Received: 27 July 2021 | Revised: 28 January 2022 | Accepted: 17 April 2022

DOI: 10.1111/1755-0998.13627

INVITED TECHNICAL REVIEW

MOLECULAR ECOLOGY RESOURCES WILEY

Systematic review and meta-analysis: Water type and temperature affect environmental DNA decay

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Handling Editor: Naiara Rodriguez-Ezpeleta

Abstract

Environmental DNA (eDNA) has been used in a variety of ecological studies and management applications. The rate at which eDNA decays has been widely studied but at present it is difficult to disentangle study-specific effects from factors that universally affect eDNA degradation. To address this, a systematic review and meta-analysis was conducted on aquatic eDNA studies. Analysis revealed eDNA decayed faster at higher temperatures and in marine environments (as opposed to freshwater). DNA type (mitochondrial or nuclear) and fragment length did not affect eDNA decay rate, although a preference for <200 bp sequences in the available literature means this relationship was not assessed with longer sequences (e.g. >800 bp). At present, factors such as ultraviolet light, pH, and microbial load lacked sufficient studies to feature in the meta-analysis. Moving forward, we advocate researching these factors to further refine our understanding of eDNA decay in aquatic environments.

KEYWORDS
aquatic eDNA, ddPCR, eDNA concentration, eDNA degradation, qPCR, species detection

1 | INTRODUCTION

The use of environmental DNA (eDNA), trace amounts of DNA in sediment, soil, air, or water, left-behind by processes such as sloughing, shedding, excretion, injury, or decomposition of tissue (Harrison et al., 2019), to identify taxa in the environment has transformed biodiversity monitoring. Monitoring methods such as direct observation can change the behaviour of organisms (Symondson, 2002), underestimate or miss rare and cryptic species (Rees et al., 2014), or may not be possible in hazardous environments. Other techniques, for instance using fishing equipment for marine biodiversity assessments are invasive or lethal for the taxa surveyed (Thomsen et al., 2012) and require taxonomic expertise at the point of extraction. Extracting and sequencing eDNA, then matching it with a vouchered sequence to reveal its taxonomic identity using a genetic database allows circumvention of these issues (assuming appropriate primers have been developed and taxonomic coverage in genetic databases is adequate). Furthermore, gathering and processing eDNA samples is rapid since it does not require specimen isolation, therefore eDNA monitoring programmes are sometimes only a fraction of the cost of traditional monitoring techniques (Goldberg et al., 2013). eDNA analyses can fall into two broad categories: targeted taxa assays (using taxa-specific primers) and community approaches (using primers to amplify and identify many taxa simultaneously using high throughput sequencing). Both approaches have seen use for applications such as the detection of rare, cryptic, or nonindigenous species, species-identification in difficult to access locations, documenting habitat preferences, and a range of biodiversity monitoring programmes (reviewed in Gilbey et al., 2021).

Despite the popularity of eDNA in biomonitoring during the past 15 years, there remain uncertainties, some of which are creating barriers for uptake in policy (Darling, 2019; Gilbey et al., 2021). One unresolved area is how long it takes for eDNA to decay in the environment. Decay rates will affect not only how long an organism can be detected with a molecular assay, but in studies involving moving water this can also change spatial interpretation (Cowart et al., 2018; Shogren et al., 2017; Thomsen et al., 2012). The literature provides many examples of investigations of factors affecting eDNA decay including biotic factors such as the amount of extracellular nucleases, microbial load and community-composition (Barnes & Turner, 2016; Lance et al., 2017; Levy-Booth et al., 2007) in addition to abiotic factors such as: temperature (Jo et al., 2019; Kasai et al., 2020; Takahara et al., 2020), eDNA fragment length (Bylemans et al., 2018; Wei et al., 2018), salinity (Collins et al., 2018), pH (van Bochove et al., 2020; Lance et al., 2017; Seymour et al., 2018), ultra violet light (Andruszkiewicz et al., 2017; Strickler et al., 2015), and oxygen load (Barnes & Turner, 2016).

Until recently, the effect of these factors on eDNA decay remained unsynthesised: that is, in the body of accumulated research it was difficult to disentangle system effects unique to the study-system from generalised phenomena that would affect eDNA in all situations. Shogren et al. (2018) conducted the first literature synthesis, although this was limited in scope, focussed on aiding the interpretation of their own research. Jo and Minamoto (2021) recently published a more comprehensive meta-analysis investigating the relationship between pore size, gene, temperature, fragment length (and interaction terms) and eDNA decay rate. In the present study we present a further original investigation of the relationship between eDNA and environmental factors by aiming to quantify heterogeneity across studies, and testing Bayesian hierarchical models to account for intrastudy autocorrelation.

2 | MATERIALS AND METHODS

2.1 | Generating search terms

Natural language processing was used to identify relevant search terms. We identified 19 studies (Table S1) for use in the scoping exercise. The R (version 4.0.2, R Core Team, 2020) package tidytext (Silge & Robinson, 2016) was used to identify the most frequent bigrams (unique two-word combinations) and words, with default stop words removed (extremely common words such as: the, and, as, and if which are unlikely to contain relevant information), in abstracts and titles. A heatmap was used to identify which combination of words would detect all the studies in the exercise. Additional words that described water-based environments were added to the search term to ensure the search-terms were not overfitted to the scoping studies. The finalised search terms were: ("environmental DNA" or edna) AND (decay* OR degrad* OR presen* OR detect*) AND (aquatic OR water OR pond* OR lake* OR river* OR lentic OR lotic OR freshwater OR marine OR sea*).

2.2 | Systematic review

The search terms were used to query Scopus using the article title, abstract, and keywords fields on 8 August 2020. Since the journal *Environmental DNA* was not indexed, yet was a likely source of relevant studies, all published articles from the journal were also included for review. A total of 1064 articles were returned from the Scopus query, and 71 articles were available from the journal *Environmental DNA* to give a total of 1135 articles to review. The first sift involved reading titles and abstracts to remove studies that were clearly not relevant to the synthesis; this narrowed the synthesis down to 66 articles. In the second sift, only original research articles that used a targeted taxa approach (qPCR or ddPCR) to quantify eDNA decay were retained narrowing the focus to 57 studies (Table S2) on which data extraction was attempted.

2.3 | Data extraction

The following metadata were extracted for each trial from the studies: water type (freshwater or marine), equipment used (qPCR or ddPCR), DNA type (mitochondrial or nuclear), organism name, temperature, and fragment length. In the few instances where the amplicon length was not reported, the study species' mitochondrial genome was downloaded from Genbank and in silico PCR performed using Amplify4 (Engles, 2015) to determine the product length. The eDNA decay constant was extracted if reported in the text, otherwise raw data was extracted from Supporting Information, from figures using WebPlotDigitizer (Rohatgi, 2017), or emailing the author (attempted in that order) and eDNA decay rates were estimated using the first order exponential decay function (e.g., Bylemans et al., 2018; Wood et al., 2020). Data extraction, in essence, also functioned as the final sift of the systematic review: articles that did not feature desired quantitative information, reused a data set from another study, or from which we could not extract data were removed from the analysis. In total, 150 trials from 30 studies (Figure 1; full information available in Table S3) were included in the meta-analysis.

2.4 | Exponential decay model

Following the collation of data on eDNA concentration (C_t) all times metrics were converted to hours. Temperature, water type (marine or freshwater), DNA type (mitochondrial or nuclear), and fragment size were used as the experimental variables in the meta-analytical model. Estimates of eDNA decay constants are then obtained using the first order exponential decay function of the form,

$$C_t = C_0 e^{-\lambda t} \quad (1a)$$

	Author	H_2O	DNA	Temperature (°C)	Fragment length (bp)	Weighting (%)
2020	Villacorta-Rath *et al.*	F	M	30 – 35	221	0.3
	Curtis *et al.*	F	M	8.2 – 23.9	208	0.1
	Skinner *et al.*	M	M	17.4	102	0
	Kasai *et al.*	F	M	10 – 30	138	4.4
	Sakata *et al.*	F	M	17.3	132	0.2
	Kutti *et al.*	M	M	8	178	0.2
	Wood *et al.*	M	M	19	90 – 150	0.3
	Jo *et al.*	M	N	13 – 28	164	4.2
	Takahara *et al.*	F	M	4 – 25	94 – 126	1.8
2019	Sengupta *et al.*	F	M	23	86	0.2
	Moushomi *et al.*	F	B	20	101 – 128	0.7
	Jo *et al.*	M	M	13 –28	127	2.4
	Ladell *et al.*	F	B	23.9	95 – 110	0.4
2018	Collins *et al.*	M	M	9.8 –16.9	132 – 153	10.4
	Nukazawa *et al.*	F	M	21.4 – 22.1	149	0.2
	Nevers *et al.*	F	M	12 – 19	150	0.3
	Cowart *et al.*	M	M	-1	70	0.4
	Bylemans *et al.*	F	B	20	95 – 515	15.1
2017	Minamoto *et al.*	M	M	18.8	151	1.1
	Weltz *et al.*	M	M	4	331	0.5
	Jo *et al.*	M	M	26	127 – 719	0.2
	Tsuji *et al.*	F	M	10 – 30	78 – 131	0.4
	Hinlo *et al.*	F	M	4 – 20	390	0.5
	Lance *et al.*	F	M	4 – 30	190	47.4
	Andruszkiewicz *et al.*	M	M	16.8	107	2.9
2016	Eichmiller *et al.*	F	M	5 – 35	149	2.7
	Sassoubre *et al.*	M	M	18.7 – 22	107	1
	Forsström *et al.*	M	M	17	75	0.1
2014	Maruyama *et al.*	F	M	20	100	0.4
2012	Thomsen *et al.*	M	M	15	101 – 104	1.1

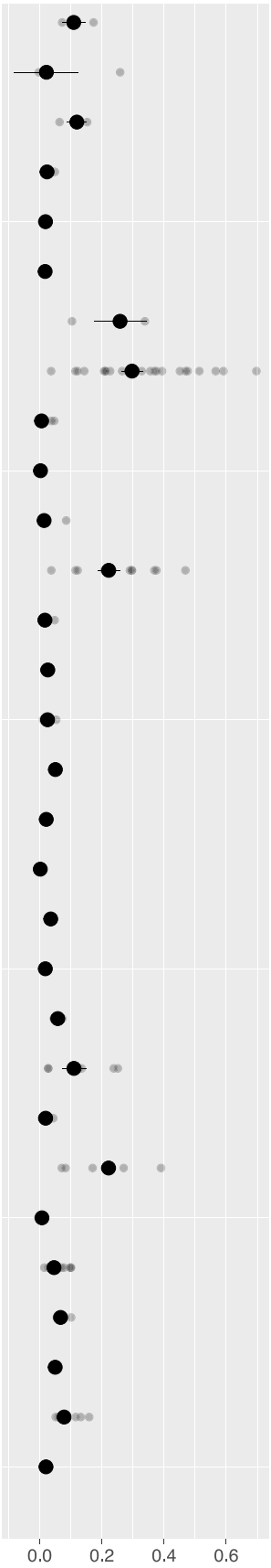

FIGURE 1 Forest plot showing summary of studies in the meta-analysis including water-type (H_2O; F, freshwater; M, marine), DNA-type (DNA; M, mitochondrial DNA; N, nuclear DNA; B, both mitochondrial and nuclear DNA), temperature (°C), fragment length (bp) and relative weighting in the meta-analysis model (%). The large opaque points show weighted study-wide estimates with 95% confidence intervals calculated using bootstrapping ($k = 1000$). Small, transparent, points show eDNA decay rates within a trial. DOIs of studies are available within Table S3

where C_0 is the eDNA concentration at time $t = 0$, that is, the initial eDNA concentration. Estimates of the eDNA decay rate λ were then combined with those collated directly from the studies to be used as the response variables in the meta-regression models.

2.5 | Multilevel mixed effect models

To obtain an eDNA decay rate across all study levels, we assumed that the observed effect size for the *ith* study y_i was normally distributed with mean α_i and sampling variance $\sigma^2_{y_i}$, where the unknown true effect size α_i is to be estimated. Therefore,

$$y_i = \alpha_i + \epsilon_i \tag{1b}$$

with a Gaussian sampling error or noise $\epsilon_i \sim Normal(0, \sigma^2_{y_i})$, $(i = 1, 2, \cdots K)$ for 150 study (K) levels. Here, y_i is the eDNA decay rate for the *ith* study level such that the observed data vector for the K study levels is given by $\mathbf{y} = (y_1, y_2, \cdots, y_K)'$. Note that in Equation (1a), we assumed that observations across study levels are independent and homogeneous, that is, the outcome measure y_i does not vary from study to study. We also assumed that there are no effects of other variables such that the variability in the outcome can only arise through the sampling error ϵ. These assumptions were made to facilitate synthesis. However, the studies considered in our work were performed under varying values of predictor variables such as temperature, pH, dissolved oxygen, and salinity so the potential for factors not included in the model to influence decay rate still exists.

Multiple levels of treatment within a given study (found in many of the included studies) meant that it was not appropriate to assume independent observations across multiple experimental levels. As a result, we extend the *null model* in Equation (1b) to allow for the incorporation of the potential sources of variability identified above such that the observed outcome of study i at experimental level j, y_{ij} is given by the *mixed effect multilevel regression model* given below,

$$\text{Level 1: } y_{ij} = \alpha_i + \epsilon_{ij}, where\ \epsilon_{ij} \sim \text{Normal}(0, \sigma^2_{y_i})$$

$$\text{Level 2: } \alpha_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \cdots + \beta_p X_p + \mu_i\ where\ \mu_i \sim \text{Normal}(0, \tau^2) \tag{2}$$

where $\boldsymbol{x} = (x_{i1}, \cdots, x_{ip})$ and $\boldsymbol{\beta} = (\beta_0, \beta_1, \cdots, \beta_p)$ are the vectors of the p predictors (temperature and fragment size), and the corresponding fixed effects parameters (DNA type and water type) to be estimated, where β_0 is the intercept. The term μ_i is the study-level random effect which adjusts for potential autocorrelation between adjacent study levels as well as capturing the potential heterogeneity across all studies. The term τ^2 measures the amount of heterogeneity across all studies. Therefore, the multilevel mixed effect model attempts to estimate the true average effect size (decay rate) $\alpha_i = \mu$ and the amount of heterogeneity across studies τ^2.

2.6 | Bayesian hierarchical regression models

To ensure more accurate representation of various sources of heterogeneity in the decay rate and quantify uncertainties in parameters estimation, data were also analysed within a Bayesian hierarchical regression modelling framework. The same model structures as defined above are adopted and only differed in approach to inference. Within the Bayesian paradigm, estimates of the unknown parameters of interest are obtained from the posterior distribution of the parameters given the data $\pi(\theta|\text{Data})$, where $\theta = \{\boldsymbol{\beta}, \mu\}$ is a generic term representing the model parameters. Mathematically, the posterior distribution is defined as

$$\pi(\theta|\text{Data}) = \text{Likelihood}(\text{Data}|\theta) \times \text{Prior}(\theta) / \text{marginal}(\text{Data}) \tag{3}$$

In most situations, the marginal distribution of the data marginal(Data) is not analytically tractable thus requiring high level computational approaches. However, methods which approximate the posterior distribution and circumvent the need for computing the marginal(Data) have been developed. Here, we utilised Markov chain Monte Carlo (MCMC; Brooks, 1998; Metropolis et al., 1953) algorithms to model and analyse our data. Specifically, the models were implemented using the rstanarm package in R (Goodrich et al., 2020). Each of the unknown parameters β and μ are assigned zero mean Gaussian priors with standard deviation of 10, that is,

$\beta \sim N(0, 100)$ and $\mu \sim N(0, 100)$.

Posterior estimates of the model parameters were based on four parallel MCMC chains. Each chain was run for 2000 iterations and a total of 4000 samples were drawn after a warmup (or burnin) period of 1000 samples each.

2.7 | Model fit statistics and publication bias

Models were checked rigorously using three fit indices: Log-likelihood, Bayesian information criterion (BIC), and Akaike information criteria (AIC). For each model, we assessed the generalised variance inflation factor (GVIF) and iteratively retained only variables with GVIF values not more than 10. Variables with GVIF values larger than two are excluded from the final model. The extent of publication bias was explored by assessing the funnel plot asymmetry with a rank correlation test.

3 | RESULTS

One hundred and fifty exponential decay coefficients were extracted from 30 published studies. Most research focussed on the decay of mitochondrial DNA ($k = 120$), with just 30 decay exponents derived from nuclear DNA. A more even split was observed between marine ($k = 82$) and freshwater ($k = 62$) research. The studies documented eDNA decay in conditions ranging between −1 and 35°C.

A total of 10 models were tested (Table S4, details of model selection and the best-fit Bayesian models are detailed in Table S5), the best-fit model describing eDNA decay included both temperature ($p < .01$) and water-type ($p = .04$) as significant terms, no other variables were included (Table 1; variables are visualised in Figure 2). Details of variables and decay estimates used for each study included in the best-fit model are detailed in Figure 1.

Significant residual heterogeneity was observed (QE = 1300, $p < .01$) indicating more variance than expected through chance alone. The large degree of variance can be clearly seen in Figure 2: with greater variance existing within variable groups than between them. However, the variance observed within any given study was small in most studies (Figure 1): this suggests studies could produce precise estimates under experimental settings where factors that could influence decay were controlled. Notable exceptions, with large intertrial eDNA decay exponent differences (Jo et al., 2019, 2020; Lance et al., 2017), tested a range of temperatures suggesting this was driven by experimental design. Therefore, variance appears to arise from interstudy differences that could not be accounted for using the meta-analysis rather than lack of precision within the studies.

The rank correlation test suggested asymmetry was present in the funnel plot, suggesting that publication bias may be present in the data included in the meta-analysis ($p < .001$, $\tau = 0.528$) (Figure 3).

4 | DISCUSSION

4.1 | What affects eDNA decay rate?

Across the 30 studies (summarised in Figure 1) included in the meta-analysis water type ($p = .04$) and temperature ($p < .01$) were included as statistically significant variables in the best-fit model. Increased temperatures and sampling from marine water (as opposed to fresh water) were associated with higher rates of eDNA decay.

DNA is a stable molecule and does not experience direct degradation in the environment unless ambient temperature exceeds 50°C (Strickler et al., 2015). Given none of the studies included in the meta-analysis exceeded this threshhold, this suggests the increase in decay rate are not the result of direct degradation. Jo et al. (2019) and Collins et al. (2018) suggest eDNA is primarily degraded by extracellular nucleases and microbes; consequently, the observed increase in eDNA decay rate with higher temperatures is likely driven by increases in enzymatic activity. This is further supported by studies that report slower DNA degradation in sterilised water when compared to untreated samples (Barnes et al., 2014; Lance et al., 2017).

Water type (marine or freshwater), significantly affected eDNA decay rate, a simple explanation for which is not immediately apparent. The marine environment differs from freshwater habitats in many regards: for example, salinity, microbial community composition and abundance, UV regimes, and temperature variability. Further research will be required to untangle which abiotic or biotic factors are driving this relationship.

DNA fragment length was not included in the best-fit model. This was unexpected as longer target fragments inherently have more nucleotides that could degenerate so it might be expected that long sequences would decay more rapidly. Many studies have

TABLE 1 Best-fit model describing eDNA decay

Variable/factor/fit indices	Estimate	SE	*p*-value	GVIF
Intercept	−0.0776	0.0260	**.0028**	
Temperature	0.0069	0.0009	**<.0001**	1.0074
Water source (marine)	0.0620	0.0307	**.0433**	1.0074
Test for heterogeneity:				
Residual: $QE(df = 147)$	1299.9670		**<.0001**	
Moderators: $QM(df = 2)$	64.7723		**<.0001**	
Variance components:				
τ^2	0.0055			
Fit indices:				
Log-like	146.037			
Deviance	−273.543			
AIC	−284.074			
BIC	−272.032			
AIC_c	−283.799			

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion; GVIF, generalized variance inflation factor; SE, standard error. All *p*-values associated with the model are reported in bold.

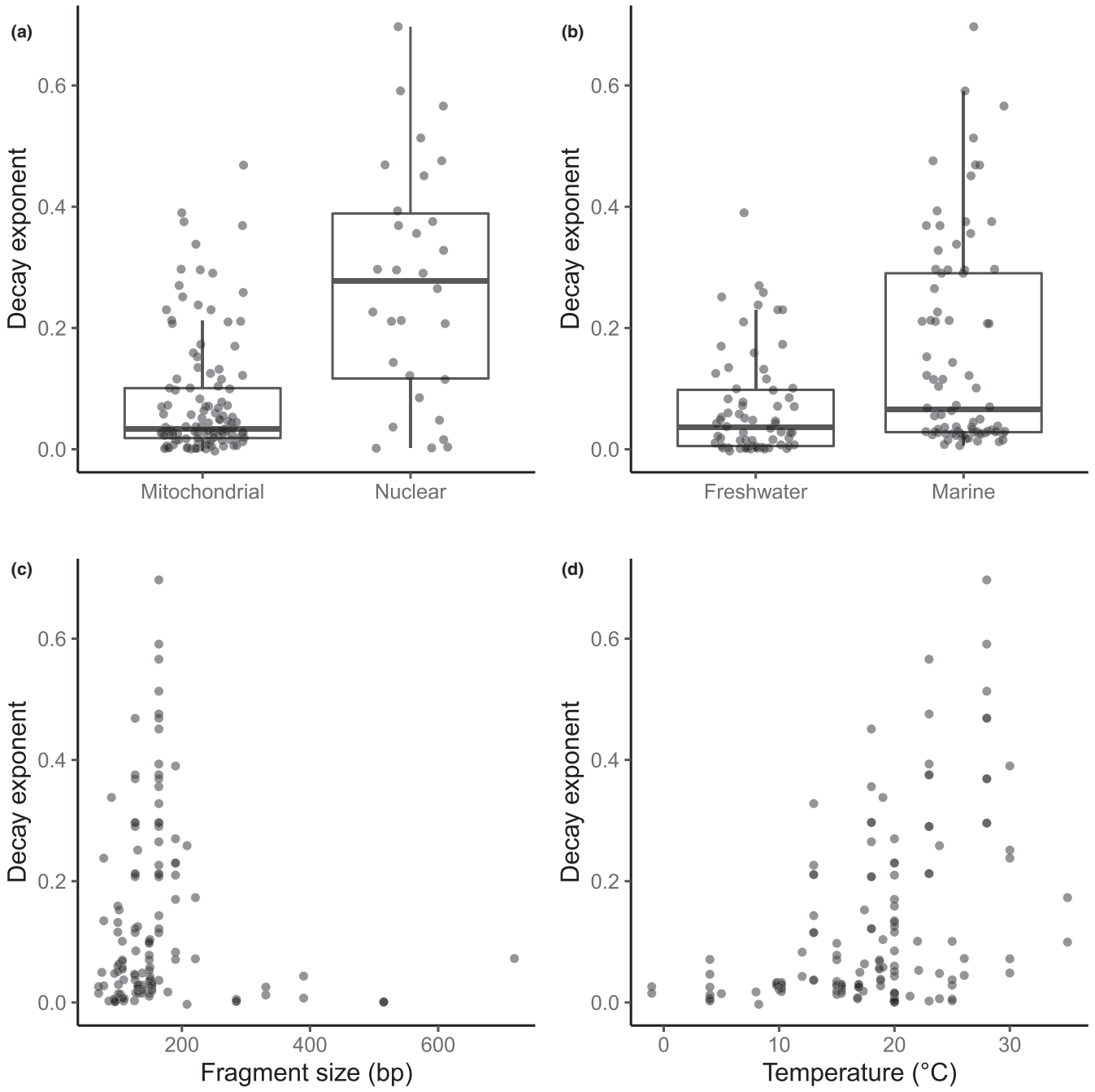

FIGURE 2 The effect of (a) DNA-type, (b) Water-type, (c) fragment size, and (d) temperature on eDNA decay rate. Please note that each point in the figure represents a trial within an experiment; trials within the same study will not be fully independent from one another. However, this nonindependence is accounted for in the meta-analysis. Boxplots denote median value, lower and upper hinges show 25th and 75th percentile values, and whiskers show minimum (lower) and maximum (upper) values (up to 1.5 times IQR in both instances)

documented a rapid decay of longer fragments and short target sequences have been advocated (Jo et al., 2017; Shogren et al., 2018; Wei et al., 2018) (but see also: Bylemans et al., 2018; Ma et al., 2016). The apparent lack of any relationship in the present analysis may be due to the similarity in fragment lengths used. Most tested amplicons were less than 200 bp, the longest targeted fragment was 719 bp, therefore it is possible that the lack of relationship was driven by absence of long amplicons. At present, whilst we would not advocate using long fragments (>800 bp; as this was untested in the meta-analysis), the results suggest that the pursuit of the shortest possible fragment may not be advisable. Marginally shorter fragments may not persist in water longer and using a slightly larger fragment with more tightly conserved primer regions between taxa may achieve higher taxonomic resolution.

The type of DNA used, nuclear or mitochondrial, was also not an explanatory variable in the best-fit model. This was surprising as it has been previously reported that nuclear DNA PCR-assays exhibit greater sensitivity than mitochondrial DNA (Dysthe et al., 2018;

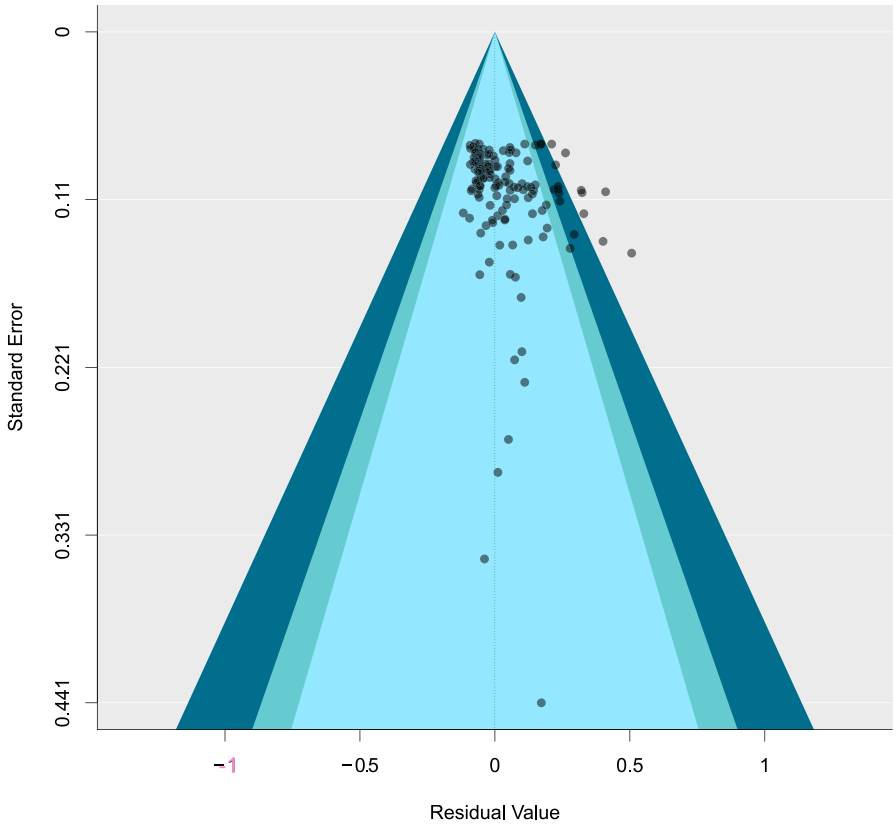

FIGURE 3 Contoured funnel plot for the best fit multivariate multilevel mixed effect publication bias model. Each point is a study level with the effect size (decay rate). Statistical significance of a study is indicated by colour: light blue ($p > .1$), light green ($p > .05$), dark blue ($p > .01$), and light grey ($p < .01$)

Minamoto, Uchii, et al., 2017). Additionally, nuclear DNA and mitochondrial DNA have different molecular structures: nuclear DNA is linear, whilst mitochondrial DNA is circular. This circular structure grants endonuclease resistance and slows enzymatic digestion (Jo et al., 2020; Moushomi et al., 2019). An explanation for this paradox could be the aforementioned short fragments used in eDNA studies: as the DNA breaks down into shorter fragments, the difference in molecular structure will become less pronounced (i.e., eDNA will become short linear fragments regardless of the origin) and the process of decay will be extremely similar in both types of DNA. It is worth highlighting that this meta-analysis looked at decay rate so the relative copy number of mitochondrial DNA to nuclear DNA has not affected the decay estimate. However, many copies of mitochondrial DNA genome exist for each nuclear genome in a cell, that is, mitochondrial DNA is found in greater abundances, therefore environmental persistence times of mitochondrial DNA may be greater in the field than would be suggested when considering decay rates alone.

4.2 | Implications of the meta-analysis

A systematic review coupled with meta-analysis is an open and repeatable method of synthesising a topic in published literature. Implicitly, a meta-analysis is only capable of capturing information compatible with the chosen statistical framework and for which there is adequate sample size. This meta-analysis captured the effect of fragment length, DNA type, water type, and temperature on eDNA decay rate. However, these factors alone are unlikely to paint the complete picture. After model fitting there remains unexplained variance and greater decay exponent variability within model factors than between them (Figure 2a,b). Additionally, model predictions do not appear particularly accurate, for instance: when considering eDNA decay in freshwater a temperature lower than 11.2°C yields a positive half-life (i.e., DNA appears to be slowly accumulating). Clearly this is at odds with our current understanding of eDNA fate. Yet this does not suggest the model is spurious: the meta-analysis featured a robust sample size and used best practice for model fitting. One possible explanation is that few trials ($k = 25$) were performed at temperatures below 11°C indicating model performance is being negatively impacted by a paucity of data. Unexplained variance and limited model performance could also suggest factors that were not included in the analysis are likely critically important to understand eDNA decay. Microbial communities are thought to be a key driver in eDNA decay (Collins et al., 2018; Jo et al., 2019) and their composition and function is affected by abiotic factors such as UV (Arrieta et al., 2000), pH (Das & Mangwani, 2015), and dissolved oxygen (Spietz et al., 2015). However, although research on the influence of microbes and the aforementioned abiotic factors on eDNA has been published (Barnes et al., 2014; Lance et al., 2017; Strickler et al., 2015), too few studies currently exist to include in meta-analysis. To improve the predictive ability of future meta-analyses we would strongly advocate further research in these areas.

This study included studies using a quantitative ddPCR or qPCR approach: literature using a detected or not-detected (often referred to as presence /absence) approach (van Bochove et al., 2020; Jones

et al., 2018; Mächler et al.,2018) or high throughput sequencing (Li et al., 2019) also address the impact of environmental variables on eDNA decay rate but could not be included in the same meta-analytical framework. We also draw attention to the loss of some detail incorporating a study into a meta-analysis; here we used exponential decay rate to compare studies, but this will not fit the eDNA decay observed in the studies equally well. Choosing an appropriate effect size is a critically important decision in all meta-analyses and in-practice a "perfect" effect size rarely exists. We are confident in our choice of effect size and that the synthesis as a whole is robust. However, for readers planning to use the decay rate of an individual study from this meta-analysis, we would strongly encourage reading of the primary literature to gain a thorough understanding of the results rather than relying exclusively on the associated effect size presented here.

Evidence of publication bias, the propensity for research to be published based on direction of results and achieving statistically significant results, was present in the studies included in the meta-analysis (Figure 3). Regrettably, data augmentation (modelling missing data points) to estimate the sensitivity of the meta-analysis to publication bias is not possible on mixed-effect models (Viechtbauer, 2010). Publication bias is widespread across scientific disciplines (Fanelli, 2012) and addressing this issue at its core is beyond the scope of this study. We emphasise, therefore, that the findings of this meta-analysis reflect the bias inherent in the published literature. Moving forward, we would encourage authors and editors to consider publication of eDNA decay trials, regardless of the outcome, to correct this issue.

It is also appropriate to reflect on other syntheses exploring the same topic: Jo and Minamoto (2021) recently published a similar meta-analysis exploring the eDNA decay using a decay exponent as an effect size. However, despite the similarities in the two studies, strikingly different results were found. We concluded that water type and temperature affect the decay of eDNA. Fragment size and DNA type were not significant predictors of eDNA decay rate. Conversely Jo and Minamoto (2021) did not include these factors individually in their best-fit model; however, significant interactions between filter pore size and water temperature, and target gene and water temperature, were present. Although only considering studies under 200 bp, a relationship between fragment size and eDNA was also found.

Divergent results from similar meta-analyses are not uncommon. Differences can arise from the choice of studies included, the choice of effect size and factors to investigate, and the statistical modelling approach (Perego & Casazza, 2012). Here, the choice of effect size (decay exponent) and factors investigated (DNA-type, water type, temperature, and fragment size) were the same. However, Jo and Minamoto (2021) included pore filter size as a tested variable. In addition, different systematic review approaches were used: 30 studies were included in our final model compared to 26 in Jo and Minamoto (2021). Much overlap (80%) was observed in the studies included in both analyses suggesting both approaches captured the available literature effectively. We believe the main source of result divergence arises from the different statistical approaches applied. We accounted for intra-study trial differences by using a nested modelling approach and tested Bayesian models. Furthermore, we assessed publication bias and used GVIF to avoid over-fitting our model. Jo and Minamoto's (2021) best-fit model could not generate GVIF since some of the levels of the best-fit model did not contain any studies which means the final model may be overfitted. However, we would encourage readers to read Jo and Minamoto (2021) as the differing approach has captured different literature and factors affecting eDNA decay and offers original perspectives on the topic.

4.3 | Applications to field research

Viewing the meta-analysis results through an applied lens, the most striking finding is that temperature affects decay rate. One of the key advantages of using eDNA workflows it that they are repeatable and reproducible (Sepulveda et al., 2020), that is, taxa detectability can be standardised between locations, time, and researchers. However, the results presented here complicate matters: identical eDNA assays conducted in different locations, weather conditions, or time of year could have markedly different detection abilities. For example, Créach et al. (2022) used a qPCR assay to monitor UK waters for the invasive ctenophore *Mnemiopsis leidyi*. Assuming all other conditions were identical, the model developed here suggests that eDNA will persist above the limit of detection 4.2 times longer at 6°C (minimum temperature) compared to 18°C (maximum temperature) (calculations shown in Figure S2). Additionally, the extra persistence time may have enabled further travel on ocean currents. Therefore, it is highly likely the temporal and spatial reach of the eDNA assay, and ultimately the detectability of *Mnemiopsis leidyi*, was variable throughout the monitoring exercise.

The meta-analysis model also suggests eDNA decays faster in marine environments compared to freshwater. Studies featuring both marine and freshwater are uncommon; however, García-Machado et al. (2021) conducted an eDNA community assessment using metabarcoding along 1,300 km of the St. Lawrence river and into the Gulf of St. Lawrence in Canada. Using the mean temperatures and water types found at two sites within the study: 23°C and freshwater in the river sites near Montreal and 4.7°C salt water in the Gulf of St. Lawrence, the best-fit model suggests eDNA will last 4.9 times longer in the marine environment (Figure S2). In this instance the higher temperature of the river results in faster decay rates, despite the freshwater typically experiencing slower rates of eDNA decline.

In specific situations it may be possible to leverage these findings to aid study design: for example, if maximum sensitivity of an eDNA assay is required the study could be conducted at the coldest time of the year. However, in many instances the ecology of many species makes this an overly simplistic recommendation and many conflating factors exist. For instance, many taxa do not maintain a year-round presence. Furthermore, even if resident population

exists other factors that vary through the year may be at play: diet (Klymus et al., 2015), growth (DNA shedding rates change with allometric scaling Maruyama et al., 2014; Yates et al., 2021), behaviour, and health (Hansen et al., 2018) could all affect the eDNA shedding rates throughout the year. Instead, the dynamic decay rate of eDNA could be accounted for using modifications to the sampling protocol (e.g., sampling more regularly in hot weather) or using statistical approaches (e.g., incorporating temperature into eDNA occupancy models).

When reflecting on real-world usage it is worth noting that decay is not the only factor to be considered when using eDNA methodologies. The movement of water serves to both dilute and spread eDNA through the environment. We are unaware of empirical studies that directly quantify the impact of decay and water body movement together. However, lotic eDNA research indicates that higher flow rates dilute the eDNA signal (Akre et al., 2019) and may lead to false-negatives (Curtis et al., 2021), although this relationship varies stream to stream (Jane et al., 2015) probably reflecting the complex idiosyncrasies of each water body. In the marine literature, Andruszkiewicz et al. (2019) used a modelling approach to incorporate the role of advection, mixing, settling rates, and eDNA decay in the transport of eDNA in Monterey Bay (USA). Whilst the influence of hydrology on eDNA was not the focus of the meta-analysis we would encourage researchers to familiarise themselves with this literature as the techniques contained within will also improve the utility of eDNA in applied situations.

5 | CONCLUSION

This meta-analysis suggests that higher temperatures and marine water (as opposed to fresh water), can speed up eDNA decay. The key implication of this is that the sensitivity of any given eDNA assay is dynamic, potentially changing with temperature and location. Moving forwards, eDNA studies looking at sites with different water types (e.g., water from an estuary compared to marine water) or varying temperatures may wish to account for this changing sensitivity by incorporating these variables within statistical models when interpreting results. No relationship was found between fragment length or DNA type and eDNA decay. However, most amplicons included in the meta-analysis were <200 bp so whilst pursuit of the shortest possible amplicon may not be necessary, we would exercise caution if targeting much longer fragments. Although we were able to include many studies in this synthesis, some abiotic factors that may affect eDNA decay such as ultraviolet radiation, pH, dissolved oxygen, and biotic factors such as microbial community and microbial load have been insufficiently studied to be included in this meta-analysis. Additionally, studies using high-throughput sequencing platforms (e.g., Li et al., 2019) were not included since sufficient methodological idiosyncrasies exist, such as community-based PCR, to make them incompatible with the our modelling approach. Moving forward, we hope future research explicitly addresses these knowledge gaps, enabling a clearer, mechanistic, understanding of factors affecting eDNA decay and facilitating easier use of environmental DNA in conservation and management applications.

ACKNOWLEDGEMENTS

We would like to thank Cefas Seedcorn for funding this research.

CONFLICT OF INTEREST

We have no conflicts of interest to report.

AUTHOR CONTRIBUTIONS

Philip D. Lamb, David L. Maxwell, and Chibuzor C. Nnanatu came up with the study idea. PDL conducted the systematic review. Chibuzor C. Nnanatu conducted the meta-analysis. Philip D. Lamb and Chibuzor C. Nnanatu wrote the first version of the manuscript. All authors assisted with manuscript revision.

DATA AVAILABILITY STATEMENT

Data are hosted on Dryad: https://doi.org/10.5061/dryad.h44j0zpnn

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How to cite this article: Lamb, P. D., Fonseca, V. G., Maxwell, D. L., & Nnanatu, C. C. (2022). Systematic review and meta-analysis: Water type and temperature affect environmental DNA decay. *Molecular Ecology Resources*, *22*, 2494–2505. https://doi.org/10.1111/1755-0998.13627