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## Release of live baitfish by recreational anglers drives fish pathogen introduction risk<sup>☆</sup>

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### ABSTRACT

Emerging diseases of wildlife are an existential threat to biodiversity, and human-mediated movements of live animals are a primary vector of their spread. Wildlife disease risk analyses offer an appealing alternative to precautionary approaches because they allow for explicit quantification of uncertainties and consideration of tradeoffs. Such considerations become particularly important in high-frequency invasion pathways with hundreds of thousands of individual vectors, where even low pathogen prevalence can lead to substantial risk. The purpose of this study was to examine the landscape-level dynamics of human behavior-mediated pathogen introduction risk in the context of a high-frequency invasion pathway. One such pathway is the use and release of live fish used as bait by recreational anglers. We used a stochastic risk assessment model parameterized by angler survey data from Minnesota, USA, to simulate one year of fishing in Minnesota and estimate the total number of risky trips for each of three pathogens: viral hemorrhagic septicemia virus, the microsporidian parasite *Ovipleistophora ovariae*, and the Asian fish tapeworm *Schizocotyle acheilognathi*. We assessed the number of introductions under four scenarios: current/baseline conditions, outbreak conditions (increased pathogen prevalence), source-focused control measures (decreased pathogen prevalence), and angler-focused control measures (decreased rates of release). We found that hundreds of thousands of introduction events can occur per year, even for regulated pathogens at low pathogen prevalence. Reducing the rate of illegal baitfish release had significant impact on risky trips in scenarios where a high number of anglers were involved, but was less impactful in circumstances with limited outbreaks and fewer affected anglers. In contrast, reducing pathogen prevalence in the source populations of baitfish had relatively little impact. In order to make meaningful changes in pathogen introduction risk, managers should focus efforts on containing local outbreaks and reducing illegal baitfish release to reduce pathogen introduction risk. Our study also demonstrates the risk associated with high-frequency invasion pathways and the importance of incorporating human behaviors into wildlife disease models and risk assessments.

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## 1. Introduction

Invasive species are among the greatest threats to biodiversity worldwide (Balvanera et al., 2019). As global trade intensifies, transportation networks facilitate their spread at local, regional, and global scales (Gertzen et al., 2008; Mills et al., 1993; O'Hanlon et al., 2018). Among the diverse taxa of organisms recognized as invasive species, infectious diseases of wildlife stand out among the more significant and costly impacts to an ecosystem, with nearly a quarter of the species on the IUCN's 100 worst invaders list referencing disease as one of the mechanisms of their harmful impacts (Hatcher et al., 2012). Pathogens may also be considered invasive species in their own right (van Helden et al., 2020), causing population declines, local extinctions, and ecosystem-level changes (Crowl et al., 2008; O'Hanlon et al., 2018; Smith et al., 2006; Tompkins et al., 2015). Pathogenic organisms are particularly problematic invaders because of their ability to be inadvertently transferred with otherwise innocuous species, allowing them to pass undetected until already well-established and virtually impossible to eradicate (Crowl et al. 2008; Peeler and Otte 2016). Similar to cryptic invaders (Morais and Reichard, 2018) or sleeper populations of invasive species (Spear et al., 2021), invasive pathogens can evade traditional detection and prevention and require special attention when considering biological invasion risks.

Aquatic ecosystems are particularly vulnerable to pathogen invasion facilitated by live animal movements (Gozlan et al., 2006; Peeler et al., 2011; Smith et al., 2006). Live fish shipments comprise over 90 % of wildlife trade into the United States (Smith et al., 2009), and fish pathogens account for a large proportion of emerging infectious disease reports (Tompkins et al., 2015). At the same time, freshwater organisms are facing precipitous declines as a result of several anthropogenic pressures (Reid et al., 2019; Tickner et al., 2020), including the emergence and spread of novel invasive species and diseases (Gozlan et al. 2006). Invasion pathways with a high frequency of human movements of live animals, water, and equipment are well-documented vectors of invasive species (Connelly et al., 2016; Johnson et al., 2006; Ludwig and Leitch, 1996; Pradhananga et al., 2015; Rothlisberger et al., 2010). Despite this pressing threat, the risk of pathogen invasion in complex interconnected landscapes such as those dominated by recreational boaters and anglers is poorly understood.

Risk analysis has been identified as an important tool for understanding and mitigating the risk of invasive species and disease spread (Lodge et al. 2006; Mandrak and Cudmore 2015; Peeler, Reese, and Thrush 2015). Risk analysis is a process of identifying the hazardous outcomes relevant to the pathway of interest, evaluating the likelihood and severity of consequences that result from these outcomes, and communicating the results of the analysis to support improved risk management (Jakob-Hoff et al., 2014; World Organization for Animal Health (OIE) and International Union for the Conservation of Nature (IUCN), 2014). Risk analysis presents an appealing alternative to precautionary principle paradigms (Garnett and Parsons, 2017; Starr, 2003) because it allows for explicit consideration of tradeoffs and objective quantification of risks, an important consideration for risk policy decisions that may affect industry or trade sectors (Peeler et al., 2015). Risk assessment is the module of Risk analysis that explicitly addresses the question "how likely is this undesirable outcome to occur" and can be qualitative or quantitative depending on the data availability and needs of the risk assessment (Vose, 2001).

Although the attitudes and behaviors of individual anglers are frequently studied to inform fisheries management decisions (Hunt et al., 2011; Matsumura et al., 2019; Ward et al., 2016), invasive species risk assessments for freshwater ecosystems have typically evaluated invasion risk via species-based evaluations of invasive traits or habitat suitability for particular species (Kolar and Lodge, 2002; Marcot et al., 2019; Sakai et al., 2001; Williams et al., 2013). Some studies have integrated characteristics of angler behaviors to evaluate introduction risk in aquatic landscapes (Drake and Mandrak, 2014; Johnson et al., 2006;

Kilian et al., 2012; Ludwig and Leitch, 1996). These studies typically require significant amounts of individual-level behavioral data and pathogen-specific information that is frequently unavailable for aquatic systems (Jones, 2000; Travis and Hueston, 2000). Efforts to develop detailed quantitative risk assessments of high-volume invasion pathways are important, as they can provide crucial decision support for risk management policies in controversial or hotly contested situations that have already been qualitatively identified as potentially high risk pathways (Peeler et al. 2007; Hulme 2009).

In this study, we examine the landscape-level dynamics of human behavior-mediated pathogen introduction risk in the context of a high-frequency invasion pathway. We ask three main questions: First, is pathway risk more influenced by intrinsic pathogen characteristics, or human behaviors? Secondly, what is the potential utility of quantitative risk assessment to inform landscape-level management of pathogen invasion risk? Finally, what is the potential role of regulations in reducing the risk to acceptable levels? We first identify the human behaviors that facilitate pathogen introduction under baseline conditions, and then model the impacts of potential management alternatives to explore the sensitivity of large-scale social-ecological systems to changes in human behavior. Specifically, we quantify the number of introductions of a harmful pathogen that could occur under a suite of conditions.

The social and ecological context of live baitfish use and release by recreational anglers in an inland fishery provides an opportunity to study these dynamics. Live baitfish, most commonly minnows of the family Leuciscidae (formerly Cyprinidae; Schönhuth et al. 2018; Tan et al., 2018), are a popular choice among recreational anglers. Although banned in much of Europe due to animal welfare concerns (Ferber et al., 2020), the use of live baitfish remains popular in the United States, where millions of baitfish are raised in aquaculture facilities or harvested from the wild annually (Gunderson, 2019; 2018 Census of Aquaculture). Baitfish are therefore an important cultural and economic contribution in fishing and aquaculture production communities across the country (Connelly and Knuth, 2014; Litvak and Mandrak, 1993). However, recent advances in diagnostic techniques and increased surveillance have revealed the presence of invasive species (Nathan et al., 2015; Snyder et al., 2020) and pathogenic microbes (McEachran et al., 2021; Mahon et al., 2018; Boonthai et al., 2017; 2018; McCann, 2012) co-occurring with live baitfish available for retail sale across the country. Consequently, live baitfish release is illegal in most jurisdictions, but compliance is imperfect (Drake et al., 2015; Gunderson, 2019; McEachran et al., 2022). The encroachment of invasive pathogens on high-value inland fisheries has thus forced a more thorough review of this highly complex and wide-ranging pathway (Connelly et al., 2016; Anderson et al., 2014; Smith et al., 2020; Kilian et al., 2012; Donnelly and Wolbers, 2019).

We developed a stochastic risk assessment model of the angler-mediated movement of live baitfish and parameterized it with angler-provided data from a survey of adult anglers in Minnesota, USA (McEachran et al., 2022). Minnesota serves as a compelling study system, with over one million anglers, thousands of water bodies, and notable pathogens encroaching or already present in the live baitfish supply (McEachran et al., 2021; Gunderson 2018). Furthermore, Minnesota serves as a 'closed system' given the ban on live baitfish importation since 1973 (MN State Statute 97C.341c), but we acknowledge that the potential for illegal importation is unknown.

As case studies for the risk assessment, we focused on the three highest-ranked pathogens identified by McEachran et al. (2020), representing a diversity of taxa, pathogenicity, and regulatory status: viral hemorrhagic septicemia virus (VHSV), the microsporidian parasite *O. variae*, and Asian fish tapeworm *Shizocotyle acheilognathi* (AFT). Each of these pathogens causes morbidity and mortality in important fish species, is easily transmitted by baitfish species, and has the potential to become established in Minnesota. For a more extensive description of each pathogen, please see [Supplementary Material: Pathogen Descriptions](#). For each pathogen, we estimated the risk of

pathogen introduction under baseline, outbreak, and increased control scenarios, which were designed to represent system responses under distinct conditions that may occur in the future.

## 2. Materials and methods

### 2.1. Project scope and risk pathway definition

To quantify the risk of fish pathogen spread via the illegal release of live baitfish in Minnesota, we defined our outcome of interest as a fishing trip that resulted in the release of a baitfish infected with one of the three priority pathogens. The risk that any given fishing trip results in the release of an infected baitfish was conceptualized as a function of both angler behaviors (e.g., propensity to release baitfish) and pathogen characteristics (e.g. prevalence in susceptible species). Numerous factors including environmental conditions, presence of host species, and pathogen fitness can modulate the likelihood of an introduction resulting in the establishment of that pathogen (Langwig et al. 2015). Given that suitable environments and susceptible species are widespread in Minnesota for each of the pathogens considered in this study (McEachran et al. 2020), we considered the release of an infected baitfish as a potential disease introduction (hereafter, a “risky trip”).

We defined the risk pathway from “shop to shore”; namely, we quantified the likelihood of an angler purchasing baitfish from a bait-shop or harvesting from the wild, the likelihood of that baitfish being infected, and the likelihood of that infected baitfish being released into a different waterbody from which it was sourced. Although factors prior to the point of sale, such as location of harvest, implementation of decontamination procedures, or inspections of live baitfish could influence pathogen prevalence, we excluded any steps not involving recreational anglers from the risk pathway.

### 2.2. Scenario descriptions

For each pathogen, we assessed the risk of fish pathogen spread by quantifying the probability of any given fishing trip being risky and the total number of risky trips that occur under a range of simulated conditions: (1) baseline conditions, (2) outbreak conditions (increased pathogen prevalence), and (3) implementation of source-focused control measures. Baseline conditions were defined as the present status of the pathogen, including distribution and host species, as confirmed by relevant fish health authorities (World Organization for Animal Health (OIE) 2017; U.S. Fish and Wildlife Service and American Fisheries Society-Fish Health Section 2007), while outbreak conditions were intended to simulate introduction or further spread of the pathogen within the state beyond where it is currently understood to be distributed. Source-focused control measures were defined as measures to reduce pathogen prevalence in the source populations for each relevant baitfish species.

### 2.3. Viral hemorrhagic septicemia virus

At the state level, Minnesota is considered VHSV-positive due to the detection of VHSV-positive fishes in Lake Superior (Gustafson et al. 2014). Despite this proximity to a positive water body, however, over a decade of disease testing has thus far not detected VHSV in any inland waters or fish production facilities in the state (Gunderson 2018; Phelps et al. 2014). Although we assume freedom from VHSV under baseline conditions in Minnesota, current testing procedures are imperfect and the stochastic nature of infectious diseases introduces uncertainty (Travis and Hueston 2000). Until recently, the list of VHSV-susceptible species subject to regulatory testing in Minnesota included emerald shiner *Notropis atherinoides* and spottail shiner *Notropis hudsonius*, and as of July 2021 now includes fathead minnow *Pimephales promelas* (MN Statute 17.4981 subd 21a). This change was made in response to an update of the susceptible species list in the American Fisheries Society –

Fish Health Section Blue Book ([USFWS] U.S. Fish and Wildlife Service and [AFS] American Fisheries Society-Fish Health Section 2014), but fathead minnow has been listed as susceptible by the OIE since 2010 (World Organization for Animal Health (OIE) 2017b).

We assessed the risk of VHSV introduction under four different hypothetical scenarios: pathogen confined to susceptible *Notropis* species in the Lake Superior Watershed (HUC-4 0401, Fig. 2) (VHSV-1); pathogen in *Notropis* species statewide (VHSV-2); pathogen in both *Notropis* species and fathead minnows in the H0507 watershed (VHSV-3); and pathogen in both *Notropis* species and fathead minnows in all watersheds in the state (VHSV-4; Fig. 1).

### 2.4. *Ovipleistophora ovariae*

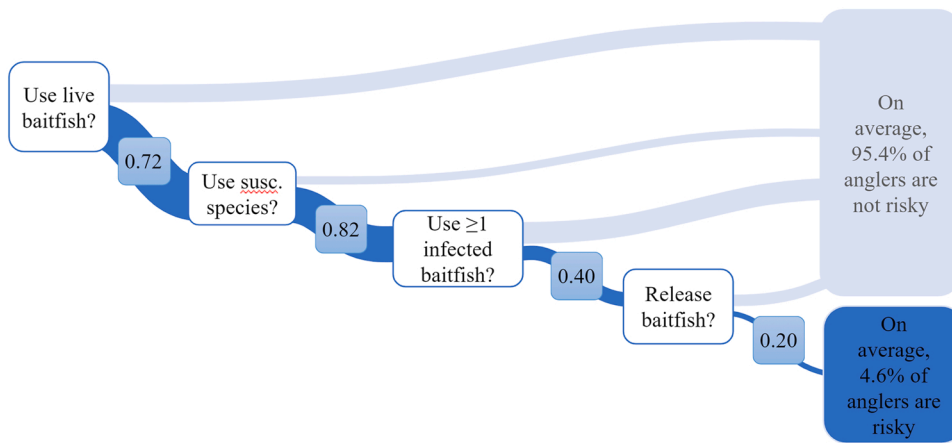
*Ovipleistophora ovariae* is not subject to regulation or testing in the state, but has been widely detected in live baitfish available for retail sale and present in wild populations of golden shiner *Notemigonus crysoleucas* in Minnesota (McEachran et al., 2021). We estimated the risk of *O. ovariae*-infected fish being released under three conditions. First, **OVIO-1**: assuming baseline conditions, including current estimated prevalence of *O. ovariae* during summer and winter seasons, and current rates of angler release. Golden shiner is a preferred baitfish species among Minnesota anglers and there are growing calls for increasing within-state production of disease-free fish, so we also estimated disease introduction risk under **OVIO-2**: 25 % of the available golden shiner currently sold were replaced with certified disease-free golden shiner and **OVIO-3**: 50 % replaced with certified disease-free golden shiner. We assumed 0 % pathogen prevalence in the certified golden shiner in the latter two scenarios.

### 2.5. Asian fish tapeworm

Similar to *O. ovariae*, the invasive AFT is not subject to any regulatory testing or surveillance at present. To date, AFT has never been detected in Minnesota; however, its detection in neighboring states’ baitfish supplies and ability to infect numerous Minnesota species (Boonthai et al., 2017) has raised concerns that the lack of in-state surveillance for AFT may be missing its true prevalence. To estimate the risk of AFT spread given incomplete knowledge of current distribution in Minnesota’s live baitfish supply, we assessed introduction risk assuming low (AFT-1) and moderate (AFT-2) pathogen prevalence.

### 2.6. Model parameterization

Probability distributions for each input variable in all scenarios were fitted using the `fitdistrplus` package in R (Dignette-Muller and Dutang, 2015; Table 1). Probability distributions for angler behaviors and characteristics were parameterized using angler-reported data collected via a mailed paper questionnaire in May–August 2019 as described in McEachran et al. (2022). Briefly, 669 anglers who had purchased an annual Minnesota fishing license during the March 2018–February 2019 fishing season responded to a mailed survey following a modified Dillman approach (Dillman et al., 2014). The average number of trips reported per year per angler was 24 trips (SD = 26) and the proportion of anglers using live baitfish was 71 %. Despite a prohibition on stocking fish without a permit (MN State Statute 17.4986 subd. 1), 20 % of live baitfish users reported releasing their leftover live baitfish into public waters where they were fishing. We used these survey results to fit Beta probability distributions for the probability of an angler using live baitfish ( $P_{use}$ ), the probability of using susceptible baitfish species ( $P_{usesusc}$ ), and the probability of an angler releasing their leftover live baitfish ( $P_{release}$ ). To fit count distributions for the number of baitfish susceptible to each pathogen used per trip ( $S_{path}$ ) and the number of fishing trips taken each year ( $T_{angyr}$ ), we first removed outlier values greater than ten times the median absolute deviation and then used the `fitdistrplus` package. For VHSV scenarios 1 and 3 where the pathogen



**Fig. 1.** Example conceptual diagram illustrating risk pathway for the VHSV-4 scenario, a statewide outbreak of VHSV in *Notropis* species and fathead minnow *Pimephales promelas* in Minnesota. Each box represents a step in the risk pathway, and numbers on each arrow indicate the average percentage of anglers for whom this step occurred in this particular scenario. The average value of  $P_{risky}$  for this scenario is 4.6%. Parameters were estimated using angler survey data from McEachran et al. (2022), which used a mailed survey questionnaire to elicit responses from adult licensed anglers in Minnesota in May-July 2019.

was confined to the Lake Superior watershed, we also estimated conditional probabilities of using fish from that watershed ( $P_{useL\text{fish}}$ , Table 1), and using susceptible fish when just *Notropis* species ( $P_{useL\text{Sshiners}}$ ) and both *Notropis* species and fathead minnow ( $P_{useL\text{Ssus}}$ ) were included in the outbreak scenario. Using historical license data, we parameterized a discrete uniform distribution centered on the number of annual license holders ( $n = 677,542$ ) during the 2018-2019 fishing season to estimate the total number of annual license holders ( $L$ ; MN DNR historical license data available at <https://www.dnr.state.mn.us/licenses/license-sales-data.html>).

For distributions of  $P_{usesusc}$ ,  $S_{path}$ , and prevalence ( $Prev$ ) that required defining which species were susceptible to each pathogen, we considered evidence for susceptibility as natural infection discovered via surveillance, or confirmed infection in experimental settings using natural infection pathways (i.e. immersion or cohabitation) that did not circumvent the host fish's immune systems (World Organization for Animal Health (OIE) 2017a). Susceptibility established via intraperitoneal injection, or natural susceptibility that was unable to be confirmed by PCR or other typing methods, was considered to be incompletely demonstrated as noted in Supplementary Material: Pathogen Descriptions, and not included in our model. To retrieve information confirming the susceptibility of the relevant baitfish species to our selected diseases, a literature search was performed via PubMed, SCOPUS, and Web of Science in June 2020. Abstracts were first scanned for the baitfish species of interest and pathogen susceptibility was verified for those species based on the methods and results of each paper (Supplementary Material: Pathogen Descriptions).

To estimate potential prevalence of VHSV in a "worst case scenario" where VHSV persists at low levels despite routine surveillance, the probability distribution for prevalence in all VHSV scenarios was determined by calculating the complement probability of VHSV detection given current surveillance standards. Although VHSV is a psychrophilic virus with peak mortalities occurring at water temperatures 5-15 °C ([USFWS] U.S. Fish and Wildlife Service and [AFS] American Fisheries Society-Fish Health Section 2014; Faisal et al. 2012), susceptible baitfish species have been found to have subclinical infections even during periods of higher water temperatures (Frattini et al. 2010). Therefore, we assumed equal probability of baitfish being infected with VHSV across both the open water (May-October) and ice fishing (November-April) seasons. The current recommended sampling plan for VHSV inspections requires 60 fish to be taken, providing a 95% certainty of freedom from disease at 5% disease prevalence or higher ([USFWS] U.S. Fish and Wildlife Service and [AFS] American Fisheries Society-Fish Health Section 2007). We then used the `phyper()` function in R to estimate probability of getting fewer than  $q$  infected individuals in a sample of 60 fish taken from a population of  $N$  fish with  $m$  infected fish present:

$$Prevalence = \text{phyper}(q, m, n, k)$$

where  $q = 0$ ,  $n = N - m$  representing the number of uninfected fish present,  $k = 60$  representing current recommended sample size, and  $m$  is the array of numbers of infected fish corresponding to prevalence values ranging from 0 to 1. Thus, the values of the *Prevalence* represent the probability of an outbreak of size  $m$  going undetected despite current surveillance protocols. To convert this to a probability density function for prevalence, we then fit a truncated exponential distribution bounded between zero and 1 to represent the probability of infection with VHSV using the `fitdistr()` function from the `fitdistrplus` package (Dlignette-Muller and Dutang 2015).

To estimate the probability of infection with *O. variae*, we fit empirical probability distributions to the percent of mature females infected per shop as reported from a statewide baitshop survey (McEachran, Mor, and Phelps 2021). Prevalence of *O. variae* was significantly higher in the summer months than in the winter months, so we fit separate probability distributions for summer ( $Prev_{summer}$ ) and winter ( $Prev_{winter}$ ) prevalence. We also estimated the probability of using live baitfish ( $P_{usesummer}$ ) and using golden shiner ( $P_{usesusc,summer}$ ) in the summer separately from the probability of using in winter ( $P_{usewinter}$  and  $P_{usesusc,winter}$ ) using data from the angler survey (McEachran et al., 2022). To test the impact of a certified disease-free supply of golden shiner becoming available, we also included a parameter representing the probability that an angler purchased golden shiner that were not from the certified disease-free source ( $P_{usedirty}$ ).

To estimate pathogen prevalence for the AFT scenarios, we defined a uniform distribution with minimum and maximum values based on published values for infection rates in representative baitfish species. In the low prevalence outbreak scenario, (AFT-1), we modeled prevalence as a uniform distribution between 0% and 2%, since the lowest prevalence of AFT in previously reported infected populations was 2% (Muzzall et al., 2016; Boonthai et al. 2017; Bean and Bonner, 2010; Marcogliese et al., 2016; Marcogliese, 2008). Given that 20% is the reported maximum prevalence in field studies of AFT in baitfish species (Marcogliese et al., 2016), we parameterized the moderate outbreak scenario prevalence using a uniform distribution between 0% and 20%. Five live baitfish species met the criteria for susceptibility to AFT and were included in the models: golden shiner, fathead minnow, spottail shiner, emerald shiner, and creek chub *Semotilus atromaculatus*.

## 2.7. Simulation modeling

To quantify the number of risky trips that could occur each year in Minnesota, we first estimated the probability of a single angler being risky under each scenario using the following equation:

**Table 1**

Input parameter distributions, values, and source of data for all modeled pathogen scenarios. All angler survey data cited as a source of parameter information is from McEachran et al. (2022). Scenario abbreviations are VHSV-1: Lake Superior watershed in susceptible shiners only, VHSV-2: statewide outbreak in susceptible *Notropis* species only, VHSV-3: LS watershed in all susceptible species, VHSV-4: statewide outbreak in all susceptible species, OVIO-1: baseline conditions; OVIO-2: 25 % golden shiner replaced with disease-free; OVIO-3 50 % golden shiner replaced with disease-free; AFT-1: low prevalence Asian fish tapeworm; AFT-2 high prevalence Asian fish tapeworm. ESH = emerald shiner *Notropis atherinoides*, SPT = spottail shiner *Notropis hudsonius*, FHM = fathead minnow *Pimephales promelas*.

Parameter	Description	Value	Source
$P_{use}$	P(use live baitfish)	$Beta(\alpha = 482, \beta = 191)$	Proportion of anglers who use live baitfish, McEachran et al. (2022)
$P_{useseason}$	P(use live baitfish in winter or summer use live baitfish)	OVIO, summer: $Beta(402, 81)$ OVIO, winter: $Beta(280, 203)$	Proportion of bait users who use live baitfish in summer or winter, McEachran et al. (2022)
$P_{release}$	P(release live baitfish)	$Beta(98, 481)$	Proportion of bait users who release live baitfish, McEachran et al. (2022)
$T_{angyr}$	Number of fishing trips per angler per year	$NegBin(mean = 36.7, s = 1.28), 1 \leq x \leq 120$	Reported number of trips per year per angler, McEachran et al. (2022)
$L$	Number of annual angling license purchases per year	$DiscreteUniform(667542, 687542)$	Historical license data; number of annual licenses (codes 111,112,121)*
$Prev$	Prevalence of pathogen in susceptible species	VHSV: $Exp(rate = 41)$ , where $0 \leq x \leq 1$ ; OVIO, winter: $Triang(min = 0.25, max = 0.5, mode = 0.5)$ ; OVIO, summer: $Triang(0.067, 0.50, 0.3)$ ; AFT, low: $Uniform(min = 0, max = 0.02)$ ; AFT, mod: $Uniform(0, 0.2)$	VHSV: hypothetical, Blue USFWS and AFS-FHS Blue Book; OVIO: McEachran et al., 2021; AFT: hypothetical, Boonthai et al., 2017
$P_{usesusc}$	P(use susceptible species use live baitfish)	VHSV-2: $Beta(92, 391)$ ; VHSV-4: $Beta(398, 85)$ ; OVIO, winter: $Beta(33, 91)$ ; OVIO, summer: $Beta(57, 304)$	Proportion of anglers using VHSV-susceptible shiners (VHSV-2), VHSV-susceptible baitfish (VHSV-4), golden shiners (OVIO), or AFT-susceptible baitfish (AFT), McEachran et al., 2022
$P_{useLSfish}$	P (purchase from infected LS watershed use live baitfish)	VHSV-1, VHSV-3: $Beta(44, 439)$	Proportion of bait users acquiring baitfish in LS watershed, McEachran et al., 2022
$P_{useLSshiners}$	P(use ESH or SPT purchase from infected area)	VHSV-1: $Beta(11, 34)$	Proportion of anglers purchasing from LS watershed using susceptible shiners, McEachran et al., 2022
$P_{useLSsusc}$	P(use ESH or SPT or FHM purchase from infected area)	VHSV-3: $Beta(39, 6)$	Proportion of anglers purchasing from LS watershed using susceptible species, McEachran et al., 2022
$S$	Number of susceptible	VHSV-1, VHSV-2: $NegBin(size = 1.2, \mu =$	Reported number of VHSV-susceptible

**Table 1 (continued)**

Parameter	Description	Value	Source
	baitfish purchased	25.13), where $1 \leq x \leq 202$ ;	baitfish purchased per angler per trip, McEachran et al., 2022
		VHSV-3, VHSV-4: $NegBin(0.7, 36)$ , where $1 \leq x \leq 264$ ;	
		OVIO: $NegBin(1.3, 22)$ ;	
		AFT: $NegBin(0.6, 34)$ ;	
		where $1 \leq x \leq 264$	

$$P_{risky} = P_{use} * P_{usesusc} * (1 - (1 - Prev)^{Spath}) * P_{release}$$

The number of risky trips occurring in a single fishing season (March-February of the following year;  $N_{risky}$ ), was then calculated for each scenario by multiplying the probability of a single angler being risky by the product of trips per angler per year ( $T_{angyr}$ ) and total number of anglers ( $L$ ):

$$N_{risky} = P_{risky} * T_{angyr} * L$$

Because the probability of infection with *O. ovariae* and angler behavior varied significantly between the open water and ice seasons (McEachran et al., 2022), we split the *O. ovariae* scenario calculations by summer and winter season and calculated  $P_{risky}$  and  $N_{risky}$  for each season using the following equations, respectively:

$$P_{risky.season} = P_{use} * P_{use.season} * P_{usesusc.season} * (1 - (1 - Prev_{season})^{Sovia}) * P_{release}$$

$$N_{risky.season} = P_{risky.season} * T_{angyr} * L$$

$$N_{risky.total} = N_{risky.summer} + N_{risky.winter}$$

These calculations were then repeated 10,000 times, drawing a new value from each input distribution with each iteration to create a distribution of values representing resulting variability of the outputs of interest.

Defining an acceptable level of risk at the outset of a risk assessment is critical for identifying which risk mitigation strategies should be undertaken and when they have been successful (Travis et al., 2014). Given the inherent disease risks associated with moving live animals, “zero” is an infeasible benchmark, so we arbitrarily chose 1 % probability of riskiness ( $P_{risky}$ ) as a threshold for evaluating the subjective risk presented by each scenario. We calculated the value of the empirical cumulative distribution function at  $P_{risky} = 0.01$  for each scenario and reported the proportion of model iterations where the estimated value of  $P_{risky}$  was  $> 0.01$ , representing the risk that at least 1 % of anglers in a given year are risky.

### 2.8. Sensitivity analyses

To examine the sensitivity of model outputs to variability in input parameters, we applied a two-stage sensitivity analysis (Martinez-Lopez et al., 2008). First, the output  $N_{risky}$  was regressed on all input parameters using a general linear model (lm() function) in R. We then calculated standardized regression coefficients ( $\beta_i$ ) by multiplying the unstandardized regression coefficients  $b_i$  by the standard deviation of each parameter  $i$  and dividing by the standard deviation of  $N_{risky}$ :

$$\beta_i = b_i * \frac{sd_{xi}}{sd_{N_{risky}}}$$

Each  $\beta_i$  could thus be interpreted as the standard deviation unit change in  $N_{risky}$  resulting from a single standard deviation unit change in each input parameter  $i$ . Standardized regression coefficient values less than 0.1 were considered evidence of low impact of an input parameter on  $N_{risky}$ . For the second stage of the sensitivity analysis, we considered how moderating certain management-relevant parameters could result

in meaningful change in the number of risky trips. Because the prevalence of disease and the probability of release are the two parameters currently managed by existing regulations and practices, we modulated these in the second stage of the sensitivity analysis. We systematically varied each by +10 % and -10 % from baseline while keeping the original distributions for all other input parameters, and the outputs and  $\beta_i$  were recalculated and compared to their initial values. Equivalent values of  $\beta_i$  to the tenths decimal point was considered evidence of noncollinearity in selected model parameters (Martinez-Lopez et al., 2008). Percent differences in mean  $N_{risky}$  resulting from 10 % increase or decrease in the select parameters were evaluated and compared to the 10 % change in the input value. A change of less than 10 % resulting from changing parameter  $i$  was considered evidence for the model's relative insensitivity to that input parameter, while a resultant change greater than 10 % was considered evidence for the model's relative sensitivity to that input.

### 3. Results

#### 3.1. Viral hemorrhagic septicemia virus

In scenarios where the outbreak was contained to the Lake Superior watershed (VHSV-1 and VHSV-3), the mean conditional probability of an angler purchasing their live baitfish from the outbreak area given that they were using live baitfish ( $P_{useL\text{fish}}$ ), was 0.091 (SD = 0.013). In VHSV-1, the mean probability of purchasing a *Notropis* species given purchase from the Lake Superior watershed ( $P_{useL\text{Sshiners}}$ ) was 0.24 (SD = 0.063), and in VHSV-3, the mean probability of purchasing a combination of *Notropis* species and fathead minnow given purchase from the Lake Superior watershed ( $P_{useL\text{Susc}}$ ) was 0.87 (SD = 0.050). In the VHSV-2 scenario, the average probability of purchasing *Notropis* species statewide ( $P_{usesusc}$ ) was 0.19 (SD = 0.018) and the average number of susceptible baitfish purchased ( $S_{vshv}$ ) was 26 (SD = 23.2 fish). When the outbreak included fathead minnows in VHSV-4, these increased to 0.82 (SD = 0.017) and 33 (SD = 29.8 fish), respectively (Fig. 1). All input parameter distributions are provided in Table 1.

Despite low modeled prevalence of VHSV in infected fish (mean = 0.024, sd = 0.025), all simulated VHSV scenarios resulted in risky trips where fish infected with VHSV were released (Table 2). VHSV-1, the least extensive outbreak which was confined only to *Notropis* species sourced from the Lake Superior watershed, had an average of 19,244 risky trips occurring each year, though the distribution was highly skewed (SD = 28,372). Broadening the outbreak by including susceptible fathead minnows in VHSV-3 resulted in a 4-fold increase to 81,581 risky trips on average (SD = 114,001). However, the impact of expanding the affected area statewide in VHSV-2 and VHSV-4 had a greater impact, resulting in approximately a 5-fold increase from 175,810 risky trips on average (SD = 247,886) in VHSV-2 to 841,992 (SD = 1,119,171) in VHSV-4. The percent of iterations where  $P_{risky} > 0.01$  was also much lower in VHSV-1 (0 %) compared to the statewide scenarios (79 % in VHSV-4). All output summary statistics are displayed in Table 2.

The number of trips per angler (*Tangyr*), prevalence of VHSV, and number of VHSV-susceptible fish purchased were influential parameters in all VHSV scenarios (Table 3). For VHSV-1 and VHSV-3, the probability of purchasing susceptible fish from the infected region was also influential, though to a lesser degree. The standardized regression coefficient for  $P_{release}$  did not meet the threshold value of 0.1 in most scenarios (Table 3). However, in the second phase of sensitivity analysis, decreasing the probability of release by 10 % had an effect on the mean number of risky trips for all scenarios. The greatest changes in  $N_{risky}$  occurred in the statewide scenarios VHSV-2 and VHSV-4 with 11 % and 12 % reduction in mean risky trips, respectively, but the change was less than 10 % for VHSV-1 and VHSV-3 (Table 4). In contrast, the values of  $\beta_i$  for the prevalence parameter were above the  $\beta_i > 0.1$  threshold, but the impacts of a 10 % decrease or increase in prevalence were  $\leq 10$  % for all

**Table 2**

Summary statistics for estimated annual number of risky trips ( $N_{risky}$ ), proportion of all annual trips that are risky ( $P_{risky}$ ), and percent of model iterations where  $P_{risky} > 1$  % for all scenarios estimating risk of fish pathogen introduction via release of live baitfish by anglers in Minnesota. VHSV-1: Lake Superior watershed in susceptible *Notropis* species only, VHSV-2: statewide outbreak in susceptible *Notropis* species only, VHSV-3: LS watershed in all susceptible species, VHSV-4: statewide outbreak in all susceptible species, OVIO-1: baseline conditions; OVIO-2: 25 % golden shiner replaced with disease-free; OVIO-3 50 % golden shiner replaced with disease-free; AFT-1: low prevalence Asian fish tapeworm; AFT-2 high prevalence Asian fish tapeworm. Note that for *O. variae* scenarios,  $P_{risky}$  is calculated separately for each season but the total number of risky trips per year ( $N_{risky,total}$ ) is presented. Season-specific parameter estimates are denoted S: summer and W: winter for OVIO scenarios.

Scenario	$P_{risky}$ (median, SD)	$N_{risky,total}$ median (SD); maximum	Percent of iterations where $P_{risky} > 0.01$
VHSV-1	0.000747 (0.00104)	8,701 (28,372); 390,553	0.0 %
VHSV-2	0.00688 (0.00823)	81,205 (247,886); 2,492,833	38 %
VHSV-3	0.00336 (0.00387)	37,605 (114,001); 1,143,523	11 %
VHSV-4	0.0355 (0.0376)	411,136 (1,119,171); 9,696,539	79 %
OVIO-1	S: 0.0175 (0.0102) W: 0.0 (0.0113)	128,974 (263,598); 2,504,575	71 %
OVIO-2	S: 0.0 (0.00848) W: 0.0132 (0.00769)	102,803 (209,182); 2,666,183	25 % 66 %
OVIO-3	S: 0.0 (0.00626) W: 0.0175 (0.0102)	67,081 (140,677); 1,376,316	37 % 20 %
AFT-1	0.0215 (0.0314)	256,499 (879,064); 10,458,152	70 %
AFT-2	0.105 (0.0424)	1,164,475 (1,693,666); 11,995,539	96 %

scenarios, indicating relative insensitivity to pathogen prevalence (Table 4).

#### 3.2. *Ovipleistophora variae*

Release of fish infected with *O. variae* was common in the scenario representing baseline prevalence and distribution of the parasite (OVIO-1, Table 1). The probability of using live baitfish in summer ( $P_{use,summer}$ , mean = 0.83, SD = 0.017) was higher than in winter (mean = 0.58, sd = 0.022). The empirical probability distributions for *O. variae* prevalence were zero-inflated, particularly for the winter estimates. As a result, the average prevalence in summer ( $Prev.s$ , mean = 0.21, sd = 0.15) was higher than in winter ( $Prev.w$ , mean = 0.10, sd = 0.18). In addition, the average number of trips per angler in summer was 17.9 (sd = 19.5), more than twice as many trips as in winter (mean = 6.39, sd = 8.72). The probability of a trip being risky in summer ( $P_{risky}$ ) was higher than in winter across all *O. variae* scenarios (Table 2). The average number of risky trips in the baseline scenario was 213,665, but as with VHSV, the distribution was highly skewed (SD = 263,598). Replacing 25 % (OVIO-2) and 50 % (OVIO-3) of the available golden shiner with certified disease-free baitfish resulted in 20 % and 48 % reduction, respectively, in the median number of risky trips as compared to the baseline scenario (Table 2). Additionally, the percent of iterations where  $P_{risky} > 0.01$  decreased from 71 % in the summer in the baseline condition, to 37 % in the summer in the 50 % clean baitfish scenario. However, even in OVIO-3 when 50 % of all golden shiner was *O. variae*-free, the number of risky trips per year was still large (mean = 113,235, SD = 141,666).

The first stage of sensitivity analyses revealed that the high number of risky trips ( $N_{risky,total}$ ) across all *O. variae* scenarios was due to the high number of trips in summer and the prevalence of *O. variae* during

**Table 3**

Standardized regression coefficients ( $\beta_i$ ) when  $N_{risky}$  is regressed on each of the input parameters  $i$  for each pathogen scenario simulated with a quantitative risk assessment model of live baitfish release by recreational anglers in Minnesota. Values of  $\beta_i$  can be interpreted as the standard deviation unit change in  $N_{risky}$  resulting from one standard deviation unit change in the input parameter, holding all others constant. Boldface type indicates  $\beta_i$  values  $> 0.1$ . Asterisks denotes significance at the  $\alpha = 0.05$  level. For *O. ovariae* scenarios, S = summer parameters, W = winter parameters.

Scenario	$P_{use}$	$P_{useseason}$	$P_{usesusc}$	$P_{useLsfish}$	$P_{useLSusc}$	$P_{useLSshiners}$	$P_{release}$	$Prev$	$S$	$T_{angyr}$	$L$
OVIO-1	0.018*	S: 0.14* W: 0.0099	0.093* 0.002*	–	–	–	<b>0.16*</b>	<b>0.38*</b> <b>0.12*</b>	0.048*	<b>0.64*</b> <b>0.15*</b>	0.011
OVIO-2	0.026*	S: 0.019* W: 0.0052	0.086* 0.021*	–	–	–	<b>0.17*</b>	<b>0.38*</b> <b>0.20*</b>	0.049*	<b>0.19*</b> <b>0.62*</b>	0.0059
OVIO-3	0.011*	S: 0.0067* W:0.0070	0.086* 0.023*	–	–	–	<b>0.16*</b>	<b>0.37*</b> <b>0.194*</b>	0.051*	<b>0.631*</b> <b>0.16*</b>	0.010*
VHSV-1	0.018*	–	–	0.010*	–	<b>0.17*</b>	0.068*	<b>0.420*</b>	<b>0.33*</b>	<b>0.54*</b>	0.0058
VHSV-2	0.012*	–	0.071*	–	–	–	0.073*	<b>0.414*</b>	<b>0.34*</b>	<b>0.58*</b>	0.0012*
VHSV-3	0.024*	–	–	<b>0.11*</b>	0.043*	–	0.061*	<b>0.359*</b>	<b>0.36*</b>	<b>0.60*</b>	0.0101*
VHSV-4	0.020*	–	0.0249*	–	–	–	0.060*	<b>0.398*</b>	<b>0.34*</b>	<b>0.61*</b>	0.0207*
AFT-1	0.020*	–	0.012	–	–	–	0.069*	<b>0.31*</b>	<b>0.49*</b>	<b>0.56*</b>	0.0002
AFT-2	0.027*	–	0.013*	–	–	–	0.099*	<b>0.24*</b>	<b>0.24*</b>	<b>0.80*</b>	0.0079*

**Table 4**

Results of second-stage sensitivity analysis using one-way balanced design to estimate change in number of risky trips ( $N_{risky}$ ) resulting from a 10 % change in prevalence ( $Prev$ ) and rate of release of live baitfish by recreational anglers ( $P_{release}$ ). Both summer and winter values for  $Prev$  in the *O. ovariae* scenarios are displayed, with summer values listed first.

Scenario	Parameter	Increase parameter 10 %			Decrease parameter 10 %		
		Difference in mean $N_{risky}$ (absolute value, percentage)	$\beta_i$	$\beta_i'$	Difference in mean $N_{risky}$ (absolute value, percentage)	$\beta_i$	$\beta_i'$
VHSV-1	$P_{release}$	3,275 (17 %)*	0.067	0.057	-1,446 (8 %)	0.067	0.064
		13,325 (7.5 %)	0.073	0.070	-19,998 (11 %)	0.073	0.075
		9,684 (12 %)	0.043	0.045	-7,458 (9 %)	0.043	0.044
		63,621 (8 %)	0.060	0.072	-104,712 (12 %)	0.071	0.072
VHSV1	$Prev$	1,953 (10 %)	0.42	0.40	-2,314 (3 %)	0.059	0.063
		6,467 (4 %)	0.41	0.40	-9,700 (6 %)	0.41	0.42
		4,901 (6 %)	0.36	0.35	-2,314 (3 %)	0.36	0.37
		36,802 (4 %)	0.39	0.38	-42,283 (5 %)	0.40	0.40
OVIO-1	$P_{release}$	21,274 (10 %)	0.16	0.15	-25,027 (11 %)	0.16	0.16
		6,848 (4 %)	0.14	0.16	-27,782 (16 %)	0.14	0.15
		6,229 (6 %)	0.15	0.16	-17,484 (16 %)	0.16	0.16
		3,137 (1 %)	0.38,	0.38,	-2,897 (1 %)	0.38,	0.38,
OVIO-1	$Prev$		0.18	0.17		0.18	0.18
		1,965 (1 %)	0.38,	0.37,	-11,972 (7 %)	0.38,	0.39,
			0.19	0.18		0.19	0.18
		5,979 (5 %)	0.39,	0.35,	-5,969 (5 %)	0.38,	0.38 0.17
AFT-1	$P_{release}$	57,236 (9 %)	0.07	0.06	56,305 (10 %)	0.07	0.06
		187,991 (11 %)	0.09	0.09	1,964,090 (12 %)	0.07	0.07
		27,788 (4 %)	0.074	0.074	-47,730 (8 %)	0.07	0.05
		98,566 (6 %)	0.09	0.09	-1,075 (0.06 %)	0.09	0.09

both seasons (Table 3; Supplementary Material). However, the proportion of anglers releasing live baitfish ( $P_{release}$ ) was also an important predictor of risk, with approximately 0.15 standard deviation increase in  $N_{risky}$  resulting from a single standard deviation increase in the probability of release (Table 3; Supplementary Material). Indeed, reducing release probability by 10 % in the second stage of sensitivity analysis led to substantial decreases in  $N_{risky}$  across all scenarios. Decreasing *O. ovariae* prevalence produced relatively small ( $\leq 10$  %) decreases in  $N_{risky}$  in both OVIO-2 and OVIO-3 (Table 4).

3.3. Asian fish tapeworm

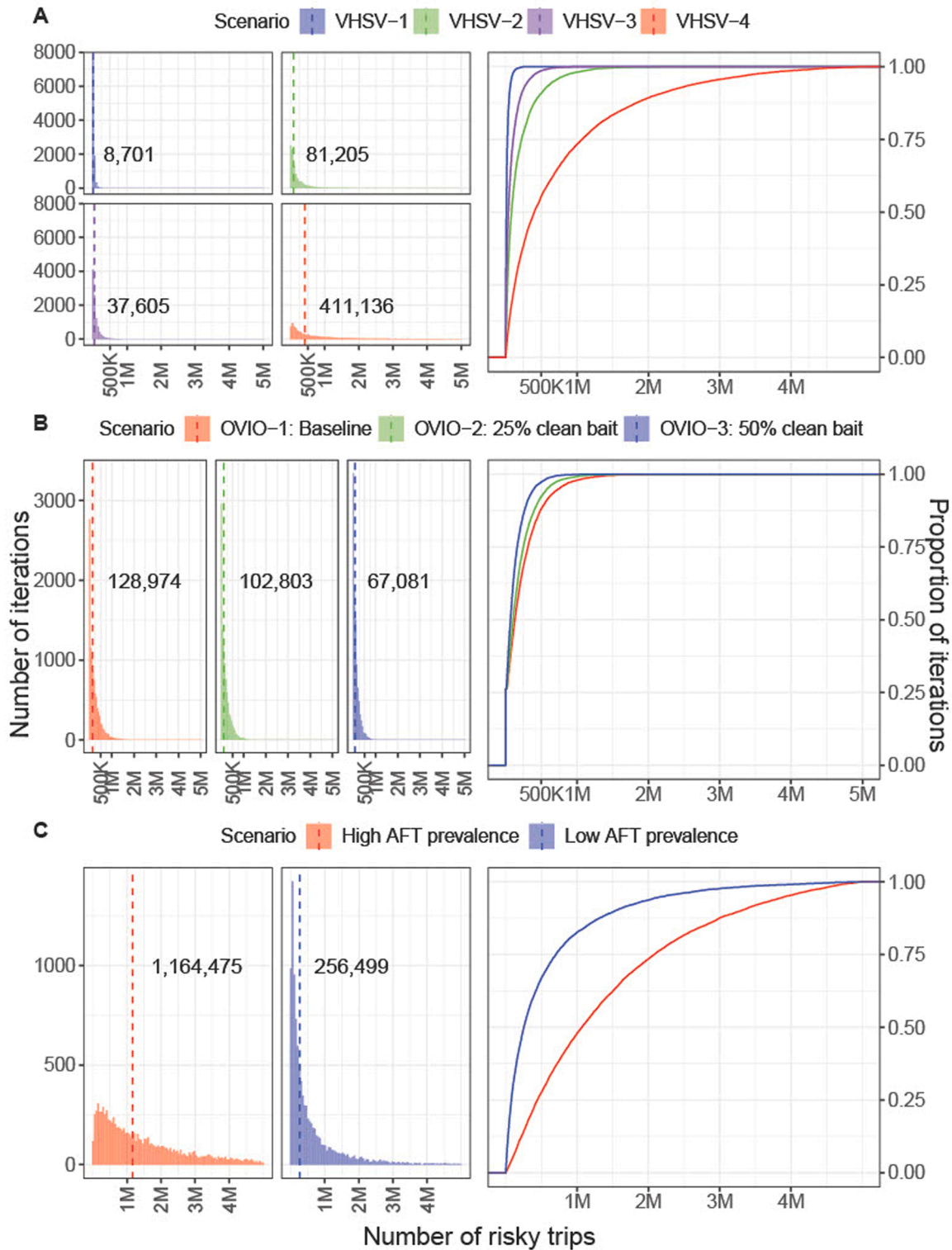
The average proportion of baitfish users purchasing one or more of the AFT-susceptible species ( $P_{usesusc}$ , Table 1) was 0.89 (sd = 0.014), and the average number of susceptible baitfish purchased was 38 (sd = 42.5). Similar to *O. ovariae* and VHSV scenarios, the simulations for AFT showed highly skewed estimates for the number of risky trips per year (Fig. 2, bottom). On average, there were 256,499 risky trips annually under the low prevalence scenario (AFT-1, SD = 879,064, Table 2) and 70 % of iterations had  $P_{risky} > 0.01$ . In AFT-2, the mean increased to 1,164,475 risky trips annually (SD = 1,693,666) and 96 % of iterations

had  $P_{risky} > 0.01$ . Changes in  $N_{risky}$  were driven largely by number of trips per angler, which corresponded to the highest  $\beta_i$  value in both scenarios (Table 3). In the second phase of sensitivity analysis, we observed similar patterns to *O. ovariae* and VHSV scenarios (Table 4). Changing pathogen prevalence resulted in small ( $< 10$  %) changes in  $N_{risky}$ , and decreasing prevalence by 10 % in the high prevalence scenario AFT-2 resulted in  $< 1$  % change in  $N_{risky}$ . We observed greater decreases in  $N_{risky}$  associated with decreased probability of release, with the greatest magnitude change (12 % reduction) observed when probability of release was decreased by 10 % in the moderate-prevalence scenario (Table 4).

4. Discussion

This study builds on previous hazard identification work to quantify the behaviors that facilitate the spread of invasive pathogens in high-frequency invasion pathways, and estimates the risk of the priority pathogens being introduced by illegal release of live baitfish by anglers. When the necessary data are available, quantitative risk assessments can provide important context for risk-based management by quantifying existing risk and providing a baseline against which to evaluate tradeoffs





**Fig. 2.** Scenario-specific histograms (left) and empirical cumulative density plots (right) depicting results of 10,000 iterations estimating the total number of risky trips during a single fishing season in Minnesota, or trips that result in the release of baitfish infected with viral hemorrhagic septicemia virus (A, top), *Ovipleistophora ovariae* (B, middle), or Asian fish tapeworm (C, bottom). Dashed vertical lines indicate median annual number of risky trips for each pathogen-scenario combination. LS watershed: Lake Superior watershed (U.S. Geological Survey HUC-0507; <https://water.usgs.gov/GIS/huc.html>).

associated with policy alternatives (Mumford and Mark, 2021). Applying our novel risk assessment framework and angler-provided behavioral data, we found that there can be substantial opportunity for fish pathogen introductions via live baitfish release in Minnesota. Indeed, across the three pathogens examined, the majority of model

iterations estimated greater than 1 % of all anglers being risky annually. Given the very high numbers of anglers in the state, even this small percentage presents considerable risk of pathogen introduction via the live baitfish pathway in Minnesota. Surveillance alone was not enough to prevent the spread of regulated pathogens, as demonstrated by

scenarios where simulated prevalence below detection thresholds still caused several thousand introductions annually. The effect was particularly true when the simulated outbreak extended across the entire study area, such as in the hypothetical scenarios where the pathogen was present in three different baitfish species statewide. For pathogens that are not currently regulated in Minnesota, such as the microsporidian *O. ovariae* and the macroparasite *S. acheilognathi*, even higher pathogen prevalence (<20 %) is possible. We estimated that the median number of *O. ovariae* introductions under baseline conditions was over 100,000, and median number of *S. acheilognathi* introductions over 200,000 when pathogen prevalence was under 2 %. For all scenarios, pathogen prevalence was an influential parameter when the number of risky trips was regressed on all inputs. However, because we only modulated the pathogen prevalence by 10 % in the second-stage sensitivity analysis, we did not see large changes in the number of risky trips under most conditions. Modulating the rate of live baitfish release was influential, however, resulting in disproportionate changes in risk, particularly when the geographic extent of the outbreak was large or there were several affected species, or both.

Our approach employs a pathway-based assessment to estimate the risk of pathogen introduction. This is a departure from most of the current regulatory criteria in Minnesota and more broadly in the United States, which are largely focused on trait-based heuristics for identifying potentially harmful invasive species (Kolar and Lodge 2002; Marcot et al. 2019). These trait-based frameworks are an important first step in identifying potential hazards, but stop short of answering important questions about introduction effort or propagule pressure of species. As a result, they fail to assess likelihood and severity of consequences occurring if the potential hazardous outcomes were realized.

Our results highlight the role that human behavioral dimensions play in driving pathogen introduction risk and the importance of including these dimensions in risk assessments for wildlife disease. For invasion pathways with numerous individual vectors, low-probability events can become near certainties (Ludwig and Leitch, 1996; Drake and Mandrak, 2014), and thus modifying risky behaviors becomes a critical task for risk management. We found that human-mediated behaviors had outsized impacts on the number of risky trips for certain scenarios where there were a high number of infected baitfish and/or high number of baitfish anglers implicated. Decreasing release probability by 10 % was associated with >10 % shift in  $N_{risky}$  in all *O. ovariae* scenarios, the statewide VHSV scenarios, and the moderate AFT prevalence scenario. Although the probability of a single angler engaging in risky behaviors is relatively low, as geographic range and prevalence of a pathogen increase, the number of anglers also increases. Under such circumstances, the relative benefit of reducing illegal release behavior may be greater. However, there were some scenarios where the outbreak was limited in geographic scope, species affected, or both. In these cases, reducing the probability of illegal baitfish release by 10 % resulted in less than 10 % reduction in the average number of risky trips annually, indicating release behavior was not a significant determinant of risky trips in those situations. Behavior change campaigns aimed at reducing risky angling behaviors have had mixed success (Cole et al., 2019; Eiswerth et al., 2011; Anderson et al., 2014), and achieving even 10 % reduction in a risky behavior may be challenging (Drake et al., 2015). Managers may therefore experience diminishing returns while trying to achieve 100 % compliance with regulations. As a result, reaching an acceptable level of risk may be impossible if high numbers of anglers are required to make behavior changes in order to accomplish core objectives (Floerl et al., 2016). Our results illustrate the importance of understanding when such measures may accomplish desired management endpoints, and when the risk dynamics of the pathway may be more resistant to moderate changes in human behaviors.

The number of fishing trips taken per angler annually was also a top predictor of the number of risky trips across all modeled scenarios. Even after accounting for outliers, the number of overall trips and trips per season were highly right skewed, with some anglers taking over 100

trips per year. As a result, the behavior of individual anglers had a large effect on the total number of risky trips. Although avid anglers who take many trips each year may represent a unique management challenge considering the increased opportunity for baitfish release, they are also more likely to be aware of invasive species prevention practices (Eiswerth et al., 2011; Seekamp et al., 2016). Nevertheless, this study highlights the importance of targeting high-frequency anglers for AIS prevention messaging to maximize the impact of the outreach efforts.

The study also illustrated the utility of using simulation modeling to evaluate proposed management strategies aimed at reducing pathogen introduction risk. For example, evidence from population genetics would suggest that higher numbers of an invasive species in a source population can support higher additive genetic variation, potentially increasing the potential fitness of the invading species (Ahlroth et al., 2003; Sakai et al., 2001). Reducing the prevalence of a pathogen can limit its evolution potential and fitness, making controlling pathogens in baitfish an attractive management alternative. However, in our study, we found that risk outcomes were generally insensitive to pathogen prevalence. In contrast to the model's sensitivity to the number of trips and probability of release, further reducing pathogen prevalence below baseline levels did not have an appreciable effect on the average number of risky trips in any scenario. Reducing prevalence was most impactful when the pathogen's range is confined to a small proportion or area of live baitfish, such as in the VHSV scenarios. Focusing disease control efforts in areas known to be high risk for pathogen outbreaks or to have high rates of an established disease may be an effective way to reduce the risk of further pathogen spread. Further, the practicality of reducing pathogen prevalence (or disease eradication) can be difficult in aquaculture settings and impossible in wild populations with minimal to no disease testing, and can add to the already substantial regulatory burdens on baitfish producers (van Senten and Engle, 2017). Quantitative risk models informed by real data could facilitate high-quality disease management decisions (Gore et al., 2009; Canessa et al., 2018) prior to implementing costly and potentially ineffective risk reduction strategies, and should be considered by natural resource managers faced with limited resources.

Developing and enforcing regulations may also play a role in reducing the drivers of pathogen introduction risk. Regulatory frameworks can provide the justification and structure for early detection, protection, and control of aquatic pathogens. For example, although Minnesota prohibits the importation of live baitfish (MN State Statute 97C.515), current regulations do not prohibit the movement of live baitfish across political or geographical boundaries within the state. Repeated introductions of a pathogen can result in unstable populations that seed subsequent invasions (Lockwood et al., 2005), so even limited, ephemeral outbreaks of pathogens in localized areas could translate to more widespread risk as anglers frequently travel long distances within the state (McEachran et al., 2022). In our study, we found that the proportion of anglers buying fish from the high-risk Lake Superior watershed was an influential predictor of risky trips, suggesting that even transitory outbreaks in the region could quickly spread to other areas of the state. State fisheries managers should take care to contain known outbreaks of disease in wild sources of live baitfish and consider within-state management interventions on baitfish movement to prevent within-state spread of pathogens that have not yet become established statewide.

There are several limitations and assumptions associated with our assessment of risk, so caution must be taken when interpreting these risk estimates. The various scenarios explored for VHSV and AFT in this study, while not unreasonable, are largely hypothetical and may not represent current reality for these pathogens. Although both VHSV and AFT have not been detected in Minnesota, both pathogens have been detected in baitfish populations in nearby states (Boonthai et al., 2017; McEachran et al., 2021; Faisal et al., 2012) and are capable of establishment, have limited or no active surveillance, and have the potential to be illegally imported into Minnesota, supporting an assumption of

non-zero risk (Escobar et al., 2016; McEachran et al., 2020; McEachran et al., 2022). Additionally, we made an assumption regarding the potential for consequential morbidity and mortality in important fish populations (McEachran et al., 2020), but did not explicitly assess the probability of establishment or consequence following introduction. A next step would be to incorporate these risk factors as part of a comprehensive risk analysis of the live baitfish pathway (Jakob-Hoff et al., 2014; Williams et al., 2013; Morant et al., 2013). Nevertheless, invasion risk is directly proportional to the rate of arriving invasive propagules at an individual location, so quantifying the rate of introduction at the waterbody-level is an important step for understanding the degree to which important fish and ecosystems are at risk (Lockwood et al., 2005; Simberloff, 2009). The high number of risky trips estimated annually in our study warrants a cautious approach and further study to understand the risk of these pathogens becoming established and impacting important fish populations.

Faced with limited resources, it is important for natural resource managers to understand whether the available management alternatives are capable of meeting desired management goals. Managers must not only assess whether interventions (e.g. enforcement) effect the desired change in behavior, but also whether changing behaviors meaningfully reduces pathogen invasion risk. Further work is necessary to understand what factors determine an angler's likelihood of release and how they might be persuaded to change their behavior. Additionally, changes to regulation or policy regarding baitfish use, release, or production should be considered in an integrated theory of change framework that considers the social, psychological, and economic dimensions of angler decision-making in order to provide tailored management recommendations (Wallen and Daut, 2018). The results of this study provide decision support for developing policy alternatives to reduce the risk of fish pathogens being introduced within Minnesota. Quantitative risk analysis is a promising approach for beginning to evaluate with the complex trade-offs and difficult decisions associated with managing emerging invasive species and wildlife diseases in an increasingly globalized world.

## Declaration of Competing Interest

The authors listed on this manuscript do not stand to gain personally, professionally, or financially from its publication and have no competing interests to declare.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.prevetmed.2023.105960](https://doi.org/10.1016/j.prevetmed.2023.105960)

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