

Research Article

Using structured decision making to evaluate potential management responses to detection of dreissenid mussel (*Dreissena* spp.) environmental DNA

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Abstract

Environmental (e)DNA tools are sensitive and cost-effective for early detection of invasive species. However, the uncertainty associated with the interpretation of positive eDNA detections makes it challenging to determine appropriate natural resource management responses. Multiple sources of error can give rise to positive detections of eDNA in a sample when individuals of that species are not present at the site or a widespread infestation is not imminent. Acting on an erroneous eDNA inference could result in needless costs or reductions in desirable resources. Alternatively, failure to rapidly act on eDNA results that truly indicate invader presence could compound negative impacts and lead to high, long-term costs to manage infestations. We used a structured decision making (SDM) process, which incorporates tradeoffs and uncertainties, to evaluate appropriate response actions following hypothetical eDNA detections of invasive dreissenid mussel (*Dreissena* spp.) eDNA in Jordanelle Reservoir, Utah (USA). We worked with decision-makers and stakeholders to identify objectives and discrete management action alternatives to assess consequences and tradeoffs. Alternatives ranged from no action to intensive and expensive control efforts. The best performing alternative was delayed containment described by immediate attempts to confirm the eDNA detections using non-molecular sampling techniques followed by mandatory watercraft exit inspections to prevent dreissenid mussel spread to regional water bodies. Non-molecular sampling increased public support for management by demonstrating a commitment to monitor the invasion state before action, whereas containment decreased likelihood of regional spread to other waters. Delayed containment had the lowest downside risk, and the highest upside gains relative to other alternative actions. Sensitivity analyses showed our results to be robust to parameter and outcome uncertainty.

Key words: containment, decision support, early detection, invasive species, rapid response, reservoir, risk

Introduction

Early detection-rapid response (EDRR) is a guiding principle for minimizing the impacts of invasive species in a cost-efficient manner (Reaser et al. 2020). The longer an infestation goes undetected and untreated, the more likely it is to spread and reach abundances capable of causing impact. Control efforts become more expensive and less effective for larger and widespread populations. The scientific literature is replete with examples of costly invasions that were only detected after they spread considerably, including dreissenid mussels (*Dreissena* spp.) in North America (Kelly et al. 2009) and lionfish (*Pterois* spp.) in the western Atlantic and Caribbean (Schofield 2009). Far fewer examples exist of successful EDRR because of a lack of effective early detection tools and multiple impediments to act once detection occurs (Reaser et al. 2020; Simberloff 2014).

Environmental (e)DNA methods are recognized as a highly sensitive and cost-effective toolset for invasive species early detection (Morisette et al. 2021). Environmental DNA methods sample for DNA released by an organism into the environment (e.g., water, soil, air; Pawlowski et al. 2020). Detections of eDNA enable inference about invasive species presence at a site. However, site-level inferences are uncertain because multiple sources of error can give rise to positive detections of eDNA in a sample when that species is not present at the site, and less sensitive, traditional methods with a higher false negative rate cannot be used for timely corroboration (Darling et al. 2021). Late detection has the potential to allow an incipient population to become established and prevent any practical control efforts. Alternatively, acting on an erroneous eDNA inference could result in needless costs and potential inconvenience to users of the resource. Moreover, there is no guarantee that timely response actions will effectively control the invader (Pluess et al. 2012). Managers need decision support tools to navigate this uncertainty and integrate eDNA methods into current EDRR frameworks.

Decision making under uncertainty is a norm in most disciplines, including natural resource management. Structured decision making (SDM) has emerged as a toolset that is adept at guiding natural resource decisions in complex socio-ecological systems characterized by uncertainty and competing objectives (Runge et al. 2020). A key feature of SDM is the decomposition of decision problems into the essential components to evaluate options relative to the desired outcomes. A coherent decision process increases the odds of meeting fundamental objectives. For example, managers have used SDM to guide decisions about proactively managing wild bighorn sheep (*Ovis canadensis*) pneumonia die-offs in Montana (USA) when the probability of a future pneumonia die-off is uncertain (Sells et al. 2015). Invasive species managers have also used SDM to develop a response plan for the invasion of myrtle rust (*Uredo rangelii*) in

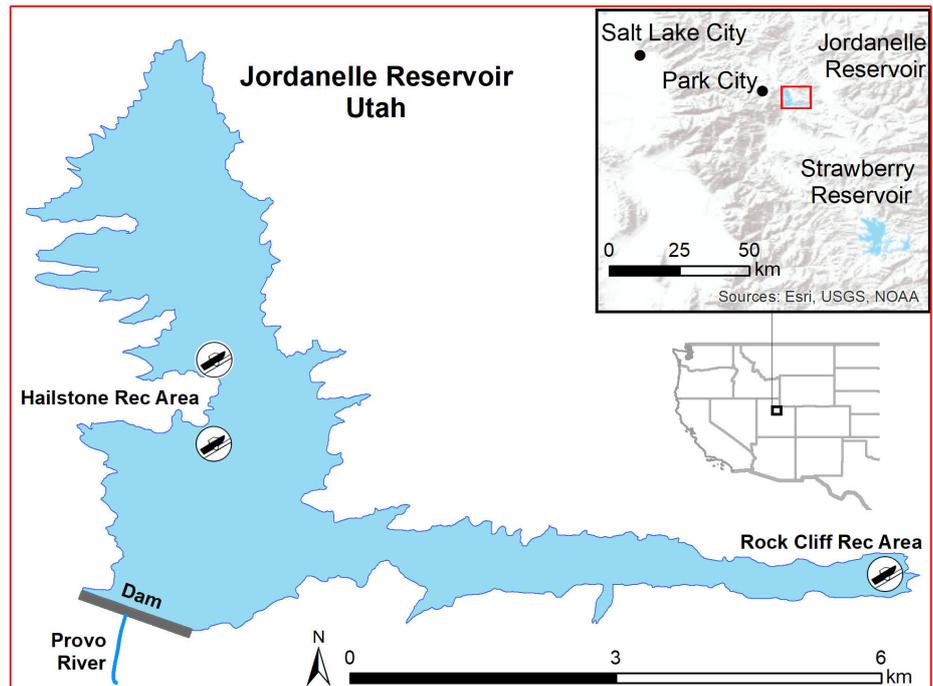


Figure 1. Map of Jordanelle Reservoir, which is to the east of Salt Lake City, Utah, USA (inset map).

Australia, even though they had limited knowledge about its ecology and the effects of response actions (Liu et al. 2012).

Here, we present a case study using SDM to help managers evaluate appropriate response actions following hypothetical eDNA detections of invasive dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) in a waterbody where dreissenid mussels are not known to occur. Our case study was intended to be representative of the larger challenges faced by managers of how to best respond to eDNA detections in the face of uncertain invasive species presence. For this process, the hypothetical detections occurred in Jordanelle Reservoir (Figure 1), which is located near Salt Lake City, Utah (USA) and provides important recreation value and critical water delivery, water storage, and power production to > 1,000,000 people. Recreational boating is the primary pathway by which dreissenid mussels spread to uninvaded waters since mussels can become entrained on watercrafts and watercraft equipment (De Ventura et al. 2017; Johnson et al. 2001). Thus, any response action is likely to have considerable socio-economic costs through inconvenience to recreational watercraft users, but delayed response that allows an invasion to proceed unchecked would likely have an even greater cost to all users. This is a similar scenario as the initial eDNA detections of invasive carp (*Hypophthalmichthys* spp.) in the Chicago Sanitary and Ship Canal that connects the invasive carp-invaded Mississippi River basin to the uninvaded Great Lakes, which is home to important fisheries and provides drinking water to 40 million people (Jerde 2021).

To clarify the selection of dreissenid mussels in this exercise, we briefly summarize the challenges associated with invasive dreissenid mussel management in western North America. Dreissenid mussels are not widely

Table 1. Decision-makers and stakeholders involved with the Jordanelle Reservoir structured decision making process.

Entity	Acronym	Authority	Representatives
U.S. Bureau of Reclamation	USBR	Water right management, dam safety and title to the Dam	Brittany White, Fish & Wildlife Biologist
Central Utah Water Conservancy District	CUWCD	Water storage, delivery, and hydropower production	Gene Shawcroft, General Manager Mike Rau, Water Quality Manager Joe Crawford, Water Quality Scientist Erik Cram, Lab Manager
Utah Div. of Wildlife Resources	UDWR	Management of the fishery and administration of watercraft inspection stations	Nathan Owens, Aquatic Invasive Species Coordinator Skylar Wolf, Research Biologist
Utah Div. of Parks & Recreation	UDPR	Management of project lands and recreation activities	

distributed in this region, yet they present difficult management and political challenges due to the magnitude of their impacts and the socio-economic and ecological importance of western waters (U.S. Department of the Interior 2017). Consequently, dreissenid mussel detections can result in strong reactions by politicians, managers, and the public. For example, the visual detection of dreissenid mussel larvae in Montana's Tiber Reservoir in 2016 led to states and federal agencies reallocating tens of millions of dollars to mussel prevention and early detection efforts across the Pacific Northwest.

We formed a collaborative team for our SDM case study. Managers with decision-making authority worked to address value-based tasks while technical experts focused on scientific tasks within the 5 constituent elements in our SDM process: (1) problem framing, (2) objectives identification, (3) a set of alternatives to choose from, (4) estimating the probable consequences of each alternative, and (5) an evaluation of the trade-offs among the alternatives.

Materials and methods

Study area

Our case study focused on Jordanelle Reservoir (hereafter JR, Figure 1), a waterbody that is ~ 60 km away from Salt Lake City, Utah (USA). The reservoir is fed and drained by the Provo River and is impounded by the Jordanelle Dam. JR has 40 km of shoreline, a surface area of 1,336 hectares and a volume of $4.445 \times 10^8 \text{ m}^3$ at capacity. The reservoir provides many services for the Salt Lake City metropolitan area (population > 1,200,000) including drinking, industrial and agricultural water, hydropower production, water storage and delivery, and recreation (e.g., fishing, boating, camping). Multiple entities have management responsibilities at JR and its dam (Table 1). Given evidence of a dreissenid mussel introduction, the Utah Division of Wildlife Resources (UDWR) would assume the lead for all rapid response actions at the reservoir and Central Utah Water Conservancy District (CUWCD) would lead any actions at the dam facility.

Dreissenid mussels are not currently known to occur in JR, but this waterbody is at high risk to introduction and establishment, especially

through spread from recreational boating. JR is one of the region's most popular state parks for boating recreation and received almost 1 million visitors in 2020, largely due to its proximity to the Salt Lake City metropolitan area. Moreover, many of the boats launched at JR have recently been used in mussel-infested waters in the region, including Lake Powell (southern Utah, ~ 500 km away) that is extremely infested by mussels. The state of Utah has several regulations in place to prevent mussel spread, including mandatory watercraft inspections and pulling of watercraft drain plugs during transport and storage, and compliance is thought to be high. The JR has water chemistry conditions that are suitable for dreissenid mussel life history, including dissolved calcium concentrations > 20 mg/L (Whittier et al. 2008); thus, if dreissenid mussels were introduced, they would have the potential to establish and thrive.

Decision Analysis Framework and Model Development

U.S. Geological Survey decision analysts and technical experts (n = 8) worked with representatives from the U.S. Bureau of Reclamation (USBR, n = 1), UDWR (n = 2), and CUWCD (n = 3) to frame the management decision problem and define the 5 constituent elements in our SDM process (Table 1). These representatives either had decision-making authority or were selected as proxies by organizational decision-makers. The problem statement contained the background to establish the fundamental and means objectives of the decision problem. Fundamental objectives define what managers with decision-making authority ultimately value, whereas means objectives provide a pathway for achieving the fundamental objectives (Keeney and McDaniels 1992). We used these objectives to create a set of management alternatives for responding to eDNA detections of invasive mussel DNA. We built a population model to evaluate the effect of each management alternative on invasive mussels in JR. We then used a multi-attribute reward function that included the results of the population model, expert opinion, and decision-maker/stakeholder values to determine the management alternative that best achieved the multiple objectives. This working group met virtually for 2 hr every 1–2 weeks, from January–March 2020.

Problem statement

The working group's focus was on actions following eDNA detections because dreissenid mussel eDNA protocols are established (Goldberg et al. 2016; Sepulveda et al. 2019a, b). We assumed that a response action would only be triggered following > 1 eDNA detection in a sampling season per Sepulveda et al. (2019b). The working group acknowledged that eDNA detections indicate the presence of target DNA in a sample and that there is uncertainty about inferring presence of the target organism at the site.

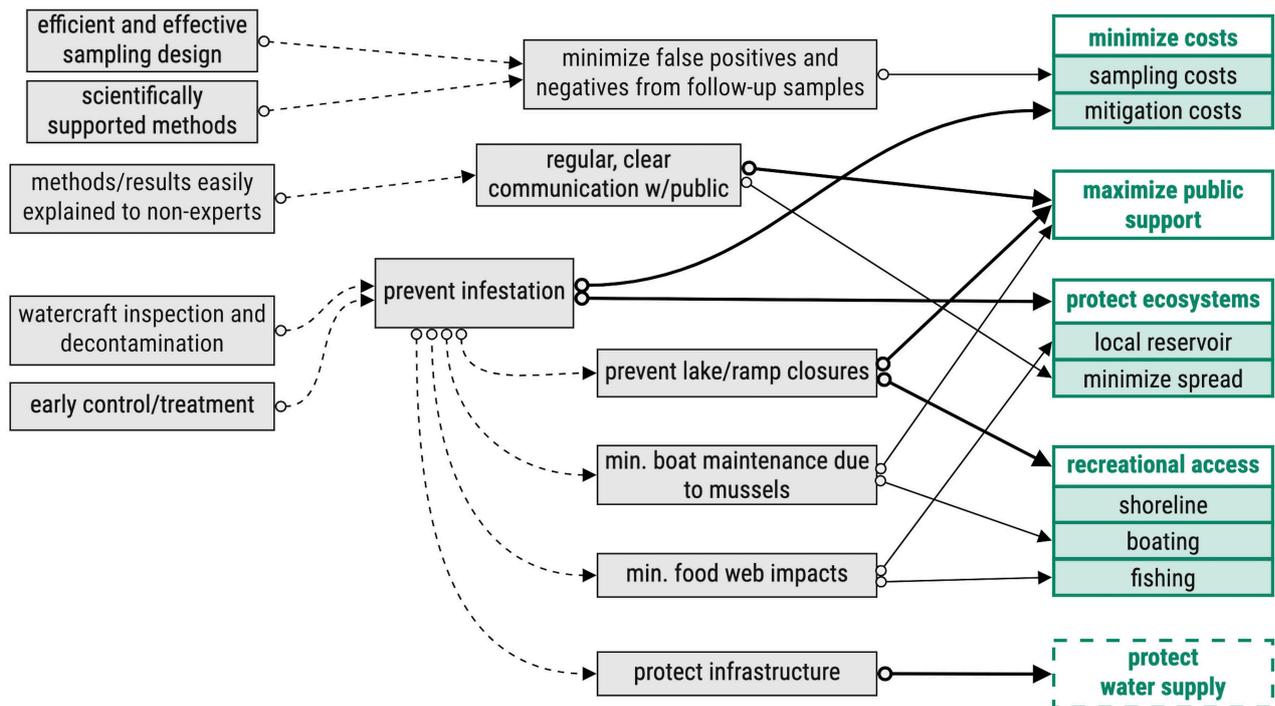


Figure 2. Hierarchy of objectives and means-ends schematic that illustrate how constraints (dotted green box), fundamental objectives (green boxes) and sub-objectives (filled green boxes) might be achieved by means objectives (grey boxes). Thicker arrows represent linkages that had strong agreement among participants.

Decision-makers and stakeholders identified the problem as: “What are the appropriate immediate and long-term actions to take following multiple detections of dreissenid mussel eDNA”. Immediate actions are those that occur within weeks of multiple positive eDNA detections and long-term actions are those that occur up to 8 years later. Eight years was selected as the time window because (1) dreissenid mussels are likely to transition to higher levels of abundance capable of negative impacts within 8 years of introduction (see Probability of Infestation section below and Strayer et al. 2019); and (2) financial costs of alternative actions after 8 years became indistinguishable in this case study.

Objectives

The working group developed a means-end diagram (Figure 2) to help identify five fundamental objectives (listed below in no particular order). The importance weights, attributes, and units for each fundamental objective are described in Table 2.

1. *Protect the water supply.* Invasive mussels threaten the water supply by attaching to and clogging up (fouling) water intake and delivery pipes. USBR and CUWCD are mandated to provide municipal, industrial, and agricultural water to meet demand. This objective is a constraint, so any alternative action cannot affect this objective.
2. *Protect the ecosystem.* Invasive mussels can have detrimental impacts to ecosystem structure and function by affecting the energetic resources available to higher trophic levels (Higgins and Zanden 2010). Actions

Table 2. Objectives, attributes, importance weights, and performance measures for the Jordanelle Reservoir structured decision making process. Two attributes were assigned importance weights of 0 because they were deemed to be constraints or triggered by the eDNA detection, so did not vary across actions, infestation state, or time. The remaining attributes varied across actions, infestation state, or time.

Objectives	Attribute	Weight	Direction	Unit
1. Protect water supply	Satisfy user demand	0	Constraint	% required supply delivered
2. Protect the ecosystem	Spatial extent of an infestation in Jordanelle Res.	1	Minimize	% area infested
	Spread to other water bodies	8	Minimize	Likelihood of spread
3. Maintain recreation	Boat ramp closures	4	Minimize	Ramp-days
4. Maintain public support	Level of support	10	Maximize	5-point scale
5. Minimize costs	Capital: infrastructure retrofit	0	Minimize	US\$
	Operating: response management & sampling costs	2	Minimize	US\$

- that minimize the spatial extent of infestation in JR and the likelihood of spread to other waterbodies will help to protect the ecosystem.
3. *Provide recreation access.* JR is a state park that is managed for recreational opportunities, including boating and fishing. Maintaining public use of boat ramps is required in order to continue to provide sufficient water-based recreational opportunities. Limited and prolonged boat ramps closures would be required for many containment and control actions.
 4. *Maximize public support of UDWR's aquatic invasive species program.* The success of UDWR's efforts to prevent, contain and control invasive species in Utah is contingent on public support. A supportive and engaged public not only does a better job self-policing to ensure that their actions do not exacerbate invasive species problems, but also increases the potential that legislators will allocate adequate funding to invasive species programs.
 5. *Minimize financial costs.* Decision-makers have limited financial resources and they must allocate these resources across multiple programs and waterbodies. Mussel containment and control actions can be costly and contribute to budget shortfalls (Chakraborti et al. 2016). Increasing invasive species containment and/or control efforts at one waterbody could result in reduced efforts at another.

Alternatives

The number of potential alternative actions is so large as to be impractical to list. Thus, we adopted a common approach of identifying a tractable set of alternative actions that spans the range of possibilities, providing contrasts among the alternatives, which are expected to generate valuable insights about the inherent trade-offs in the decision (Gregory et al. 2012). First, we mapped alternative actions to two discrete decision points (Figure 3). Decision point 1 (DP1) includes the alternative actions that follow the eDNA detections and consisted of: (1a) Attempts to confirm the eDNA detections using non-molecular sampling techniques; (1b) Containment efforts using mandatory watercraft inspections upon exiting JR; or (1c) Containment + control efforts (could include chemical or physical).

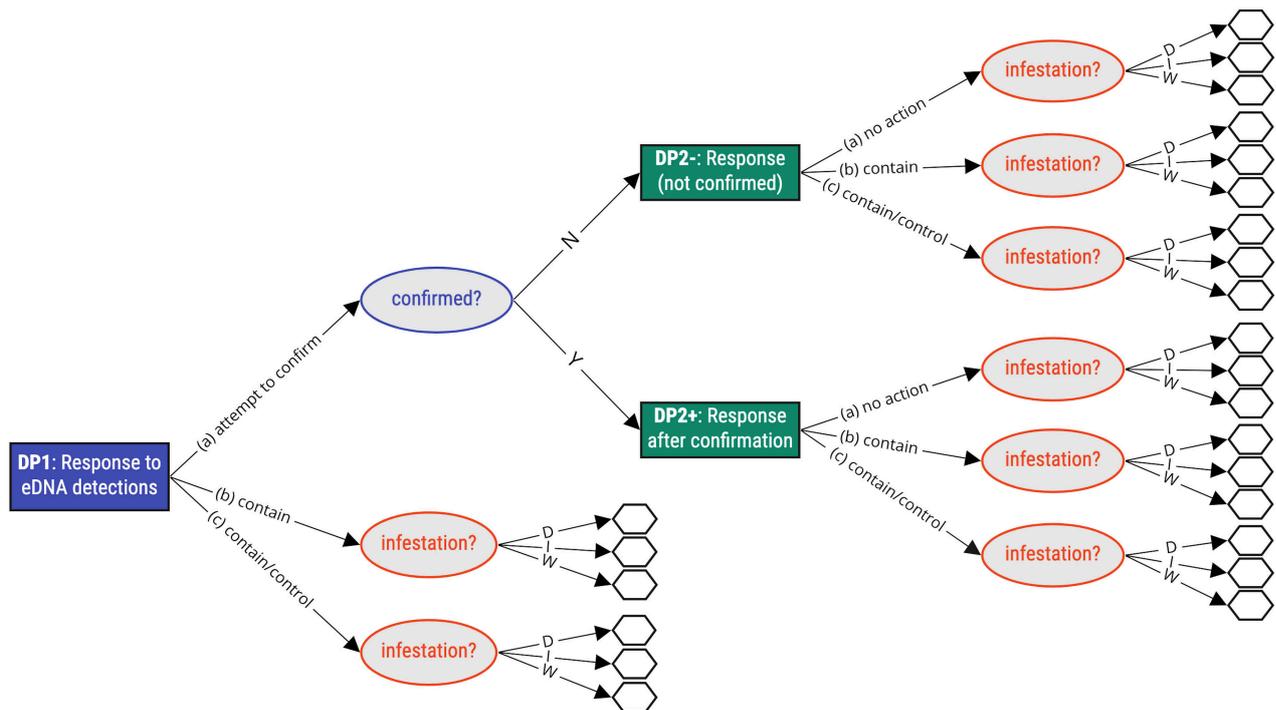


Figure 3. Annotated decision tree that describes the alternative actions following decision points (DP) 1 and 2 and probabilistic outcomes. Hexagons indicate the likelihood of the dreissenid mussel infestation state (*D*) eDNA presence only or non-reproducing individuals; (*I*) Isolated areas of reproduction or (*W*) Widespread infestation given the alternative action.

Decision point 2 (DP2) includes the alternative actions that follow if 1a (sampling with non-molecular methods) is selected and containment or control actions are delayed. Alternative actions were evaluated if attempts to confirm eDNA detections fail because no dreissenid mussels are observed; or if attempts succeed because dreissenid mussels are observed. The three alternative actions were: (2a) No action; (2b) Delayed containment; and (2c) Delayed containment + control efforts.

Non-molecular sampling efforts were evaluated at four levels of intensity (Table 3). Baseline sampling intensity assumed one plankton tow sampling survey per month for six months. Low intensity sampling included plankton tow sampling for dreissenid mussel veligers twice per month, moderate intensity consisted of sampling three times per month and high intensity included two additional times per month plus SCUBA and remote operated vehicle (ROV) surveys. Costs increased proportionally with the level of sampling intensity.

Containment actions followed standard procedures for dreissenid mussel detections in Utah, which are consistent with procedures used by most western states (Western Regional Panel on Aquatic Nuisance Species 2019). Inspections would be required for all watercraft leaving JR at the two boat ramps located at Hailstone Recreation Area (Figure 1). The third boat ramp at Rock Cliff Recreation Area (Figure 1) would be permanently closed since it is not feasible to operate a watercraft inspection station at that location.

Chemical and physical control actions were considered, but we ultimately selected chemical control, which was the least expensive option,

Table 3. Consequence table describing the typical-case (median) outcomes for each alternative action at the start of the 2nd-year based on the likelihood of mussels being in states (*D*) eDNA presence only or non-reproducing individuals; (*I*) Isolated areas of reproduction or (*W*) Widespread infestation. Colors indicate the objective outcome ranking relative to the 5 management response actions, green = best, gold = middle, red = worst. Outcomes when dreissenid mussels are confirmed with non-molecular sampling are only shown for the public support objective, as confirmation success only influenced this objective's potential outcomes. Further description of attributes, units, and importance weights are in Table 2.

Objective	Attribute	Units	Confirm	State	Typical-case				
					Contain (1b)	Contain + control (1c)	No action (2a)	Delay contain (2b)	Delay contain+ control (2c)
Water supply	Meet demand	% delivered	–	<i>D</i>	100	100	100	100	100
				<i>I</i>	100	100	100	100	100
				<i>W</i>	100	100	100	100	100
Ecosystem	JR infestation	% area infested	–	<i>D</i>	0	0	0	0	0
				<i>I</i>	20	10	40	40	20
				<i>W</i>	20	10	40	40	20
	Spread to other waters	Likelihood of spread	–	<i>D</i>	2.5E-08	2.5E-08	1.6E-01	2.5E-08	2.5E-08
				<i>I</i>	1.8E-02	1.8E-02	4.5E-01	1.8E-02	1.8E-02
				<i>W</i>	9.8E-02	9.8E-02	8.3E-01	9.8E-02	9.8E-02
				Utility	<i>D</i>	1.00	1.00	0.85	1.00
			<i>I</i>	0.98	0.98	0.64	0.98	0.98	
			<i>W</i>	0.91	0.91	0.44	0.91	0.91	
Recreation	Number of closures	Ramp days	–	<i>D</i>	182	208	0	167	191
				<i>I</i>	182	208	0	167	191
				<i>W</i>	182	208	0	167	191
Public support	Level of support	5-point scale	Yes	<i>D</i>	3.1	2.6	2.7	3.8	3.9
				<i>I</i>	3.0	3.1	1.8	3.2	3.3
			Yes	<i>W</i>	3.0	3.1	1.8	3.2	3.3
				<i>D</i>	3.1	2.6	3.1	3.2	2.5
			No	<i>I</i>	3.0	3.1	2.3	3.5	3.1
				<i>W</i>	3.0	3.1	2.3	3.5	3.1
Costs	Capital	\$US * 1000	–	<i>D</i>	750	750	750	750	750
				<i>I</i>	750	750	750	750	750
				<i>W</i>	750	750	750	750	750
	Operating	\$US * 1000	–	<i>D</i>	410	3660	8	376	3626
				<i>I</i>	410	3660	8	376	3626
				<i>W</i>	410	3660	8	376	3626

for the analysis. We estimated costs of entire lake and partial lake chemical treatments using a copper sulfate product called EarthTec QZ at US\$0.06 per cubic meter (Hammond and Ferris 2019). Entire lake volume was based on the lowest record volume at JR that met the constraint of providing water supply. Partial lake treatments only covered the bays where boat ramps were located. Bathymetric maps are not available, so we assumed the minimum surface area: minimum volume relationship of these bays was the same as the minimum surface area: minimum volume relationship for the entire lake.

Predicting Consequences

We used models and expert opinion to predict the consequences of each alternative for each objective. Consequences were estimated based on the following outcomes: (1) If 1a was selected, the eDNA detections were confirmed or not, and (2) as a function of the alternative actions, dreissenid mussels probabilistically transitioned among infestation levels or demographic states in JR. In the proceeding sections, we describe how

we estimated these outcomes and how we estimated consequences of each alternative contingent on these outcomes. To evaluate if the optimal decision was affected by the decision time horizon, we estimated consequences from 1 to 8 years after the initial eDNA detections. The consequences were accumulated over time as one-time or total measurements, annual metrics summed over years, or year-specific measures as appropriate.

The consequences depended potentially on action type, state of the infestation, and time since eDNA detection. Two of the attributes did not vary because they were deemed to be constraints or triggered by the eDNA detection. Protecting water supply was a constraint; thus, 100% of demand would be met regardless of action. Infrastructure retrofitting (e.g., replacement with larger diameter pipes that minimize potential of mussel fouling to impact water delivery) would be triggered by eDNA detection; thus, capital expenditure would be the same for all actions regardless of state. However, the potential capital cost ranged from 0.5 to 1 million \$USD. The remaining attributes varied across actions, infestation state, or time. Annualized operating expenses associated with management and monitoring increased steeply with action and varied to a minor degree on sampling intensity.

Probability of confirming eDNA detections

We used dreissenid mussel veliger detection probability estimates from Winder et al. (*in review*) as a starting place for considering the probability of confirming eDNA detections. Winder et al. (*in review*) used multi-season occupancy models to analyze dreissenid mussel veliger plankton tow survey data from across the western United States (2012–2020), which included 11,442 samples from 302 distinct lakes. Plankton tow surveys are the standard for early detection of dreissenid mussels across the western United States (Western Regional Panel on Aquatic Nuisance Species 2019). Water and debris are collected using a 64- μ m mesh plankton tow net; debris from each of 5 tows are aggregated into a single composite sample. Cross-polarized microscopy is used on composite samples to scan for dreissenid mussel veligers. Winder et al. (*in review*) estimated the mean (\pm 97.5% credible intervals) detection probability (p) as 0.0382 (0.0078–0.0749). These estimates are in line with those from Lake George (New York), where zebra mussels occur at very low abundance (Frischer et al. 2005). We calculated the cumulative probability of detection (p^*) for different sampling intensities as,

$$p^* = 1 - (1 - p)^n,$$

where p is the mean detection probability from Winder et al. (*in review*) and n is the number of samples (Supplementary material Table S1).

Probability of an infestation

We created a state-based simulation model to predict the state of the dreissenid mussel infestation of JR following eDNA detections (Figure S1).

Invasion states included (*D*) presence of eDNA or non-reproducing individuals; (*I*) isolated areas of reproduction or (*W*) widespread infestation. Importantly, dreissenid mussels, especially non-reproducing individuals, may be present in invasion state *D*, however presence is difficult to observe because they are rare. JR is routinely monitored for dreissenid mussels, so it is more likely that invasion state would be *D* rather than *I*, and *I* than *W*. Beginning at year 1 (immediately after eDNA detections), we assumed that $D = 0.90$, $I = 0.10$, and $W = 0$. We simulated annual transitions for each alternative for 8 years using two contrasting scenarios of dreissenid mussel population dynamics, given that there is uncertainty about how rapidly an invasion would establish and spread (Karatayev et al. 2015).

The first scenario assumed rapid spread since dreissenid mussels can become sexually mature in the 1st-year of life and have fecundities that range from 30,000 to 1,610,000 eggs per female (Mackie and Schloesser 1996). Rapid spread within an invaded waterbody is the expectation for zebra mussels, as the time between when they are first detected in a waterbody and when they reach maximum population size is ~ 2.5 years (Karatayev et al. 2011). Indeed, zebra mussels constituted > 70% of the zoobenthic biomass only 17 months after their first detection in the Hudson River, New York (Strayer et al. 1999). In the “rapid spread” scenario, we assumed that the annual transition probabilities from *D* to *D* and from *D* to *I* was 0.50, from *I* to *I* was 0.95, from *I* to *W* was 0.05, and from and *W* to *W* was 1.00.

The second scenario was more conservative and assumed that most introductions fail, and if they do succeed, then they take a relatively longer time to reach widespread infestation levels than expected under the rapid spread scenario. For the second scenario, we applied the “rule of 10s” (Williamson and Fitter 1996) which assumed a 0.10 probability of transition between infestation states *D*, *I* and *W*. Thus, annual transition probabilities from *D* to *D* and *I* to *I* were 0.91, from *D* to *I* and *I* to *W* were 0.09, and from *W* to *W* were 1.00.

For each scenario, we simulated how control actions (alternatives 1c and 2c) might affect annual transition probabilities. We assumed that the amount of time that elapsed between DP1 and DP2 was 4 weeks, which is not enough time to transition from presence only to widespread infestation (i.e., states *D* to *W*) since mussels have not had adequate time to reproduce in this dimictic reservoir which is ice-covered during the winter. We also assumed that no action (2a) and containment (1b, 2b) alternative actions had no influence on the mussel invasion state within JR; containment affects spread but not infestation within the reservoir. Under rapid spread, control actions affected the invasion stage transitions as follows: D to $D = 0.90$, D to $I = 0.10$, I to $D = 0.70$, I to $I = 0.25$, I to $W = 0.05$, W to $I = 0.2$ and W to $W = 0.80$ (transitions D to W and W to $D = 0$). Control actions

were assumed to be slightly more effective for the “rule of 10s” scenario since control actions are usually more effective when invader abundance is low. Invasion stage transitions were the same as those used in the rapid spread model with the exception that I to I was 0.3 and I to W was 0.

Protect the ecosystem

Spread within JR. Decision-makers and stakeholders familiar with the JR physio-chemical attributes forecasted the percent area infested (Table 1). Dreissenid mussels were expected to infest less than half of JR within eight years, since it is a steep-sloped and deep reservoir with mean and maximum depths of 33 m and 89 m. The maximum depth is within the known limits for dreissenid mussels, especially quagga mussels which have higher growth rates than zebra mussels in colder, deeper waters (Karatayev et al. 2015). However, mussel settlement may be reduced at depths below 32 m (Muetting et al. 2010), and the more favorable but limited, littoral areas of JR are exposed to freezing temperatures and desiccation during reservoir drawdowns each fall and winter. For outcomes where mussels failed to successfully invade, the area infested was 0%. Successful invasions resulted in predictions of 10% to 40% area infested. We assumed that the delay caused by attempts to confirm with non-molecular tools would result in increased percent area infested. If 1a (confirm with non-molecular) was selected, the area infested for 2a and 2b was 40% and the area infested for 2c was 20% regardless of the outcome of confirmation. If rapid response actions were taken following eDNA detection, the area infested for 1b was 20% and for 1c was 10%.

The expected area of an infestation within JR depended on infestation state and action implemented. The spatial extent was 0% for all alternative actions when mussels remained in state D . Only control actions affected area of an infestation. When the mussels transitioned to states I or W , the spatial extent was minimized when control + containment occurred at DP1, moderately reduced when control + containment was delayed until DP2 (~ four weeks), and not reduced when taking no action or only containment actions.

Spread outside JR. We used empirical data and literature values to simulate the potential for spread outside of JR (Table S2). For this exercise, we focused on the risk to Strawberry Reservoir (Utah), a premier recreational trout fishery 70 km away from JR. We used an event-tree simulation model (Gregory et al. 2012) conditional on the dreissenid mussel state (D , I , or W) to estimate the annual probability that dreissenid mussels from JR would be transported overland on watercraft and establish in Strawberry Reservoir (Figure S2). The event-tree model followed the framework proposed by De Ventura et al. (2016). Annual establishment probability in Strawberry Reservoir was a function of (1) the annual number of watercraft

being transported to Strawberry Reservoir from JR ($n = 515$) based on UDWR watercraft inspection data in 2020; (2) the probability of mussel fouling of the watercraft conditional on boat type; (3) if fouled, the number of mussels on the watercraft; (4) the probability of fouled watercraft being stopped by watercraft inspection stations when leaving JR and prior to launching at Strawberry Reservoir; (5) the probability that individuals are compliant with laws that require self-inspection for mussels and cleaning prior to re-launching (e.g., Clean, Drain, Dry); (6) the average number of live mussels that detach from a boat after rewetting in a recipient environment; and (7) the probability of mussel establishment given introduction. For function (2), watercraft types more likely to be moored for multiple days (e.g., cabin-cruisers) or those that are more difficult to inspect (e.g., wakeboard boats) were deemed “higher risk”, while watercraft types associated with day-use and uncomplicated to inspect were deemed “lower risk” for mussel fouling (De Ventura et al. 2016).

We simulated the event tree 100 times each for 515 watercraft traveling from JR to Strawberry Reservoir under “no action”, “containment”, and “containment and control” alternative actions assuming that JR is in state *D*, *I*, or *W*. We modeled the probability that the watercraft is effectively inspected (i.e., if mussel-fouled boats were decontaminated) when exiting JR for alternative actions that included containment, but ignored this step for no action. The probabilities of being fouled and of detaching alive into Strawberry Reservoir were drawn from beta distributions based on shape parameters derived from the mean and standard deviations (Table S2). The number of mussels on a fouled boat were drawn from a random distribution derived from the mean and standard deviation (Table S2). All other variables were randomly sampled according to the proportions provided in Table S2. Finally, we used a general model from Leung et al. (2004) to estimate the probability of population establishment based on the number of mussels that detached. We used the “Allee Model” with $c = 2$ and α value drawn from a normal distribution with a $\mu = 0.0050$ and $\sigma = 0.0025$.

The model-based probability of regional spread depended on the infestation state and whether containment was implemented. The probability of regional spread was high (mean probability = 0.8) once the infestation became widespread (state *W*) and was equally likely as not (mean probability approximately 0.5) for the initial stage of an infestation (state *I*). The probability of spread was converted to a utility score between 0 and 1 to account for the non-linear relationship between this attribute and the working group’s expressed concern and risk attitude regarding regional spread. Utility scores were determined by eliciting the decision-makers’ and stakeholders’ preference for fixed outcomes vs gambles that could potentially reduce or increase the spread of dreissenid mussel in Utah (cf probability equivalence method; Goodwin and Wright 2014). There was

consensus, as all pertinent working group participants expressed a similar utility curve regarding the potential for spread to other reservoirs.

Maintain recreation

We used the number of boat ramp closures as the attribute for this objective. No action would result in 0 closures. Containment and containment + control actions would result in the temporary (daily) shutdown of the two primary boat ramps and seasonal (monthly) shutdown of a third boat ramp. The primary difference between DP1 and DP2 alternatives is the length of the seasonal closure. DP2 alternatives that delay decisions until non-molecular confirmation attempts have occurred would result in a multi-week delay relative to DP1.

Potential ramp closures were annualized and increased with action but were primarily determined by the containment action. Recreational access was maximized in the no action alternative since no boat ramps were closed. Containment resulted in moderate losses to recreational access with reduced access when containment occurred at DP1 rather than DP2. Containment + control resulted in the greatest loss of access similarly for DP1 and DP2.

Public support

Public support of natural resource management actions emerges from complex individual and social reactions to policies and outcomes (Novoa et al. 2017). In this process, decision-makers used two proxies for public support: compliance with watercraft inspections and appropriated funding. We defined 5 levels of public support as follows: 1 = decrease in compliance and appropriated funding; 2 = decrease in compliance but no decrease in appropriated funding; 3 = no change in compliance or appropriated funding; 4 = increase in appropriated funding and compliance when inspection is enforced; 5 = increase in appropriated funding and compliance when inspection is not enforced.

We relied on expert judgment of the decision-makers and stakeholders to gauge the public support that would result from each course of action and resulting infestation state. To incorporate the uncertainty in the predictions, decision-makers (experts) distributed 100 points across the 5 public support levels to indicate their strength of belief that the actual public support would fall within each of the 16 action/state combinations. Experts completed this elicitation for 3 time points (1, 3, and 8 years after initial eDNA detection), and a linear interpolation was used to calculate annualized public support.

Public support of management was year-specific and depended on infestation state, action, and whether the initial detection was confirmed. Public support was the only attribute that varied with non-molecular

confirmation of the eDNA detection because confirmation does not alter the infestation but can affect the public perception of management. Public support of management ranged from 1.8 to 3.0 when mussels were confirmed, and 2.3–3.5 when mussels were not confirmed using non-molecular sampling (Table 3). Under both scenarios, infestation states of *I* or *W*, along with the alternative of no action, were expected to result in low levels of public support.

Minimize costs

Capital. Given the potential for a mussel invasion, CUWCD would take mitigation actions (e.g., retrofitting with larger diameter pipes) to ensure that water storage, delivery and hydropower generation are maintained at the mandated level. Mitigations costs include a \$750,000 initial investment with \$30,000 in cleaning and maintenance costs each year thereafter. CUWCD assumes that it will have to do this retrofit at some point in the future in case mussels are introduced, so eDNA detections would fast track this investment. Consequently, the costs were the same across all alternatives.

Operating costs. The UDWR estimated the annual costs of non-molecular sampling as \$8,000, which includes plankton tow sampling (twice per month; \$5400), scuba (6 divers, 2 events; \$2400) and settlement plates (6 plates; \$360). The annual costs of two mandatory watercraft inspection stations, which includes personnel and infrastructure, when exiting JR plus public outreach would total \$410,000. Control efforts consisting of an Earthtec QZ molluscicide application to only the bays where boat ramps are located would cost \$1.5 million. Annual non-molecular sampling cost would vary with sampling intensity when included as an option. Thus, the no action alternative had the lowest costs and DP1 and DP2 containment + control alternatives had the highest costs, regardless of infestation state.

Trade-off Analyses

We calculated the expected cumulative performance of each alternative. First, decision-makers and stakeholders collectively assigned importance weights to each objective accounting for the range of consequences. Second, we normalized the attributes linearly to a numeric scale where 0 is the worst and 1 is the best. Third, we averaged the attributes for each action across infestation states and time since eDNA detection. Fourth, we combined the attributes into a cumulative reward for each action by a linear weighted average, where the weights reflect the importance managers placed on each attribute (Table 2). Last, we calculated the expected overall performance of each alternative as the sum product of outcome conditioned on infestation state and the probability of infestation state. The alternative with the greatest expected overall performance was considered the optimal

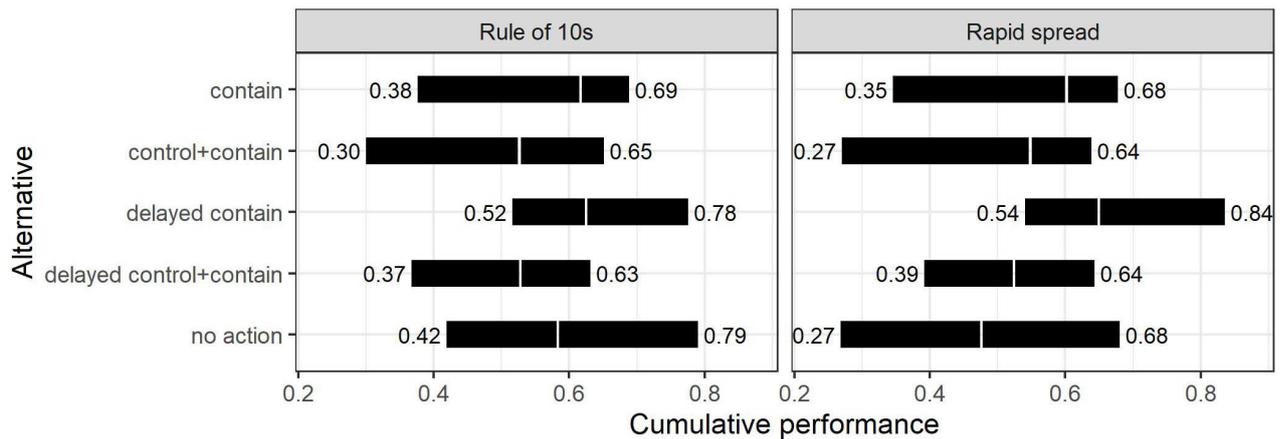


Figure 4. Tornado plots of multi-attribute utility scores of alternative actions after 8 years conditional on non-molecular sampling confirming or not confirming dreissenid mussels. For each scenario combination, objective attributes representing the worst case (10th percentile), typical case (median), or best case (90th percentile) estimates were used as inputs.

decision. For this case study, delayed containment (alternative 2b) had the highest expected cumulative performance across time and regardless of confirmation (Figure 4).

We evaluated how uncertainty affects the decision. In the context of SDM, sensitivity analyses examine the potential for the optimal decision to change. To conduct the sensitivity analysis, we repeated the trade-off analyses across uncertainty by inputting attribute worst case (10th percentile), typical case (median), or best case (90th percentile) as described in Table 3 and Tables S3, S4. The underlying transition model of infestation state (i.e., rapid spread vs rule of 10s) did not greatly affect overall performance regardless of confirmation (Figure 4). A single attribute was varied from worst to best case and all other attributes were held at typical case values. Delayed containment had the highest maximum cumulative performance value for 99% (83 out of 84) of these simulations. We then evaluated how expected cumulative performance for each action varied as a function of the probability of confirmation, which is the expected value across the uncertainty regarding confirmation (Figure 5). We simulated a range of probability of confirmation from 0.05 to 0.90. Again, we found that maximum performance was a result of delayed containment under both models and was close but slightly higher under the rapid spread model. We also examined the effect when all attributes varied from worst to best case. Public support had the greatest uncertainty for all scenario combinations, as indicated by the width of the maximum performance values (Figure 6). Regardless of this uncertainty, delayed containment had the highest maximum cumulative performance value across all simulations.

Results and discussion

We used an SDM approach to evaluate potential management action responses to eDNA detections of invasive dreissenid mussels in JR, a western waterbody that provides important socio-economic benefits to a large

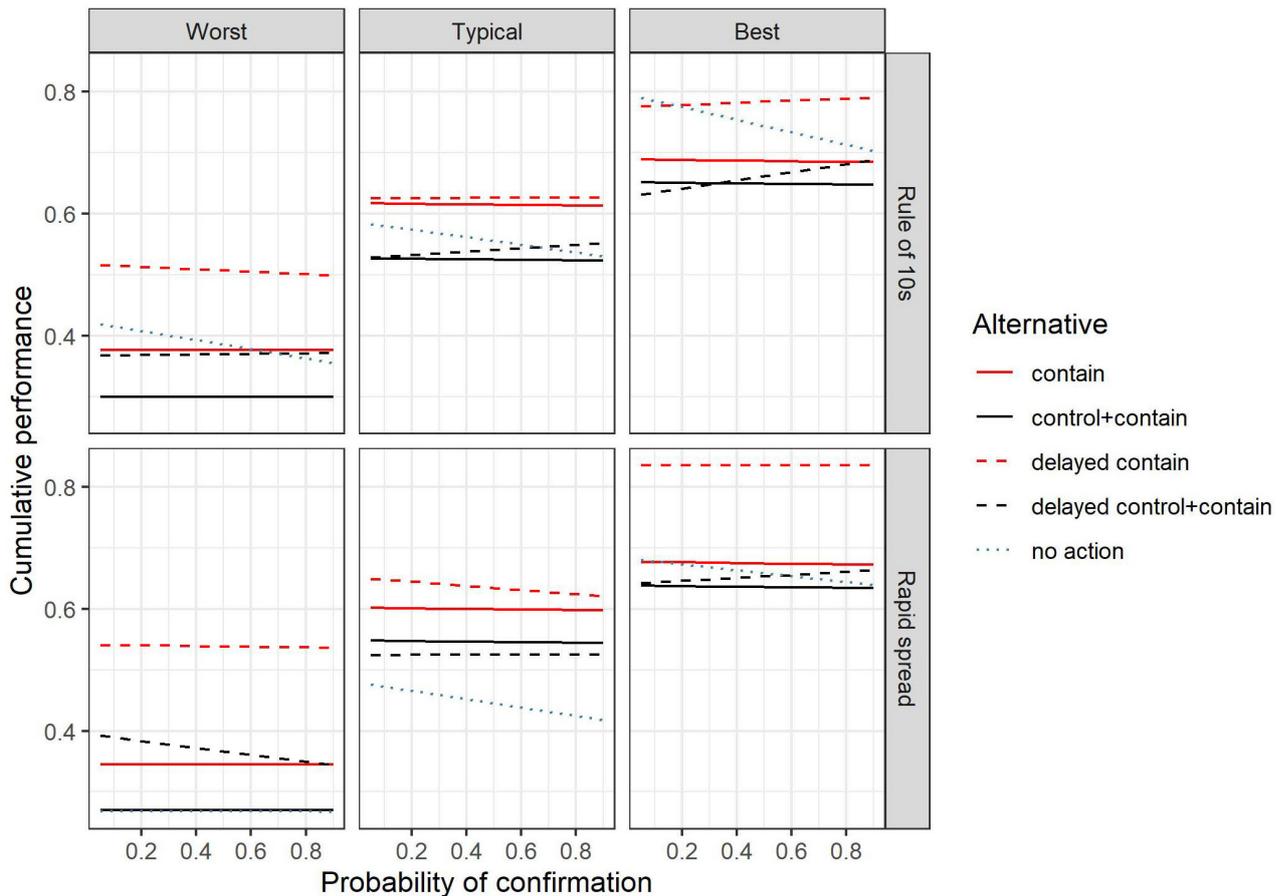


Figure 5. The maximum performance of each alternative action as a function of the probability of dreissenid mussel confirmation using non-molecular methods given the worst case (10th percentile), typical case (median), and best case (90th percentile) attribute inputs for rapid spread and rule of 10s mussel invasion scenarios.

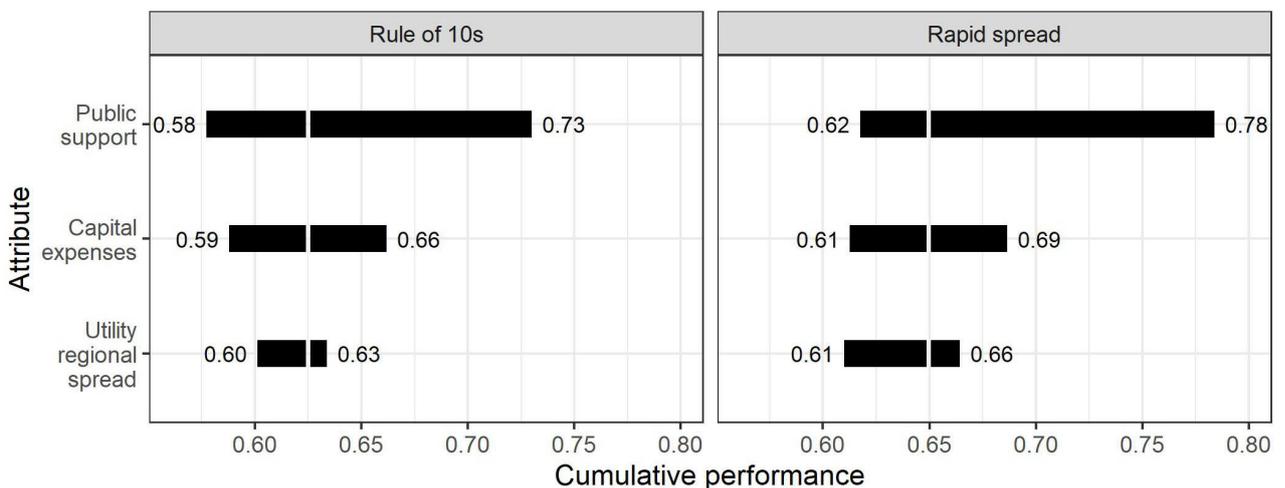


Figure 6. The sensitivity of expected cumulative performance to uncertainty in objective attribute inputs across combinations of rule of 10s and a rapid spread mussel invasion scenario. Attribute values were averaged at a baseline probability of confirmation of 0.50, given that confirmation success did not change the optimal alternative action. Uncertainty was simulated by using the worst case (10th percentile), typical case (median), or best case (90th percentile) estimates for each objective attribute. We only display those attributes containing uncertainty.

population. These responses were compared relative to how likely they are to satisfy multiple objectives identified by decision-makers and stakeholders. We predicted the consequences of each action under different invasion and

detection scenarios, given that information provided by eDNA detections is imperfect and invasion and management outcomes are uncertain. We found that delayed containment had the lowest downside risk and the highest upside gains relative to other alternative actions. The expected cumulative performance of delayed containment was robust to non-molecular confirmation success, different scenarios of invasion, parameter uncertainty, and for 3, 5, and 8 years from initial eDNA detection (Figures 4–6). We underscore that our results are specific to eDNA detections in JR and the objectives identified by the surveyed stakeholders, but the SDM approach and decision framing could be applied to other eDNA response situations.

The delayed containment process consists of actions taken at two decision points (Figure 3). At the first decision point, managers use non-molecular sampling to confirm eDNA detections. Once the non-molecular sampling is completed about ~ 4 weeks after eDNA detection, managers next make the decision to institute containment actions that require mandatory inspections for all watercraft leaving JR. This second decision point is not conditional on the confirmation of eDNA results. The large upsides of delayed containment are driven by gains in public support when non-molecular sampling confirm dreissenid mussel presence (Table 3, Tables S3, S4), even though the confirmation probability may be low (Table S2). The exposure to downside risk is minimal because the 4-week delay in containment has negligible influence on mussel spread to other waters relative to immediate containment actions. The downside risk is especially minimal when non-molecular sampling does not confirm dreissenid mussel presence (Figure 5), as this suggests that mussels are more likely to be rare (state *D* or *I*), rather than at abundance levels likely to foul watercraft (state *W*) and lead to spread. Delayed containment is a “free roll” as in the game of poker, since it potentially improves the upside with minimal downside risk.

Another way of describing why this decision is optimal is that it balances the tradeoffs between time and certainty when the accuracy of site-level inferences from eDNA detection and infestation outcomes are unknown. It takes time to collect enough information to be certain about these inferences and outcomes. However, as time passes the infestation has the potential to get worse (i.e., speed-accuracy tradeoffs; Busemeyer and Townsend 1993). In our case, non-molecular confirmation delayed containment or control actions, but provided insight and demonstrated a commitment to monitor infestation state. However, the short delay was not likely to exacerbate negative outcomes.

Other alternative actions had larger downside risks and smaller upside gains than delayed containment. Control actions were prohibitively expensive in this system. Immediate containment actions had similar upsides but larger downsides since they decreased recreational access for a longer time, potentially unnecessarily translating to low public support. The no action

alternative had large downsides because of increased potential for regional spread, especially by year 8 when mussel abundance was likely to be in state *W* if initial eDNA detections were indeed indicative of mussel presence.

To our knowledge, our case study is the first example of using decision science approaches to evaluate management responses to eDNA detections. We framed the problem as a classic “value of information decision” to assess the value of continued information gathering to benefit a multi-attribute reward (Howard 2007; Smith 2020). Our optimal decision of delayed containment for JR tracks some current management practices, in that they use eDNA detections as triggers for intensive non-molecular sampling (Woldt et al. 2020; Sepulveda et al. 2020). When non-molecular sampling fails to confirm eDNA detections, managers have usually adopted a “wait and see” approach where they continue to monitor for intrusions. However, our analysis indicates that regardless of the non-molecular sampling outcomes, the moderately costly, containment action is still warranted, assuming that monitoring efforts continue. If dreissenid mussels are truly present and spread to other waters, the downsides of doing nothing are greater than the financial, recreational, and public support downsides of containment when dreissenid mussels fail to infest (Table 3, Tables S3, S4). Thus, opportunity costs of containment are small when applying this process of alternative actions. For eDNA detections of controversial taxa such as dreissenid mussels, measured responses that minimize downside risk of an infestation, whether you win or lose, may provide a more tractable alternative to more extreme risk-tolerant or risk-adverse responses. Overly risk-tolerant actions may minimize downside risks when the species is absent or the invasion fails but have considerable downside risks when the species becomes established and an infestation occurs.

Investing in further research or learning to reduce uncertainty in the various consequence outcomes was not likely to change the optimal alternative actions after eDNA detections in JR. This is an important result because further investments are costly, delay implementation of a decision, and, as time passes, the outcome has the potential to worsen. We modeled consequence outcomes using worst, typical and best-case values across two contrasting invasion scenarios and found that delayed containment was the optimal decision in 83 of 84 simulations at year 8. The top ranked model did not deviate for comparable simulations at years 3 and 5. Moreover, delayed containment was optimal when the probability of non-molecular confirmation varied from 0.05–0.90, indicating that the specific decision problem evaluated in this case study gains nothing by improving the accuracy of confirmation probabilities. However, better information about detection probabilities would be beneficial if later decision points (e.g., when to end containment or control efforts) were contingent on multiple failures to confirm an infestation. If decision-makers do choose to invest additional resources to improve outcome certainty, then the effort should

focus on improving public support estimates. Sensitivity analyses revealed that public support had a range of maximum utility values across the two contrasting invasion scenarios that was more than two times any other objective (Figure 6). Moreover, public support had the highest importance weight of any objective, resulting in considerable leverage on the expected cumulative performance of any alternative action. Thus, efforts to increase public awareness about the negative impacts of the species targeted for management might increase public support for management action (Novoa et al. 2017).

Our decision analysis also suggests minimal benefit to adding additional molecular sampling to reduce the uncertainty to managers and to the public about the mussel invasion state. Occupancy analyses (Schmidt et al. 2013; Stratton et al. 2020), the number and strength (e.g., copy number) of detections (Ficetola et al. 2016; Furlan et al. 2016; Hunter et al. 2017), analyses using multiple markers (Sepulveda et al. 2019b), and potentially newer approaches like environmental RNA that provide biological context (e.g., life stage) of the RNA source (Yates et al. 2021), can be used to increase confidence in site-level inference of the target. However, these tools do not provide reliable insight into the future state of the invasion (i.e., if mussels are present, will they become widespread). Our means-end diagram (Figure 2) indicated that the eventual state of the invasion is what managers ultimately care about, especially given that current control options are limited. We did not specify the quantity or attributes of eDNA detections required to precipitate a manager response, aside from more than one detection over time or space that meets best practices. Even when more rigorous eDNA detection thresholds are used to trigger rapid response, non-molecular confirmation surveys will still have high value and minimal downside risk when the decision time window is rapid (i.e., weeks). Higher eDNA detection thresholds (e.g., a higher number of positive samples) may increase public support for containment and thereby increase the expected cumulative value of delayed containment. But increased eDNA thresholds are unlikely to have any influence on control since large costs drove the downsides of this action. Thus, reducing the uncertainty of eDNA detections was not an efficient use of limited resources or time in this scenario because it would not change the decision; it is only likely to make the optimal decision better.

Limitations

We present our decision-analysis as a case study since we only evaluated alternative actions at one waterbody for two invasive mussel species. Multiple aspects of our decision analysis may be generalizable, but additional scrutiny is warranted before the broad adoption of our optimal decision. The range of fundamental objectives and alternative actions we identified and evaluated encompass the breadth of objectives and alternatives

that most managers are likely to consider. In addition, attributes of JR, such as high recreation importance and drinking and irrigation water source, are common to many large waterbodies. Dreissenid mussels also have attributes common to other less vagile aquatic invaders, such as plants, snails, and clams, that rely on human vectors for secondary spread (Johnson et al. 2001).

Several nuances of our case study could limit the generality of our results, such as the core values of the decision-makers and stakeholders, the ecosystem structure of JR, and available dreissenid mussel control technologies. Decision-makers assigned importance weights to objectives on a 0–10 scale, such that the assigned weights were proportionate to the value that decision-makers and stakeholders placed on those objectives. A basic tenet of decision analysis is that decision-makers values should be incorporated. Thus, structured decision making accounts for both values and science. Objectives such as maximizing public support and minimizing regional spread were weighted much higher than other objectives to reflect decision-maker values, so they had greater influence on the overall performance of each alternative. Protection of the JR ecosystem was determined by decision-makers and stakeholders to be of relatively lower importance because it is a recently created reservoir with a put-and-take fishery and supports no threatened or endangered species, though threatened fish (*Chasmistes liorus*) spawn downstream of the reservoir. Rather, minimizing spread potential to protect other lake ecosystems, such as premier fishery destinations like Strawberry Reservoir, was determined to be extremely important. Waterbodies with vulnerable or important species assemblages or those valued for their pristine nature may have a different decision outcome. Dreissenid mussels also differ from many other invasive species since they currently have few, tenable control options and those that do exist are expensive and have uncertain effectiveness in open waters. Other invasive species have cheaper and more effective control options, such as herbicide and piscicide applications for plants and fish (Hussner et al. 2017; Rytwinski et al. 2019). These nuances and the consequence outcomes associated with the alternative actions may make the optimal decision specific to JR, however we posit that the decision process is generalizable to other systems and could be used to guide rapid response decision making following eDNA detections.

It would be useful to evaluate additional variations in the responses to eDNA detections. We did not evaluate the intuitive strategy of discontinuing containment actions after multiple failures to confirm an infestation, which is a function of the statistical power (detection probabilities) of the non-molecular sampling. For example, most western USA agencies can discontinue mandatory watercraft inspections if a water positive for dreissenid mussels (i.e., when non-molecular sampling has resulted in an initial detection plus at least one subsequent detection) has five consecutive

years of undetected/negative testing (Western Regional Panel on Aquatic Nuisance Species 2019). Another variation worth considering is the potential effect of public outreach to provide information on risks and benefits of alternative actions, which could affect the public support or tolerance for various actions.

Conclusion

Structured decision making is a process that is likely to be useful for determining whether and how to respond to eDNA detections of invasive species and pathogens, given that eDNA detections and the eventual outcome of invasions are uncertain and that there are divergent views and objectives across decision-makers and stakeholders (Runge et al. 2020). However, SDM must be used strategically in preparation for the need to respond rapidly. An SDM process can require days – months since adequate time must be invested in discussions with decision-makers and stakeholders to identify objectives, values, and alternatives and researchers must invest time to develop statistical models that account for uncertainty. The greatest benefits of SDM are likely to be reaped when they occur as a table-top exercise and are included in an operations and communication plan, prior to the initiation of eDNA sampling. This would ensure that there is decision-maker, stakeholder and public trust in the decision process and that all decisions are transparent.

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Authors’ contribution

Research conceptualization: AJS, DRS, KMO; sample design and methodology: AJS, DRS, KMO; investigation and data collection: AJS, DRS, KMO, NO, SLW, MEH, CAR, CMM, BW, MR, MEN, WMD; data analysis and interpretation: AJS, DRS, KMO; ethics approval: NA; funding provision: AJS; writing – original draft: AJS, DRS; writing – review and edit: AJS, DRS, KMO, NO, SLW, MEH, CAR, CMM, BW, MR, WMD.

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Supplementary material

The following supplementary material is available for this article:

Table S1. The cumulative probability of dreissenid mussel detection (p^*) given four levels of sampling intensity.

Table S2. Parameter inputs and sources for each step of the event tree used to estimate the probability of dreissenid mussel spread from Jordanelle Reservoir to Strawberry Reservoir given watercraft inspection and decontamination stations.

Table S3. Consequence table describing the worst-case (10th-percentile) outcomes for each alternative action at the start of the 2nd-year based on the likelihood of mussels being in state *D*, *I*, or *W*.

Table S4. Consequence table describing the best-case (90th-percentile) outcomes for each alternative action at the start of the 2nd-year based on the likelihood of mussels being in state *D*, *I*, or *W*.

Figure S1. Distribution and transition matrices used to simulate the likelihood of the dreissenid mussel invasion state.

Figure S2. Event tree that describes the probability of dreissenid mussel spread from Jordanelle Reservoir to Strawberry Reservoir as functions of higher and lower risk watercraft movements between water bodies.

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