGD peak discharge of only 1,890 cfs, locations more frequently increased than decreased in percent cover across all substrate types. The opposite was observed for samples collected in 2014 and again in 2016, where decreases were more commonly observed than increases across all substrate types (Table 2), as shown visually in Figure 3. A likely mechanism for the higher frequency of observed decreases in percent cover across sampled locations is scour and bed mobility resulting from the peak discharge event of 11,200 cfs that occurred in March 2016. Notably, increases detected from 2014 to 2016 were largely limited to shallow, marginal sand habitat (sandy deposits near river banks). One explanation for this result is that polychaetes disturbed during the high discharge event of March 2016 had settled in these areas by July when sampling occurred. Polychaetes were no longer observed in these locations during subsequent sampling (August 2016, J Alexander OSU pers. comm.).

**Infection Prevalence.** The infection prevalence of polychaetes in the Klamath River is less understood than polychaete distribution. However, several studies and ongoing monitoring efforts (conducted by Oregon State University, Yurok Tribal Fisheries) have measured incidence of infection among sampled polychaetes. Spatial and temporal (within and among years) variation in prevalence of infection among polychaete host assemblages creates a very context dependent picture that requires further study. Variation may be explained in part by spawning adult salmon abundance, known to bring *C. shasta* to the sections of river directly downstream of Iron Gate Dam, and other unknown factors contributing to myxospore production, survival and availability for infecting polychaetes.

Table 2. Change in percent cover over two different time periods summarized across sampling sites and within each substrate type. “B/B” represents bedrock and boulder substrates, and “S/S” represents sand and silt substrates. Numbers represent, for each substrate, the proportion of locations that decreased, did not change, or increased in percent cover of polychaetes between the beginning and end of the specified time period. Peak flow between sampling periods is parenthetically noted.

Time Period (peak discharge cfs)	Change	Substrate			
		B/B	Cobble	Gravel	S/S
2013-2014 (1,890 cfs)	Decrease	15%	6%	0%	0%
	No Change	36%	75%	78%	78%
	Increase	49%	19%	22%	22%
2014-2016 (11,200 cfs)	Decrease	59%	20%	29%	25%
	No Change	38%	78%	71%	59%
	Increase	3%	2%	0%	16%

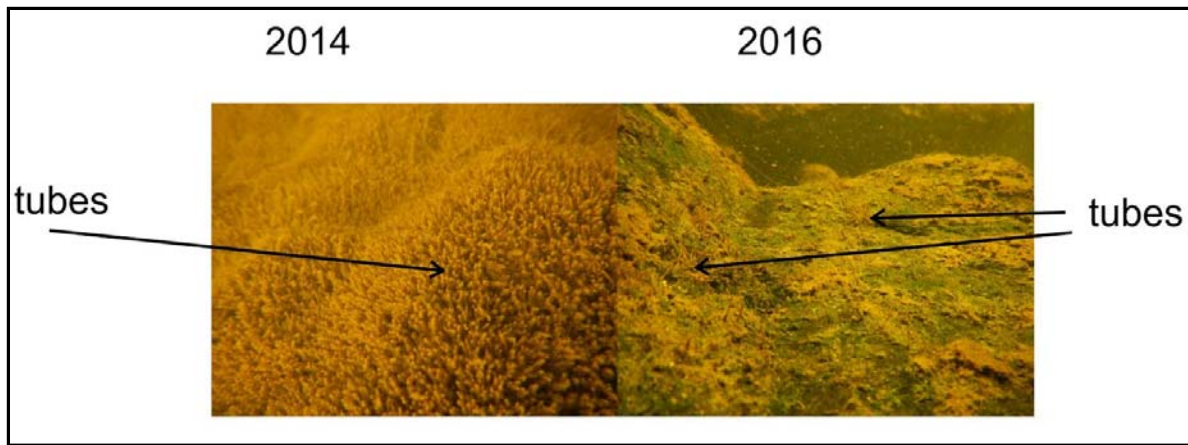


Figure 3. Split screen picture of an identical rock in the mainstem Klamath River taken in 2014 (left) and in 2016 (right) following the March 2016 peak release of 11,200 cfs from Iron Gate Dam.

Generally, myxozoan infection prevalence tends to be very low (0.1-2.0%) in naturally exposed invertebrate host populations (Zendt and Bergersen 2000, Ozer et al. 2002). Prevalence of *C. shasta* infection is also typically low in Klamath River polychaetes, but zones or patches of high infection prevalence have been described. For example, Stocking and Bartholomew (2007) reported 8.24% in one population sampled near the I-5 rest area, downstream from Iron Gate Dam. If factors resulting in these potential focal centers of infection could be identified, then management actions could potentially be targeted.

The sampling associated with Alexander et al. (2016) may provide some insight into the distribution of polychaetes prone to infection. To validate the relative abundance measure recorded at all sampling locations, a subset of locations were selected as validation samples, whereby all benthic material was collected and a more precise enumeration of polychaetes was conducted, as well as an assessment to diagnose the prevalence of *C. shasta* infections among the subsampled polychaetes. Though these data are still under preparation and formal analysis, graphical evidence suggests that infected polychaetes exhibit a smaller range of peak-flow discharge depths and velocities than the general population of polychaetes distributed throughout the infectious zone of the Klamath River (Figure 4). The preliminary findings of this on-going study also suggest that management actions targeted to reduce the impact of *C. shasta* on native salmonids of the Klamath River may not need to target the hydraulic habitat preferences of all polychaetes.

There is evidence from sampled polychaetes that the prevalence of infection is correlated with peak flow regime. Following the 2006 peak flow event (12,400 cfs at IGD), Alexander (2014) reported maximum prevalence of infection in polychaetes of 0.17-0.35% in populations sampled from June-September. Following moderate peak discharges (4,380 cfs in 2004; 5,700 cfs in 2011; measured at IGD), maximum infection prevalence reached 4.96% (Stocking and Bartholomew 2007) and 5.38% (Jordan 2012), respectively. Additionally, preliminary data shows that the highest polychaete prevalence of infection on record (10%, Alexander in prep.) was observed in drought years of 2014 and 2015 (peak IGD discharges of 1,890 and 3,580, respectively).

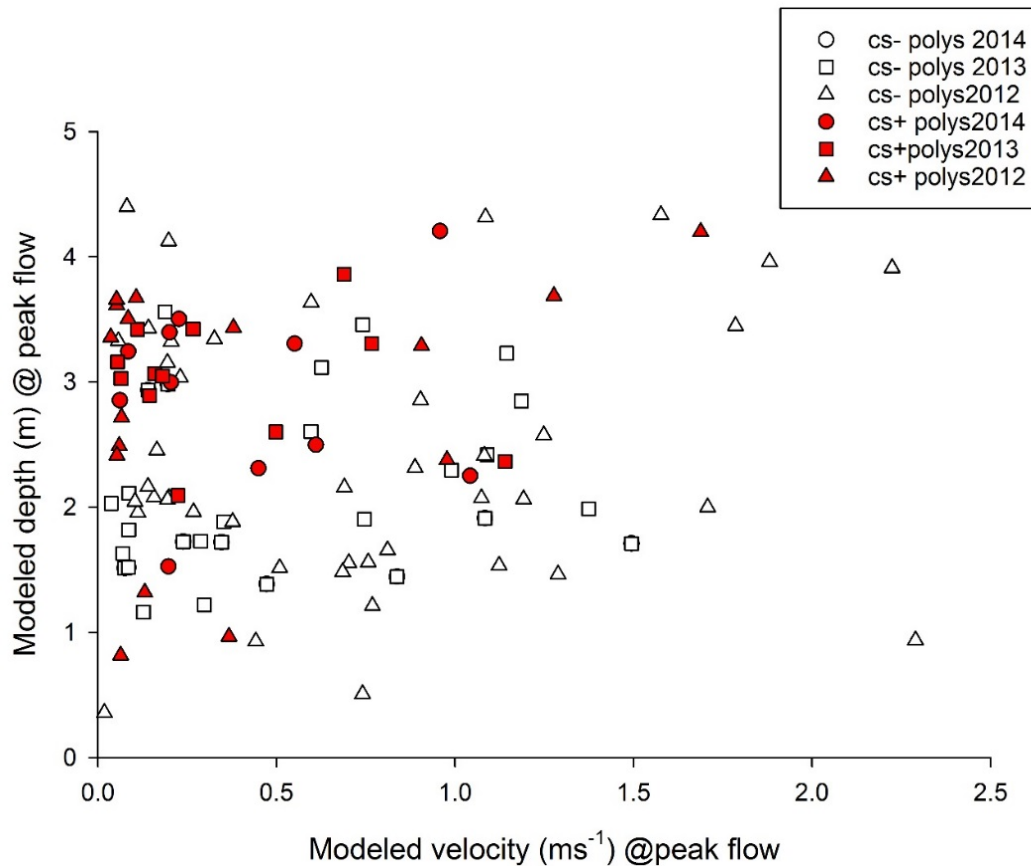


Figure 4. Infected (filled shapes) and uninfected (open shapes) polychaete host assemblages related to the peak-flow water depths and velocities as predicted by the 2-dimensional hydrodynamic model of Wright et al. (2014), and assessed under the sampling design of Alexander et al. (2016). Note that symbols in this figure reference only locations of polychaete presence and do not represent the full suite of depth and velocity combinations considered in the sampling design of Alexander et al. (2016).

**Summary Guidelines.**

- The polychaete *M. speciosa* has been documented as the obligate intermediate host for the parasite *C. shasta*.
- Polychaetes in the Klamath River have been documented to be sessile suspension feeders and may also have flexibility to feed on organic matter in deposited sediments.
- Polychaete reproduction typically peaks in spring to early summer, coinciding with increasing water temperatures.
- Studies indicate that dislodgement of *M. speciosa* increases with increasing water velocities and decreasing substrate stability.
- Results of 2-D hydrodynamic model runs predict decreasing WUA of suitable polychaete habitat with increasing discharge.
- Results of repeat samples at specific locations in the Klamath River indicate a decrease in *M. speciosa* following the March 2016 peak discharge event of 11,200 cfs.



- Evidence suggests that the prevalence of *C. shasta* infection in polychaetes is negatively correlated with the peak flow regime.
- Preliminary results indicate that infected polychaetes are more likely to occur within a smaller range of peak-flow depths and velocities than the general population, with infected polychaetes more associated with deeper and lower-velocity depositional habitats.

**Key Questions.** There are several aspects regarding the role of *M. speciosa* in the life-cycle of *C. shasta* that remain unknown, and that could help inform how the disease cycle is completed in the Klamath River. For instance, exactly when and how the infections occur, and if infection differs by parasite genotype, via suspension or deposit feeding, etc. would help inform the transmission mechanism and could help evaluate the potential efficacy and timing of pulse flow events/managed flow events. Additionally, how infection and genotype may affect the life span and survival of *M. speciosa* remains a key question.

### References

- Alexander, J. D., S. L. Hallett, R. L. Stocking, L. Xue, and J. L. Bartholomew. 2014. Host and parasite populations after a ten year flood: *Manayunkia speciosa* and *Ceratomyxa shasta* in the Klamath River. *Northwest Science* 88:219–233.
- Alexander, J. D., J. L. Bartholomew, K. A. Wright, N. A. Som, and N. J. Hetrick. 2016. Integrating models to predict distribution of the invertebrate host of myxosporean parasites. *Freshwater Science*. Online Early. doi: 10.1086/688342.
- Alexander, J.D., M. S. Jordan, R. A. Ray, and J.L. Bartholomew. In prep. Life history and demographics of the invertebrate host of salmon parasites.
- Bartholomew, J. L., C. E. Smith, J. S. Rohovec, and J. L. Fryer. 1989. Characterization of a host response to the myxosporean parasite, *Ceratomyxa shasta* (Noble), by histology, scanning electron-microscopy and immunological techniques. *Journal of Fish Diseases* 12:509–522.
- Bartholomew, J. L., M. J. Whipple, D. G. Stevens, and J. L. Fryer. 1997. The life cycle of *Ceratomyxa shasta*, a myxosporean parasite of salmonids, requires a freshwater polychaete as an alternate host. *Journal of Parasitology* 83:859–868.
- Bartholomew, J. L. 1998. Host resistance to infection by the myxosporean parasite *Ceratomyxa shasta*: A review. *Journal of Aquatic Animal Health*: 10:112-120.
- Bartholomew, J. L., M. J. Whipple, and D. Campton. 2001. Inheritance of resistance to *Ceratomyxa shasta* in progeny from crosses between high- and low-susceptibility strains of rainbow trout (*Oncorhynchus mykiss*). *Bulletin of the National Research Institute of Aquaculture*. Supplement 5:71-75.
- Ching, H. L., and D. R. Munday. 1984. Geographic and seasonal distribution of the infectious stage of *Ceratomyxa shasta* Noble, 1950, a myxozoan salmonid pathogen in the Frazer River system. *Canadian Journal of Zoology* 62:1423–1424.
- Eckelbarger, K.J. 2005. Oogenesis and oocytes. In: *Morphology, Molecules, Evolution and Phylogeny in Polychaeta and Related Taxa*. Bartolomaes T & Purschue G, eds., pp. 179-198. Springer.

- Esch, G. W., and J. c. Fernandez. 1993. Evolutionary Aspects. pp. 231-267 in: A Functional Biology of Parasitism: Ecological and Evolutionary Implications. Chapman and Hall, London.
- Foott, J. S., J. D. Williamson, and K. C. True. 1999. Health, physiology, and migration characteristics of Iron Gate Hatchery Chinook, 1995 releases. U.S. Fish and Wildlife Service, California-Nevada Fish Health Center, Anderson, CA.
- Foott J.S., R. J.L. Barthomew, R. W. Perry, and C. E. Walker. 2011. Conceptual Model for Disease Effects in the Klamath River. Whitepaper prepared for the Klamath Basin Restoration Agreement Secretarial Overview Report Process. 12 pp.
- 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 140:1380–1391.
- Hendrickson G. L., M. A. Wilzbach, and K. W. Cummins. 2008. Final Report: *Manayunkia speciosa*: Life History, Rearing, and Associated Development of *Ceratomyxa shasta* (2005-FP-10). Prepared for the Arcata Fish and Wildlife Office of the US Fish and Wildlife Service under FWS Agreement No: 13336G008.
- Holmquist, C. H. 1973. Fresh-water polychaete worms of Alaska with notes on the anatomy of *Manayunkia speciosa* Leidy. Zool. Jb. Syst. Bd. 100: 497-516. Leidy, J. 1883. *Manayunkia speciosa*. Proceedings of the National Academy of Sciences of Philadelphia 35:204-212.
- Jordan, M. S. 2012. Hydraulic predictors and seasonal distribution of *Manayunkia speciosa* density in the Klamath River, CA, with implications for ceratomyxosis, a disease of salmon and trout. Oregon State University, Corvallis, Oregon.
- Leidy, J. 1883. *Manayunkia speciosa*. Proc Acad Nat Sci Phil 35:204–212
- Lewis, DB. 1968. Feeding and tube-building in the Fabriciinae (Annelida, Polychaeta). Proc. Linn. Soc. Lond. 179(1): 37-49.
- Malakauskas, D. M., S. J. Willson, M. A. Wilzbach, and N. A. Som. 2013. Flow and substrate type affect dislodgement of the freshwater polychaete, *Manayunkia speciosa*. Freshwater Science 32:862–873.
- Malakauskas, D. M., and M. A. Wilzbach. 2012. Invertebrate assemblages in the lower Klamath River, with reference to *Manayunkia speciosa*. California Fish and Game 98:214–235.
- Meaders, M. D., and G. L. Hendrickson. 2009. Chronological development of *Ceratomyxa shasta* in the polychaete host, *Manayunkia speciosa*. American Society of Parasitologists 95: 1397–1407.
- Nichols, K, and J. S. Foott. 2006. FY2004 Investigational Report: Health monitoring of juvenile Klamath River Chinook salmon. U.S. Fish and Wildlife Service, California –Nevada Fish Health Center, Anderson, CA.
- Ozer A., R. Wootten, and A. P. Shinn. 2002. Infection prevalence, seasonality and host specificity of actinosporean types (Myxozoa) in an Atlantic salmon fish farm in Northern Scotland. Folia Parasitologica 49:263-268.
- Ratliff, D. E. 1981. *Ceratomyxa shasta*: epizootiology in Chinook salmon of central Oregon. Transactions of the American Fisheries Society 110:507–513.
- Rouse G. 1995. Spermathecae of *Fabricia* and *Manayunkia* (Sabellidae, Polychaeta). Invertebr. Biol. 114: 248-255.

- Schloesser, D. W., D. M. Malakauskas and S. J. Malakauskas. 2016. Freshwater polychaetes (*Manayunkia speciosa*) near the Detroit River, western Lake Erie: Abundance and life-history characteristics, *Journal of Great Lakes Research*. doi: 10.1016/j.jglr.2016.07.006.
- 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* 93:78–88.
- Stone, R., J. S. Foott, and R. Fogerty. 2008. Comparative susceptibility to infection and disease from *Ceratomyxa shasta* and *Parvicapsula minibicornis* in Klamath River basin juvenile Chinook, coho and steelhead populations. U.S. Fish and Wildlife Service, California-Nevada Fish Health Center, Anderson, CA.
- Thompson, J. N. (1994). *The Coevolutionary Process*. University of Chicago Press, Chicago.
- Thorp, James H., and D. Christopher Rogers. "Class Polychaeta." *Thorp and Covich's Freshwater Invertebrates: Keys to Nearctic Fauna* (2015): 509.
- Toft, C. A., and A. Aeschlimann. 1991. Introduction: Coexistence or Conflict? pp. 1-12 in *Parasite-Host Associations: Coexistence or Conflict?* Oxford University Press. Oxford.
- True, K., Bolick, A., and J. S. Foott. 2013. Myxosporean parasite (*Ceratomyxa shasta* and *Parvicapsula minibicornis*) prevalence of infection in Klamath River Basin juvenile Chinook salmon, April–August 2012. California–Nevada Fish Health Center, US Fish and Wildlife Service, Anderson, California. (Available from: <https://www.fws.gov/canvfhc/CANVReports.html>)
- True, K., A. Voss, and J.S. Foott. 2016. Myxosporean parasite Prevalence of infection in Klamath River Basin juvenile Chinook salmon, April–July 2015. California–Nevada Fish Health Center, US Fish and Wildlife Service, Anderson, California. (Available from: <https://www.fws.gov/canvfhc/CANVReports.html>)
- Vogel, S. (1996). *Life in moving fluids: the physical biology of flow*. Princeton, NJ [u.a.]: Princeton Univ. Press.
- Webster, J. P., J. Shrivastava, P. Johnson, and L. Blair. 2007. Is host-schistosome coevolution going anywhere? *BMC Evolutionary Biology*, 7:91.
- Willson, S. J., M. A. Wilzbach, D. M. Malakauskas, K. W. Cummins (2010) Lab Rearing of a Freshwater Polychaete (*Manayunkia speciosa*, Sabellidae) Host for Salmon Pathogens. *Northwest Science* 84: 183-191. doi: <http://dx.doi.org/10.3955/046.084.0207>.
- Wright, K.A., D.H. Goodman, N.A. Som, and T.B. Hardy. 2014. Development of two-dimensional hydraulic models to predict distribution of *Manayunkia speciosa* in the Klamath River. U.S. Fish and Wildlife Service. Arcata Fish and Wildlife Office, Arcata Fisheries Technical Report Number TR 2014-19, Arcata, California.
- Zendt J. S. and E. P. Bergersen. 2000. Distribution and abundance of the aquatic oligochaete host *Tubifex tubifex* for the salmonid whirling disease parasite *Myxobolus cerebralis* in the Upper Colorado River basin. *North American Journal of Fisheries Management* 20:502-512.