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Can we manage fisheries with the inherent uncertainty from eDNA?

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Abstract

Environmental (e)DNA, as a general approach in aquatic systems, seeks to connect the presence of species' genetic material in the water and hence to infer the species' physical presence. However, fisheries managers face making decisions with risk and uncertainty when eDNA indicates a fish is present but traditional methods fail to capture the fish. In comparison with traditional methods such as nets, electrofishing and piscicides, eDNA approaches have more sources of underlying error that could give rise to false positives. This has resulted in some managers to question whether eDNA can be used to make management decisions because there is no fish in hand. As a relatively new approach, the methods and techniques have quickly evolved to improve confidence in eDNA. By evaluating an eDNA based research programmes through the pattern of the eDNA signal, assay design, experimental design, quality assurance and quality control checks, data analyses and concurrent search for fish using traditional gears, the evidence for fish presence can be evaluated to build confidence in the eDNA approach. The benefits for fisheries management from adopting an eDNA approach are numerous but include cost effectiveness, broader geographic coverage of habitat occupancy, early detection of invasive species, non-lethal stock assessments, exploration of previously inaccessible aquatic environments and discovery of new species hidden beneath the water's surface. At a time when global freshwater and marine fisheries are facing growing threats from overharvest, pollution and climate change, we anticipate that growing confidence in eDNA will overcome the inherent uncertainty of not having a fish in hand and will empower the informed management actions necessary to protect and restore our fisheries.

KEYWORDS

Asian carp, environmental DNA, error analysis, evidence, invasive species, species richness

1 | THE PROBLEM

On 10 July 2009, I collected the first water samples from the Chicago Area Waterway System (CAWS) in search of invasive bighead carp *Hypophthalmichthys nobilis* (Richardson 1845) (Figure 1a) and silver carp *Hypophthalmichthys molitrix* (Valenciennes 1844) (Figure 1b) environmental DNA (eDNA) where no traditional gears had detected these fish previously (Jerde *et al*., 2011). Finding evidence for these fishes' presence and at these locations, would have costly management implications (Reeves, 2019). At the time, I had no idea of the controversy my colleagues and I were about to create just by pursuing applied fisheries science (Mahon *et al*., 2013; Jerde *et al*., 2013).

FIGURE 1 (a) Bighead carp (*Hypophthalmichthys nobilis*) caught in June 2010 and (b) silver carp (*Hypophthalmichthys molitrix*) caught in June 2017 above the electric barrier with access to Lake Michigan in the Chicago Area Water System (CAWS)

2 | THE ASIAN CARP STORY

In the spring of 2009, Andrew Mahon, a molecular biologist, and I worked on numerous projects focused on the Laurentian Great Lakes with Lindsay Chadderton and David Lodge, experts in aquatic invasive species. As detailed in Andrew Reeves's (2019) book, our path to eDNA started with a question by Chadderton, "If we take a water sample, would there be enough DNA in it to tell if an invasive species is present?" We immediately saw the opportunity before us.

At the time, we were working with the U.S. Army Corps of Engineers (USACE) to conduct an invasive-species risk assessment of the Chicago Sanitary and Ship Canal (CSSC). The CSSC connects the Mississippi River basin (where Asian carp *Hypophthalmichthys* spp. have invaded) to the Great Lakes (home to a binational valued freshwater fishery, vast restored and natural wetlands and drinking water source to 40 million people). This discussion led to marker development, tissue acquisition, and water samples from a location in the Illinois River thought to be modestly populated with bighead and silver carp. In coordination with the USACE, we collected water samples in a range of volumes, and eDNA screening using PCR, gel electrophoresis and applied to invasive fish worked (Jerde *et al*., 2011).

The water management of the Great Lakes through the 50 km long CSSC has been disputed for over a hundred years (Annin, 2006). The opening of the CSSC (2 January 1900) resulted in on-going federal litigation regarding sewage and pollution, water rights, and invasive species, a point I will return to. In 1996, the US National Invasive Species Act (www.govinfo.gov/content/pkg/PLAW-104publ332/pdf/PLAW-104publ332.pdf) funded the construction of an aquatic nuisance species dispersal barrier, originally conceived to prevent nonnative round goby *Neogobius melanostomus* (Pallas 1814) from leaving the Great Lakes and entering the Mississippi River basin. An electrified barrier was conceived to meet the needs maintaining navigation of commerce in the canal, while also preventing the spread of aquatic invasive species (AIS; Moy *et al*., 2011). A second electric barrier (active April 2009), a third barrier (active April 2011), and additional efforts to deter Asian carps swimming through locks in the system have been added (ACRCC, 2018). The CSSC represents the bottle neck for preventing Asian carps (and other species) passage into the Great Lakes from the Mississippi River basin and is the largest and only continuous connection between the two basins.

From 29 June 2009 to 20 May 2010, we collected over 1000 2 l water samples from the CSSC, and from 15 September 2010 to 22 September 2011, we collected over 2000 2 l water samples from the Great Lakes (Jerde *et al*., 2011, 2013; Mahon *et al*., 2013). We found Asian carp DNA present throughout the CSSC (bighead 66 positive samples; silver 72 positive samples) and the waterways leading to the Great Lakes. In contrast, we had only six positive detections throughout the Great Lakes (bighead four positive samples; silver two positive samples) in Lake Erie – where historically bighead carp have been captured, but never silver carp. Since our original eDNA efforts in the CSSC and the Great Lakes, the USACE, and then largely the US Fish and Wildlife Service have taken over the surveillance effort, reproduced our results, and have now taken over 30,000 water samples in the search of Asian carp (USFWS; www.fws.gov/midwest/fisheries/eDNA.html).

So what was the controversy? We found multiple positive eDNA detections of both species on the Lake Michigan side of the electric barrier on repeated trips spanning 2 years. When multiple positives occurred, and traditional gears were deployed where the eDNA positive occurred, sometimes 2–3 months after the sample was collected, no physical fish were captured, which was somewhat unexpected. However, at that time, we had no way of comparing the incidence rate of positive Asian carp detections in the CAWS to any manipulated calibration study. Consequently, this left fishery and resource managers in a predicament: are there Asian carp in the CAWS, or is eDNA a false alarm?

Ultimately, the argument about the incipient invasion of the Great Lakes by Asian carps ended up in the US Federal court systems with repeated motions to close the locks and dams in the CAWS to prevent invasion. eDNA figured prominently in the arguments of evidence for fish presence (Reeves, 2019). The controversies that comprise the Asian carp story have spurred ongoing research into deterrents and improved capture methods for Asian carps that keeps many (including myself) cautiously optimistic that solutions can be found to prevent further spread and effects of bighead and silver carp into the Great Lakes.

3 | INVASIVE SPECIES AND INTERPRETING POTENTIAL ERRORS

Today the story of the Asian carps is less about the interpretation of eDNA results and more about blocking introduction pathways to prevent Asian carp establishment in the Laurentian Great Lakes. But before both species were eventually captured upstream (Supporting Information Press Releases S1, S2, S3) and on the Lake Michigan side of the electric barrier meant to stop their spread into the Great Lakes, eDNA was the only indicator that bighead and silver carp were present. In the intervening time between first eDNA detections and physical capture, other scientists took on the Asian carp eDNA research effort with methodological advances and had similar findings in the CAWS and across the Great Lakes (Amberg *et al*., 2015; Klymus *et al*., 2015; Turner *et al*., 2014b; USFWS, 2019; Wilson *et al*., 2014). However, using eDNA for early detection of invasive species will remain contentious among managers because of the inherent uncertainty from its application; we can detect the fish's DNA to infer presence, but we do not capture the fish and cannot prove, with eDNA alone, nor with absolute certainty, that the fish was present when we sampled. An anonymous fisheries manager, tasked with preventing Asian carp spread into the Great Lakes, told me, "I will never believe an eDNA positive detection until we capture a fish."

The environmental DNA positive detections put fisheries managers in a predicament: the DNA signalled Asian carp were present, but they had no way of capturing them and thus, stop the invasion. Asian carps are difficult to capture in the best of circumstances (Chapmen & Hoff, 2011: p. 136) and near impossible to capture at low density and in locations not conducive to traditional gears (Jerde *et al*., 2011). Adding pressure to the situation was the probable damage to a valued American and Canadian fishery (Rothlisberger *et al*., 2010) if Asian carp established (Wittmann *et al*., 2015) and the economic implications and considerations (Finnoff *et al*., 2005) that come from multijurisdictional management of aquatic invasive species (Peters & Lodge, 2009).

The Asian carp issue in North America is one of invasive species being detected in places we do not expect them. However, threatened and endangered fish being found in unexpected locations can trigger equally costly management actions, such as blocking of proposed development, imposing limitations on water use, added regulations to recreation and closures of fisheries (Leidy & Moyle, 1998). The absence of a fish in hand provides an opportunity for stakeholders in a fisheries management action to argue the veracity of the eDNA results through questioning the rigour of the sampling, the accuracy of the results and the underlying intentions of the scientists and institutions conducting the research. The target of criticism is inference and emphasises false positives: the idea that eDNA indicates the fish is present, when it is not (Darling & Mahon, 2011).

All sampling methods for fish have potential errors (Figure 2a). When comparing the inferences and errors of eDNA detection *v*. traditional fish capture methods (such as electrofishing, netting, application of piscicides, hook and line methods) there are clear differences in the mechanisms that can give rise to errors (Figure 3b). The first recognisable feature is that there are more mechanisms for eDNA methods to indicate a false presence, or finding the DNA of a fish species when the fish is not present. Some of these mechanisms are due to the ecology of eDNA (Barnes & Turner, 2016), in that DNA may persist in the environment after the fish swam far away some time ago. Another example includes hybridisation of bighead and silver carp, where the captured fish may look and act like a bighead carp, but the mitochondrial DNA being tested comes from a maternal silver carp (Lamer *et al*., 2010). Thirdly, issues of cross contamination before screening can also confound results. However, these later false detections can be addressed largely through continual improvement in field collection and laboratory practices (Goldberg *et al*., 2016). The technological advancements of eDNA screening platforms, be they active (PCR, quantitative (q)PCR, digital droplet (dd)PCR) or passive approaches (high-throughput sequencing, HTS; Simmons *et al*., 2015), are rapidly evolving and come with their own unique sources of error (Darling & Mahon, 2011; Mahon & Jerde, 2016; Olds *et al*., 2016).

The other error, concluding the fish is absent when present, *i.e*., false absence, is well known to occur in traditional gears and often gets short shrift discussion, but see Reynolds (1996) and Bayley and Peterson (2001). Nevertheless, traditional and eDNA applications are both susceptible to false negatives and in some circumstances, false negatives are presumably likely to occur when deploying insufficient sampling effort for rare species (Green & Young, 1993) or with eDNA, may occur if the sample is inadequately preserved (Renshaw *et al*., 2015).

4 | DETECTION OF RARE SPECIES

As eDNA surveillance is now considered the newest method in the field, it becomes desirable and necessary to compare it with traditional approaches (Hänfling *et al*., 2016; Jerde *et al*., 2011; Olds *et al*., 2016; Valentini *et al*., 2016; Wilcox *et al*., 2016). One criticism emerging from the Asian carp research was that after multiple positive eDNA detections for bighead and silver carp, no Asian carps were found using traditional fisheries methods. In one location, thousands of hours of net sets and electroshocking failed to capture any Asian carp. However, after more time and effort, two Asian carps were eventually found above the electric barriers and near where repeated eDNA positive detections for both species occurred (§2, Supporting Information Press Releases S1, S2, S3; Jerde *et al*., 2013).

In a modelling context, if one assumes a constant fish population, then repeated efforts to detect the presence of fish, would follow something like a geometric distribution (time to event analysis; Jerde & Lewis, 2007). If probability of detection (D_{prob}) is high, then irrespective of method, it becomes very likely there will be a detection very soon upon repeated sampling efforts. Think of the geometric distribution like flipping a coin until you see a head. With a fair coin, the probability of a head on the first trial is 0.5. The probability of a tail is 0.5. Stepping through repeated sampling efforts (n), the probability that a species remains undetected (repeated tails only) is $(1 - D_{prob})^n$, such that two trials is $(1–0.5)^2 = 0.25$, three trials is $(1–0.5)^3 = 0.125$,

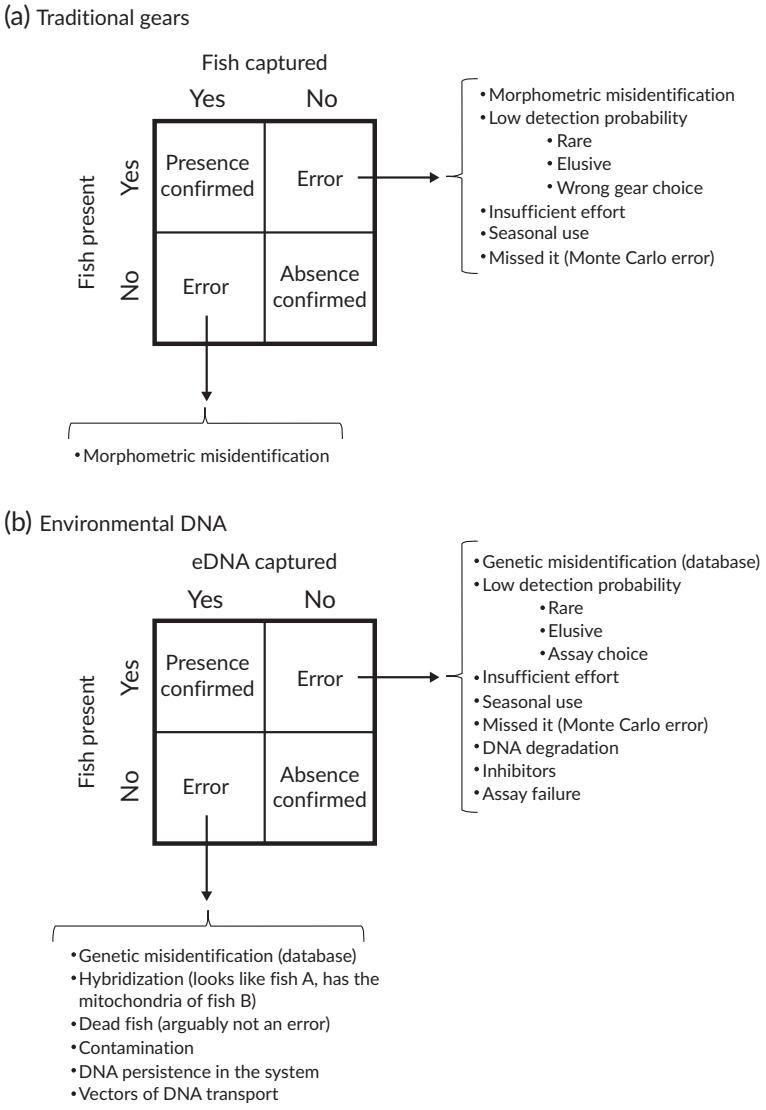

FIGURE 2 Sources of errors for (a) traditional gears and (b) eDNA. Many of the errors affecting traditional gears also affect eDNA, but there are more sources of error for eDNA than traditional gears

four trials is $(1–0.5)^4$ = 0.063 and so on. More relevant to incipient biological invasion applications, is to make this process applicable to small probabilities of detection, say D_{prob} = 0.001. This results in a probability of remaining undetected for n = 1, 2, 3 and 4 are $(1–0.001)^n$ = 0.999, 0.998, 0.997, 0.996 and so on, respectively. That there is a need for improved invasive species monitoring (*i.e.*, early detection) because of low detection probability when individuals are rare and eradication or control is still a feasible management option has been a call of invasive species policy and management for many years (Lodge *et al*., 2006).

Following the waiting time formulations in Jerde and Lewis (2007), consider two methods of fish detection; name them eDNA and traditional. Each method would have a probability of detection during a sampling event, $D_{prob.eDNA}$ and $D_{prob.Trad}$. The resulting probability of eDNA detection before traditional detection is: $(D_{prob.eDNA} - D_{prob.Trad}\ D_{prob.eDNA})(D_{prob.TTrad} + D_{prob.eDNA} - D_{prob.eDNA}\ D_{prob.Trad})^{-1}$. When both detection probabilities are small, the chance that both methods detect the target species on the same sampling effort attempt is negligible and the probability that traditional methods detect the species before eDNA is the complement of this formula. If we let $R = D_{prob.Trad}D_{prob.eDNA}^{-1}$, we can approximate this function by $(1 + R)^{-1}$ and the interpretation of R is relative, such that R = 0.25 means eDNA is four times more sensitive to detection than traditional methods. In the case of R = 0.25, the probability that eDNA detects before traditional methods is $(1 + 0.25)^{-1}$, or *c*. 0.8 (Figure 3).

Using the results from the Brandon Road pool discussed in Jerde *et al*. (2011), eDNA detections of Asian carps occurred every time it was used, $D_{prob.eDNA}$ = 1. In contrast, over 31 days (three people each working an 8 h day) only one silver carp was observed using traditional methods (electrofishing). If we take the naïve probability estimate of 1/31 of $D_{prob.Trad}$ = 0.032, then the probability of eDNA detecting Asian carp before electrofishing is $R = 1.032^{-1}$ = 0.97. Presumably this is the case for many of the locations testing positive for Asian carp eDNA found throughout the CAWS (§2; Jerde *et al*., 2011, 2013; Mahon *et al*., 2013). Similarly, Wilcox *et al*. (2016) estimated the probability of detecting brook trout *Salvelinus fontinalis* (Mitchill 1814) at low densities (1 fish 100 m^{-1}) for eDNA and electrofishing which were *c*. 0.93 and 0.45, respectively. Working through the same

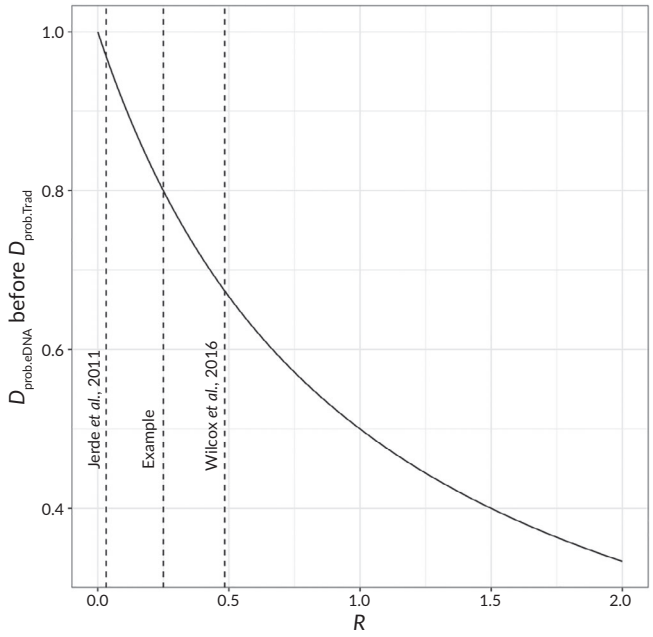

FIGURE 3 The probability of eDNA detection before traditional detection as function of the ratio of (R) of probability of detection by traditional sampling methods ($D_{prob.Trad}$) and detection by eDNA ($D_{prob.eDNA}$): $R = D_{prob.Trad}\ D_{prob.eDNA}^{-1}$. When eDNA is four times more likely to detect than traditional methods, $R = 0.25$; then 80% of the time eDNA will detect the species before traditional methods. , Examples from Jerde *et al*. (2011; $R = 0.032/1.000$), the example just given ($R = 0.25$), and Wilcox *et al*. (2016; $R = 0.45/0.93$)

calculation, the probability that eDNA detects brook trout before electroshocking is 0.69. Figure 3 shows the probability of eDNA detecting fish before electrofishing as a function of the ratio of detection probabilities for Jerde *et al*. the R = 0.25 example (above) and Wilcox *et al*. The examples provided use single species eDNA approaches, but the inferences should hold for rare species using the metabarcoding eDNA approach as exemplified by Hänfling *et al*. (2016).

Mesocosm and small-pond studies have provided evidence for the reliability of eDNA detection when fish presence and densities are known or manipulated (Barnes *et al*., 2014; Doi *et al*., 2015; Evans *et al*., 2016; Kelly *et al*., 2014; Nathan *et al*., 2014; Sassoubre *et al*., 2016). Additional studies have used comparisons of eDNA to traditional fisheries methods with conclusions ranging from eDNA being more effective (Jerde *et al*., 2011; Lawson Handley *et al*., 2019; McKelvey *et al*., 2016; Wilcox *et al*., 2016), consistent with each other (Wilson *et al*., 2014) or preferential for one approach over the other for different species, thus justifying the potential need for a combined approach (Cilleros *et al*., 2019; Hinlo *et al*., 2017). As the mathematical formulation demonstrates, however, two methods with different detection probabilities will result in one method, on average, detecting the species before the other. The key for detecting rare species is to choose a method with the greater detection probability (Thompson, 2013). However, under the presumption that eDNA approaches are more sensitive at detecting rare species, convincingly demonstrated by Wilcox *et al*. (2016), we will continue to carry the management predicament of having evidence for the presence of a species from eDNA well before we have the species in hand.

5 | SIGNIFICANCE OF CURRENT EDNA APPLICATIONS

Applications of eDNA, through either active or passive surveillance efforts, represent one of the most significant advances in aquatic conservation science in the last decade (Ricciardi *et al*., 2017; Sutherland *et al*., 2013, 2017). From conception, it was thought eDNA offered path forward to early detection of invasive species (Ficetola *et al*., 2008; Jerde *et al*., 2011). Lodge *et al*. (2006) recommended that priority US invasive species policy and management requires the development of new tools for monitoring early detection if there was ever a hope to control or manage incipient invasions. Also, while the manager's dilemma of positive eDNA detections without a fish in hand poses difficulties in terms of initiating costly institutional control or eradication efforts, it does not affect the effectiveness of policy to limit human mediated activities that reduce the risk for invasive species introduction or spread (Leung *et al*., 2002). Examples of such preventative actions include reducing the risk of invasive species introductions associated with angler dumping of contaminated live bait trade (Drake & Mandrak, 2014) or limiting transport of invasive species by recreational boats through quarantine and inspections (Morandi *et al*., 2015).

Avoiding direct fish capture can also avoid unintentional damage to threatened and endangered species and sensitive habitats. Traditional capture methods range from always lethal (*e.g*., piscicides) to stressful, due to direct handling even when steps are taken to mitigate the severity (Cook *et al*., 2019). Other traditional capture methods, such as trawling, may damage sensitive benthic habitats or other microhabitats in aquatic environments. Furthermore, traditional survey methods can have direct associated with securing regulatory permits, gaining vertebrate handling permissions and procuring vessel and capturing equipment. As an indirect detection tool, eDNA eliminates the potential effect on small populations from any handling (Beja-Pereira *et al*., 2009). Such is the case for eDNA detection of species of conservation concern such as chinook salmon (*Oncorhynchus tshawytscha* (Walbaum 1892) (Laramie *et al*., 2015), largetooth sawfish *Pristis pristis* (L. 1758) (Simpfendorfer *et al*., 2016), green sturgeon *Acipenser medirostris* Ayres 1854 (Bergman *et al*., 2016), European weather loach *Misgurnus fossilis* (L. 1758) (Brys *et al*., 2020) and spotted gar *Lepisosteus oculatus* Winchell 1864 (Boothroyd *et al*., 2016). More broadly applicable to fisheries management, there are many applications for eDNA related to delimiting species distributions (Dorazio & Erickson, 2018) for the purposes of testing ecological theory (Yoccoz, 2012), monitoring biodiversity trends (Lodge *et al*., 2012), connecting interactions between wildlife and emerging infectious diseases (Titcomb *et al*., 2019) and pathogens (Mahon *et al*., 2018), across diverse taxa (Rees *et al*., 2014) and in aquatic and terrestrial environments (Epp *et al*., 2012). The broader research agenda of

eDNA will move forward irrespective of fisheries management use and there are numerous avenues for improved fisheries management that do not require a fish in hand.

6 | ADDRESSING SCEPTICISM WITH EVIDENCE

When will an eDNA detection be considered the same as a fish in hand? In Jerde *et al*. (2011), we provided strong evidence for the presence of Asian carps based solely on the pattern of detection. A single positive sample was indicated as the weakest form of evidence. At the other end of the evidence gradient was repeated sampling efforts (trips) with multiple positive samples per effort, over multiple years. Of course, embedded into this were numerous critical factors related to specificity and sensitivity of the marker design, the sampling effort undertaken, the quality checks and assurances implemented (positive and negative controls) and the low confidence we had that fish were absent as assessed by traditional methods in the CAWS. Today, we know much more goes into establishing confidence in eDNA results, which necessities a new take on the strength of evidence for fish presence.

6.1 | The evidence for fish presence

Any eDNA research programme must address reliability and confidence across six key categories: the eDNA signal, assay design, experimental design, Quality Control and Quality Assurance (QAQC), analyses and ultimately the concurrence of the data with fish capture using traditional methods (Figure 4).

6.1.1 | eDNA signal

There is evidence in the pattern of detection that should not be ignored. Presumably as more samples are positive, there is evidence for more DNA in the water and probably more fish (Jerde *et al*., 2011). The pattern may be spatially clustered, particularly if the water is not well mixed, the species is rare but aggregated or there are microhabitats being selected for by the fish. Some have implied, at least with Asian carps, the pattern of detection may be arising from sources of DNA other than live fish, such as piscivorous birds, sewer discharge, fishing gear and commercial navigation that transport DNA from downstream into upstream Asian carp-free waters (Guilfoyle & Schultz, 2017; Schultz *et al*., 2013). However, there is currently no way to conclude that detected eDNA is sourced from a live fish or not, but see Pochon *et al*. (2017). This is particularly true in the Great Lakes wide observed pattern of positive detections that occurred close to recent and historic captures of potentially hybridised Asian carps (Jerde *et al*., 2013). Nevertheless, being transparent in the alternative sources of target species DNA should be evaluated. Ideally this evaluation is also considered in relation to the probability of the source being live fish and should not be driven by the fish presence or absence conclusions determined only from using traditional methods (see §4).

Similarly, there is concern about transport of eDNA in lotic systems giving rise to the DNA signal downstream from where the fish is

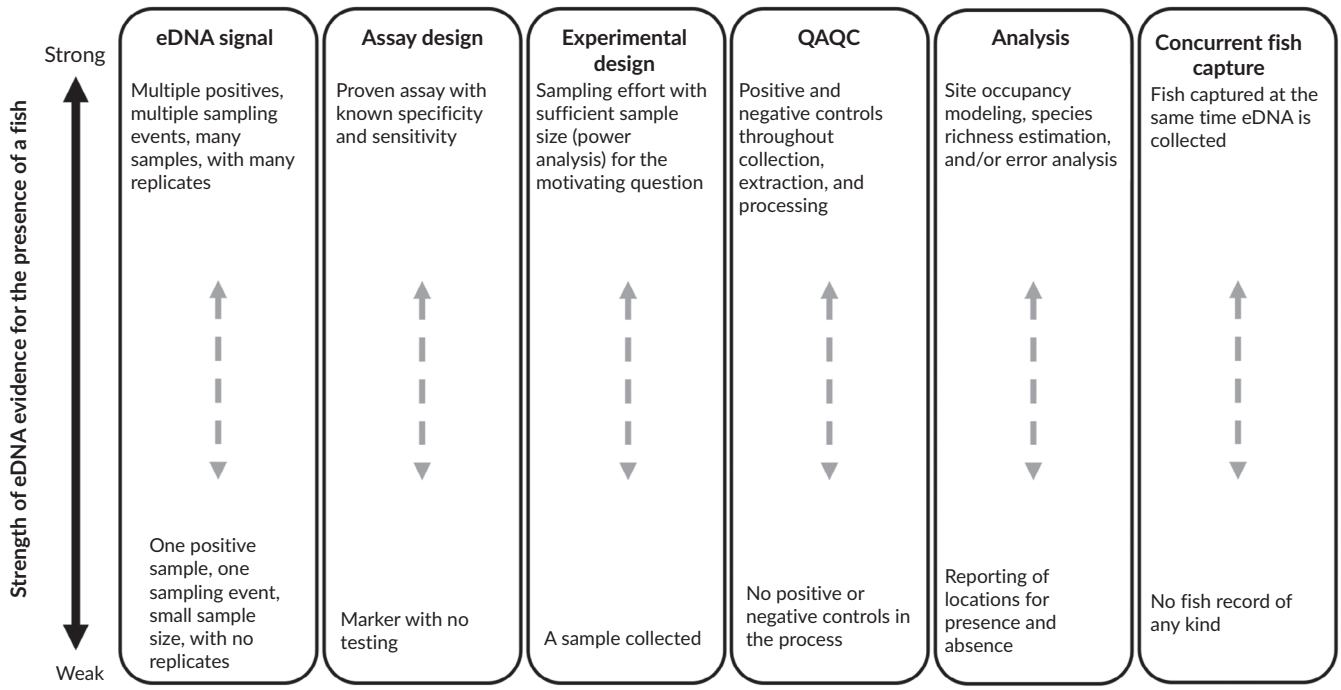

FIGURE 4 The strength of evidence for the presence of a fish from environmental DNA in each of six categories. QAQC, Quality assurance–quality control

present (Jane *et al*., 2015; Jerde & Mahon, 2015; McDevitt *et al*., 2020). The roles of substrate (Jerde *et al*., 2016; Shogren *et al*., 2016) and the underlying mechanisms of transport, retention and resuspension are being uncovered (Shogren *et al*., 2017) in the hope of linking observed patterns of the eDNA signal to projected upstream sources of DNA (Jerde & Mahon, 2015). These results will help guide fisheries management to locations where traditional capture methods could be more effective and more accurately connect eDNA to fish occupancy models (Ficetola *et al*., 2015).

A point absent from the original formulation is what to make of no positive detections. Is the fish absent, or undetected? (Gu & Swihart, 2004). Clearly negative detection is connected to the sensitivity of the assay design and the sample size used to make an inference. As is the case with rare species, a highly sensitive assay with many samples may be insufficient, thus resulting in a false negative conclusion (Figure 2). However, there are growing analyses that are providing a path forward for building a framework to infer confidence in patterns of detections (Lahoz-Monfort *et al*., 2016).

6.1.2 | Assay design

Today there are few studies that use the electrophoresis screening methodology we started with on the Asian carp project. The current advancements from our original and antiquated methodologies represent a wide range of platforms, each with strengths and weaknesses, but with more consistency across platforms than not (Nathan *et al*., 2014). Active surveillance, using a species-specific marker to look for a target species can be reliably conducted with qPCR and ddPCR platforms (Simmons *et al*., 2015). Passive surveillance, using more generalised markers and then high throughput sequencing (HTS) can assess communities (in contrast to single species detections) across diverse taxa (Thomsen *et al*., 2012). The rapidly evolving technology associated with HTS allows for more and longer DNA reads. There is much more to assay design, including evaluation of assay's sensitivity through field trials (Furlan *et al*., 2016) and evaluating specificity (Wilcox *et al*., 2013) with tissue samples of conspecifics (Mahon & Jerde, 2016). Irrespective of platform, the ultimate goal of assay design is one of reliability. If DNA from the target organism is in the sample, then it screens positive. If the DNA from the target organism is not in the sample, then it screens negative.

6.1.3 | Experimental design

Searching for the leading edge of a species invasion in a lotic system (Jerde *et al*., 2011) is going to have a very different spatial sampling design than attempting to quantify the species richness in a lentic system (Evans *et al*., 2017a). Yet the principles of survey design in fisheries is as relevant to eDNA as it is to traditional methods (Cadima *et al*., 2005). Sampling effort for purposeful detection of rare species can be justified and explored with power analysis using established approaches that have been demonstrated in aquatic systems (Green & Young, 1993). Recent studies have shown that sufficient eDNA sampling, when applied across large geographies, can reveal unexpected patterns and new occurrences of species missed by traditional approaches (McKelvey *et al*., 2016; Tucker *et al*., 2016).

6.1.4 | Quality assurance–quality control

The very first eDNA studies emphasised the importance of building confidence with checks of quality. Notably this included the use of sampling in places presumably lacking the bullfrogs (Table 1; Ficetola *et al*., 2008). In Jerde *et al*. (2011), we implemented cooler blanks that were deionised water put into collection bottles that were transported into the field and then processed (filtered, extracted, amplified and screened) between field samples in the lab and blind to the molecular technician assessing the positive or negative detection. Better practices have been devised (Goldberg *et al*., 2016; Piggott, 2016) since our early independent external peer review (IEPR) overseen by the US Environmental Protection Agency (USEPA) to evaluate quality assurance–quality control (QAQC) for Asian carps (Blume *et al*., 2010).

6.1.5 | Analysis

One of the most exciting areas of research has been connecting the eDNA signal to ecological and methodological inferences. Occupancy models have been put forth as a way to justify replication levels and assess false presences (Ficetola *et al*., 2016; Lahoz-Monfort *et al*., 2016). Chao Estimators (Chao *et al*., 2009) have been applied to eDNA data to estimate lower bounds on species richness (Olds *et al*., 2016) and justify sampling sizes and spatial distribution to characterise communities (Evans *et al*., 2017a). Currently, we are moving in a direction where eDNA produces species distribution models (SDM) useful for ecological inferences across landscape and global scales and to assess the effects of climate on fish and other species distributions (Lodge *et al*., 2012; Rees *et al*., 2014; Wilcox *et al*., 2018).

6.1.6 | Concurrent fish capture

As mentioned in §4, many eDNA studies have conducted mesocosm or semi-natural pond manipulations of fish stocks or compare traditional fisheries methods directly with eDNA. This is not the same as conducting field evaluations, but can be very compelling when trying to assess detection sensitivity and demonstrating proof of concept (Evans *et al*., 2016). While the pitfalls of comparing a detection method with a different detection method are clear when there are large differences in detection probability, ultimately a captured fish can resolve the managers dilemma. When detection probabilities for traditional gears are not small, field trials can also be beneficial for assessing proof of concept (Hänfling *et al*., 2016; Olds *et al*., 2016).

Each one of these six categories falls on a gradient (Figure 4). The weak end of the gradient means the information from an eDNA

positive comes with some caveats and where the strong end of the gradient means that given the current state of the science, this is the most confidence we can have that the positive results in the result of a false positive (Figure 2). The eDNA signal at the weak end may be one positive detection from one sampling effort. The assay design may be completely untested as to specificity and sensitivity; few samples may have been collected, with no controls and without further additional analysis or effort to capture the fish using traditional methods. It should be recognised that not all research questions need the level of evidential scrutiny of fish presence that Asian carps have motivated. That said, considering each of these categories when explaining the evidence for the presence of fish will allow for a systematic evaluation on which fisheries managers, policy makers, stakeholders and the public can debate and make informed decisions.

Lafferty *et al*. (2018) used digital droplet PCR to screen for white shark *Carcharodon carcharias* (L. 1758) presence in Southern California, USA. On the stronger side of evidence for fish presence, there were positive detections at the two locations where white sharks were present and no detection at nearby locations where white sharks were presumably absent based on historic records (Lowe *et al*., 2012). The ddPCR platform is very reliable with positive and negative controls working as expected. All methods from sterilisation of supplies to filtering protocol and DNA extraction followed peer-reviewed published protocols. Importantly, with external acoustic transmitters attached to six juvenile white sharks, we were confident the species was present at the two location that tested positive. However, this was really the first test of the marker beyond standard *in silico* design and tissue testing with conspecific species. We only collected three samples from each of the four locations and there was no analysis beyond reporting the detection pattern. In the discussion, Lafferty *et al*. described the next steps to increase the confidence in the assay with the idea that confidence can be built as research is ongoing and is based largely on filling the knowledge gaps about potential sources of error found across the six categories of evidence of fish presence (Figure 4).

The question that remains is, if we implemented an eDNA programme with best practices across all categories, could we provide enough evidence, without a fish in hand, to confidently conclude the fish is present, but uncaptured? We may have to accept that some fisheries managers will never be convinced. In that circumstance, fisheries managers must then answer the complementary question, "how confident are you the fish is absent when the eDNA evidence indicates it is present?" Arguably, every new technique in fisheries faces the same scrutiny when initially being deployed; electroshocking approaches come to mind (Bayley & Peterson, 2001; Reynolds, 1996) and eDNA is no different. As research improves, however, eDNA methodology and studies are demonstrably useful for ecological inferences and fisheries management, I am confident we will see perspectives change. Furthermore, for the sake of global fisheries, I hope the change comes quickly, because while eDNA comes with inherent uncertainty, it also comes with some inherent benefits that are very compelling for fisheries management.

7 | BENEFITS

It may not be a question of can we manage fisheries with the inherent uncertainty of eDNA, but more of a statement that to manage fisheries without using advanced detection technologies like eDNA represents an opportunity loss. The need for informed fisheries management has never been more acute and eDNA can potentially provide more cost effective (Evans *et al*., 2017b), accurate and precise fisheries data on which to study the effects of overharvest, climate change, pollution, keystone species loss and ocean acidification (Gray, 1997; Hendriks *et al*., 2010). EDNA surveillance can cover broad geographic spaces (McKelvey *et al*., 2016) and access aquatic systems inaccessible to traditional gears (Tucker *et al*., 2016). With improved sample filtration (Spens *et al*., 2017) and preservation (Renshaw *et al*., 2015), eDNA can be collected and transported in remote environments and by autonomous vehicles (Ore *et al*., 2015). The general applicability across diverse aquatic environments, while needing more proof of concept, implies that eDNA could be a general fisheries technique suitable for rare species and managed stocks, in freshwater and marine environments, that does not damage protected areas, nor the species present there.

8 | GLOBAL BIODIVERSITY & REMOTE FISHERIES

How well do we really know what fish occupy freshwater and marine systems? Historical records of commercial and recreational fish catches, coupled with accumulation of research studies documenting new occurrences populate many databases (Froese, 2011; Froese & Pauly, 2019) of global fish species distributions and form the basis for subsequent analyses of these data (Abell *et al*., 2008, Perry *et al*., 2005). However, it is rare to have comprehensive snapshots, or seasonal snapshots (Milhau *et al*., 2020), of species richness across large geographic scales to make inferences about localised extinctions, range shifts, migration trends, or new introductions (Sax & Gaines, 2003). Environmental DNA, particularly through the application of metabarcoding (Hänfling *et al*., 2016; Lacoursiere-Roussel & Deiner, 2020; Lawson Handley *et al*., 2019; Thomsen *et al*., 2012) can address this knowledge gap (Jerde *et al*., 2019).

Some freshwater systems are difficult to access and can contain such diverse fish species, that transporting traditional fisheries gear is difficult and expensive, but eDNA metabarcoding is already making inroads to challenging, species rich ecosystems (Cilleros *et al*., 2019). Additionally, there are locations, specifically polar, open-ocean and deep-sea locations that are vastly under-surveyed fisheries due to difficulties in accessibility and use of traditional capture methods in these locations (Consalvey *et al*., 2016). The first efforts to study the spawning ecology of Japanese eel *Anguilla japonica* Temminck & Schlegel 1846 nicely demonstrate the potential effectiveness of eDNA in deep, open ocean (Takeuchi *et al*., 2019). The eDNA approach allows for fisheries exploration and discovery in ways we did not believe possible.

9 | MONITORING FISHERIES STOCKS: LOCALLY, REGIONALLY AND GLOBALLY

One of the most commonly asked questions by fisheries managers is, can we estimate abundance from eDNA? Many fisheries managers see the opportunity to set harvest quotas, defend the effectiveness of protected areas, or justify fisheries being open or closed based on the amount of DNA contained in a sample. There is growing evidence for the positive correlation between fish abundance and eDNA concentrations (Doi *et al*., 2015; Knudsen *et al*., 2019; Lawson Handley *et al*., 2019; Lacoursière-Roussel *et al*., 2016; Stoeckle *et al*., 2017; Tillotson *et al*., 2018; Tomoya *et al*., 2020). However, the links between measured DNA concentrations from shedding rates, degradation rates, fish physiology and behaviour warrant further investigation (Hinlo *et al*., 2018). For many eDNA based studies to date, the emphasis has been on rare species with conservation implications or for detecting rare species for purposes estimating species richness (Olds *et al*., 2016) as a proxy to biodiversity.

Biodiversity requires both species identity and abundance (Colwell, 2009). Connecting eDNA concentrations to relative measures of abundance would allow for estimation of biodiversity. Notably, the growing interest in bringing the population genetics toolkit to bear on eDNA shows considerable promise (Adams *et al*., 2019). Commercially fished species management could be dramatically improved by distribution and biodiversity data (Walters & Pearse, 1996) given the attempts to rebuild global fisheries (Worm *et al*., 2009) in the face of growing pressures from pollution, climate change and ocean acidification (Gray, 1997; Hendriks *et al*., 2010). While few examples of eDNA applications to commercial fish stocks exist, but see Thomsen *et al*. (2016), the use of eDNA based metagenetic approaches is a very promising avenue of research that could have global implications for informed fisheries management (Point *et al*., 2020).

10 | CAN WE SQUEEZE MORE OUT OF A WATER SAMPLE?

We know from size fractionation studies of eDNA, cells and pieces of tissues are captured in water samples (Turner *et al*., 2014a). This means there is more genetic information than short fragments of the mitochondria in the water sample. Technology, specifically HTS, is rapidly advancing with sequencers that are able to do more reads, longer reads, accurate reads, in portable, potentially laptop-connected machines (Lahoz-Monfort & Tingley, 2018; Reuter *et al*., 2015). Portable, single-species detectors are also becoming a reality (Egan *et al*., 2013). There are also existing tools in the population genetics world that could be applied to eDNA samples to estimate genetic variably (Adams *et al*., 2019) and the use of RNA to delineate live from dead fish shows considerable promise (Pochon *et al*., 2017). This latter idea of using RNA may solve some Asian carp presence concerns in the CAWS, but detection sensitivities, RNA handling protocols and feasibility need to be looked at closely. Lastly, there is the coupling of molecular lab techniques to bioinformatic filtering, mapping and assembly that can give rise to the sequencing of whole mitogenomes, providing clearer connections to species identity and genotype variability form environmental samples (Deiner *et al*., 2017). Maybe one of the greatest benefits of eDNA is its potential to infer much more than species presence from a sample.

So, to answer the question, can we squeeze more out of the water sample? Clearly a resounding Yes! is in order. Some may continue to focus on the inherent uncertainty of species detection from eDNA, nevertheless this exciting research will progress, adding to the confidence in our detections (and absences), building new insights into the plight and progress of our fisheries and building confidence in the eDNA approach as a path to improved fisheries management overall. Also, just like we did with Asian carps, and now with white sharks, we will pursue those knowledge gaps that get us ever closer to the having the confidence in eDNA that we do when we have a fish in hand. Management of fisheries is sympathetically difficult with growing pressures on stocks, large costs to implementing management actions and public and political pressure to make decisions that have risk and uncertainty (Finnoff *et al*., 2007). But as we build eDNA science out (Gleeson *et al*., 2020), we hope it instils confidence in managers to act upon the information gained by eDNA data and empowers the action necessary to protect and restore our fisheries.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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