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An epidemiological model of virus transmission in salmonid fishes of the Columbia River Basin

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ABSTRACT

We have developed a dynamic epidemiological model informed by records of viral presence and genotypes to evaluate potential transmission routes maintaining a viral pathogen in economically and culturally important anadromous fish populations. In the Columbia River Basin, infectious hematopoietic necrosis virus (IHNV) causes severe disease, predominantly in juvenile steelhead trout (*Oncorhynchus mykiss*) and less frequently in Chinook salmon (*O. tshawytscha*). Mortality events following IHNV infection can be devastating for individual hatchery programs. Despite reports of high local mortality and extensive surveillance efforts, there are questions about how viral transmission is maintained. Modeling this system offers important insights into disease transmission in natural aquatic systems, as well as about the data requirements for generating accurate estimates about transmission routes and infection probabilities. We simulated six scenarios in which testing rates and the relative importance of different transmission routes varied. The simulations demonstrated that the model accurately identified routes of transmission and inferred infection probabilities accurately when there was testing of all cohort-sites. When testing records were incomplete, the model accurately inferred which transmission routes exposed particular cohort-sites but generated biased infection probabilities given exposure. After validating the model and generating guidelines for result interpretation, we applied the model to data from 14 annual cohorts (2000–2013) at 24 focal sites in a sub-region of the Columbia River Basin, the lower Columbia River (LCR), to quantify the relative importance of potential transmission routes in this focal sub-region. We demonstrate that exposure to IHNV via the return migration of adult fish is an important route for maintaining IHNV in the LCR sub-region, and the probability of infection following this exposure was relatively high at 0.16. Although only 1% of cohort-sites experienced self-exposure by infected juvenile fish, this transmission route had the greatest probability of infection (0.22). Increased testing and/or determining whether transmission can occur from cohort-sites without testing records (e.g., determining there was no testing record because there were no fish at the cohort-site) are expected to improve inference about infection probabilities. Increased use of secure water supplies and continued use of biosecurity protocols may reduce IHNV transmission from adult fish and juvenile fish within the site, respectively, to juvenile salmonids at hatcheries. Models and conclusions from this study are potentially relevant to understanding the relative importance of transmission routes for other important aquatic pathogens in salmonids, including the agents of bacterial kidney disease and coldwater disease, and the basic approach may be useful for other pathogens and hosts in other geographic regions.

1. Introduction

Dynamic models (both statistical and mathematical) that categorize host populations by susceptible-exposed-infected-recovered (SEIR) status have been important tools for describing pathogen transmission, although much of the work has focused on human and livestock systems. Even simple SEIR models can capture enough of the critical transmission process to inform disease control measures (e.g., Anderson and May, 1979, 1992; Bjornstad et al., 2002; Smith et al., 2014). However, while all models are limited by the availability and quality of the data to inform and validate parameterization, this is a significant challenge in modeling infectious transmission in non-human systems,

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where even fundamental estimates of host population size are often uncertain (Heisey et al., 2010; LaDeau et al., 2011; Morris et al., 2015). Wildlife populations are difficult to access and monitor, and consequently, infection dynamics are often poorly understood.

Semi-wildlife systems with a combination of free-ranging animals and husbandry programs at various stages of animals' life history, such as those associated with salmon (*Oncorhynchus mykiss*, *Salmo salar*) and carp (*Cyprinus carpio*), have provided some of the most productive application of SEIR models to investigate transmission of infectious pathogens in non-human systems. Previous studies have evaluated drivers of epidemics, likely infection routes, effect of distance to an infectious fish farm on transmission, and epidemic control options through the use of compartment models and population-dependent and -independent transmission models (e.g., Murray, 2006; Aldrin et al., 2010; Taylor et al., 2011).

In this paper, we build on the existing literature to develop and apply a dynamic epidemiological model that categorizes and tracks transitions from susceptible to infected host groups in anadromous fish populations of the Columbia River Basin. The model evaluates the role of potential transmission routes in maintaining a viral pathogen, with specific consideration for how missing data influence identification of critical transmission routes. Infectious hematopoietic necrosis virus (IHNV, species *Salmonid novirhabdovirus*) proliferates in a semi-wildlife system with intensive data collection at critical life stages and in this sense represents an important system for making data-driven inference about transmission in the wild. The model structure and evaluation presented offer important insights into disease transmission in natural aquatic systems, as well as about the data requirements for generating accurate inference about transmission routes and infection probabilities. Once key transmission routes are identified, opportunities for surveillance, intervention, and control can be enhanced (Archie et al., 2009; Aldrin et al., 2011).

The Columbia River Basin is a large, complex watershed that occupies much of the states of Washington, Oregon, and Idaho, as well as smaller portions of other states and two Canadian provinces. A large number of fish culture facilities (hatcheries) in the Columbia River Basin support breeding and juvenile rearing of the predominant wild salmonid species in the watershed, including Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Juvenile hatchery fish are released from freshwater hatcheries to migrate to the ocean, where they spend the majority of their lives before returning to freshwater natal sites (including hatcheries) to breed. Therefore this is a semi-wildlife system where populations of diverse species mix and disperse across a complex landscape (Aldrin et al., 2011, 2015) with intense human management and data collection at the beginning and end of the fishes' life cycle.

Infectious hematopoietic necrosis virus (IHNV, species *Salmonid novirhabdovirus*), an RNA virus of the rhabdovirus family, is endemic to the Pacific Northwest of North America and currently infects a broad range of salmonid species globally (Bootland and Leong, 2011; Dixon et al., 2016). In the Columbia River Basin, IHN disease is predominantly observed in juvenile steelhead, and occasionally in Chinook salmon (Bootland and Leong, 1999; Breyta et al., 2016a). Mortality events following IHNV infection at a hatchery can result in the loss of an entire juvenile cohort and can be devastating for individual hatchery programs (Wolf, 1988, LaPatra, 1998; Bootland and Leong, 1999). Spawning adults returning to hatcheries are routinely tested for a suite of pathogens, including IHNV, but IHNV infection is largely asymptomatic in adult steelhead and Chinook. Thus, IHNV infection in adult fish is detected mostly through routine surveillance testing. In contrast, infection in juvenile fish is most often detected by diagnostic testing of moribund or dead fish, with a smaller component of routine surveillance testing throughout the Columbia River Basin. Surveillance and diagnostic testing is currently conducted by seven distinct groups in the Columbia River Basin, including Federal, State and tribal agencies (Breyta et al., 2016a, 2017a). If a test is negative for IHNV, the chance of a false negative is very low because in regions where the virus is routinely detected, a sampling method with a lower limit of detection between 5–9% is used. In regions where the virus is not routinely detected, sampling with a lower detection limit of 1.5–2% is used. A lower detection limit of 5% means that if IHNV were present in at least 5% of the fish, it would be detected.

Salmonid populations in the Columbia River Basin are both culturally and economically important. Due to the extensive programmatic losses and economic costs associated with fish mortality following IHNV infection, the molecular and immunological characteristics of the virus have been well documented (Bootland and Leong, 2011). Genotyping of IHNV isolates has been used for molecular epidemiological studies across the endemic region (Garver et al., 2003; Kurath et al., 2003; Breyta et al., 2016a,b) and globally (Nishizawa et al., 2006; Enzmann et al., 2010; Kurath, 2012). Viral genotypes isolated from IHNV-positive fish at North American hatcheries are defined by sequencing a 303 nucleotide segment of the viral glycoprotein gene called the midG region (data are publically available in the MEAP-IHNV database, http://gis.nacse.org/ihnv). The genotyping method detects the majority genotype, with a lower limit of detection of minority genotypes around 10–20%. For the purpose of studying transmission mechanisms, knowing the majority genotype is sufficient because transmission is a bottleneck event (i.e., only a few genomes likely establish a new infection). IHN virology testing data collected by each of seven fish health agencies in the Columbia River Basin from 2000 to 2012, along with available genotyping data, have been compiled in a novel database linking fish species, fish age class, testing location, test date, test type, and test result (Breyta et al., 2017b). This database of IHNV virological and genetic surveillance data is referred to hereafter as the IHNV-VGS database.

Although IHN disease outbreaks in hatcheries can result in high mortality, the spatial and temporal frequency of these events is relatively low, with an average of 5% of sites having virus-positive juveniles for any given year (10 positive sites per year on average/222 total sites with tested juveniles in the IHNV-VGS database) (Breyta et al., 2017b, access data = 3 November 2016). As with many disease systems, a persistent challenge is differentiating lack of testing from absence of virus. Testing across all sites in the IHNV-VGS database (n = 324) for the years 2000–2013 occurred at rates of 22% of site-years for juvenile fish (27% of site-years with diagnostic tests, 57% with surveillance tests, and 29% with unknown test type because some site-years had multiple test types) and 36% of site-years for adult fish (9% of site-years with diagnostic tests, 58% with surveillance tests, and 44% with unknown test type because some site-years had multiple test types). Positive IHNV results occurred in 14% of tested site-years for juveniles and 25% of tested site-years for adults.

Controlling viral outbreaks relies on specific understanding of how IHNV is maintained in the environment at local, regional, and landscape scales. While biosecurity protocols at hatcheries are intended to eliminate parent-to-offspring transmission and cross-contamination between fish cohorts, inadvertent transmission among hatchery juveniles and transmission by water-borne virus entering a hatchery from non-secure water sources are possible (Mulcahy and Bauersfeld, 1983; Mulcahy et al., 1983; Mulcahy and Pascho, 1985; Bootland and Leong, 1999; Winton, 1991; Anderson et al., 2000; Bendorf et al., 2007; Tompkins et al., 2011; Breyta et al., 2016b). It is also possible that juvenile fish that survive clinical IHN disease or were sub-clinically infected might be released from hatcheries while still harboring, and possibly shedding, infectious virus. Finally, asymptomatic adult fish are frequently recorded with high titers of infectious virus at the time of spawning (Mulcahy et al., 1982; Bootland and Leong, 1999). It is not clear whether adult infection is the result of virus acquired during return migration or life-long persistence of virus in a small proportion of fish that survive infection as juveniles, possibly with virus reactivated in response to stress or reduced immune function at spawning (Bootland and Leong, 2011). As described by Breyta et al. (2017a),

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