Allometric scaling of eDNA production in stream-dwelling brook trout (*Salvelinus fontinalis*) inferred from population size structure

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Abstract

Environmental DNA (eDNA) concentration exhibits a positive correlation with organism abundance in nature, but modeling this relationship could be substantially improved by incorporating the biology of eDNA production. A recent model (Molecular Ecology, 10.1111/mec.15543) extended models of physiological allometric scaling to eDNA production, hypothesizing that brook trout eDNA production scales non-linearly with mass as a power function with scaling coefficients <1 in lakes. To validate this hypothesis, we reanalyzed previously published data (Biological Conservation, 10.1016/j.biocon.2015.12.023) that examined the correlation between eDNA concentration and brook trout abundance in streams. We found that allometrically scaled mass (ASM) (e.g., \(\sum (\text{individual mass}^{0.36})\)) best described patterns of eDNA concentration across streams \(r^2 = 0.43\). ASM exhibited substantially improved model fit relative to biomass \(r^2 = 0.31, \Delta AIC = 5.19\), indicating that eDNA production did not scale linearly with biomass. However, the explanatory power of ASM was comparable to density \(r^2 = 0.40, \Delta AIC = 1.25\). Additionally, the optimal scaling coefficient estimated from the data (0.36) was substantially lower than that found in the previous study. Discrepancies between datasets could be attributable to ecological differences between study habitats (streams vs. lakes) or due to the exclusion of juveniles (i.e., individuals <75 mm) that can be abundant in stream environments. Nevertheless, this study adds to the growing body of literature demonstrating that individual eDNA production does not scale linearly with biomass.

Keywords

abundance, allometric scaling, allometry, biomass, brook trout, eDNA, fishes
1 | INTRODUCTION

Inferring animal abundance from environmental DNA (eDNA) sampling in aquatic ecosystems is a promising approach (Pilliod et al., 2013). However, substantial unexplained variation in eDNA concentration across environments persists, with observed eDNA concentration in natural systems explaining, on average, approximately 50% of the variation in organism abundance (Yates et al., 2019). To improve our power to infer animal abundance from eDNA sampling, we need more sophisticated models that incorporate an understanding of the origins and fate of eDNA (Barnes & Turner, 2016).

The biology of eDNA production remains understudied in comparison with the significant consideration given to the role of degradation and dispersion in eDNA persistence (e.g., Barnes et al., 2014; Goldberg et al., 2018; Harrison et al., 2019; Strickler et al., 2015). The production of eDNA is likely dominated by two major physiological processes in aquatic organisms: shedding and excretion (Stewart, 2019). Metabolic waste excretion rates scale allometrically according to a power function of individual mass, with mean scaling coefficient values between 0.57 and 0.68 (Vanni & McIntyre, 2016). Similarly, eDNA shedding is likely a function of organism surface area, which also increases with body mass in fish according to a power function with scaling coefficient values between 0.59 and 0.65, depending on the species (Shea et al., 2006). As a result, eDNA production is also likely to scale nonlinearly with individual mass approximately according to the following function:

\[ I = I_0 \times M^b \]

where \( I \) = metabolic rate, \( I_0 \) = a normalization constant, \( M \) = organism body mass, and \( b \) = an allometric scaling coefficient (Brown et al., 2004; Yates et al., 2020). In functional terms, a scaling coefficient (\( b \)) value <1 predicts that larger individuals will have a lower eDNA production rate per unit of mass. Traditional metrics of abundance (density or biomass) represent extremes of a continuum of values of \( b \), with a value of 0 corresponding to density/unit area (i.e., \( \sum(\text{individual biomass}^0)/\text{area} \)), and a value of 1 corresponding to biomass/unit area (i.e., \( \sum(\text{individual biomass}^1)/\text{area} \)) (Post et al., 1999). At a population level, eDNA concentration can therefore be modeled using \( \sum(\text{individual biomass}^0) \) as an alternative metric of abundance (Yates et al., 2020).

Using brook trout (Salvelinus fontinalis) populations that inhabit lakes in the Rocky Mountains, Canada, Yates et al. (2020) observed that a scaling coefficient of 0.72 best explained patterns of eDNA particle concentration. This was the first study to formally propose and evaluate this hypothesis, and further studies are necessary to examine the extent to which this pattern can be extrapolated to other species, locations, or habitats. Consequently, we conducted a similar analysis on brook trout inhabiting stream systems in western Montana, USA, using data from Wilcox et al. (2016). We applied these data to test the prediction that incorporating allometric scaling coefficients (i.e., \( \sum(\text{individual biomass}^0) \)), or “allometrically scaled mass” (ASM) would substantially improve models of abundance and eDNA particle concentration relative to traditional metrics of abundance (density and biomass).

2 | MATERIALS AND METHODS

2.1 | Collection of brook trout density, biomass, and aqueous eDNA

Wilcox et al. (2016) sampled 49 sites distributed across 16 streams in the Blackfoot River and Shields River watersheds in Montana, USA, located in the Middle Rockies ecoregion (elevation between 1,200 and 2,100 m) between July and September 2013. At each site, 5 L of water was filtered at the bottom and top of each sampled stream reach (mean reach length = 108 m); for these calculations, we used estimated eDNA copy numbers from the downstream site. For further details regarding eDNA sample collection, see Wilcox et al. (2016). After eDNA sample collection, stream discharge was also estimated at the downstream site for each reach (midstream method; Hauer and Lambert (2007)), except for three sites where estimates were obtained from nearby streams. For Deep and Buck creek, stream discharge was estimated from the average discharge at three transects. After eDNA sampling, each stream reach was sampled using a backpack electrofisher to estimate the abundance of brook trout ≥75 mm total length. Abundance at 15 sites was estimated using removal methods in which two or three passes were conducted (Otis et al., 1978). At 34 sites, abundance was estimated from a single pass based on capture efficiencies estimated from the multi-pass sites (see Wilcox et al. (2016) Appendix A for details). Total length and weight were estimated for all brook trout captured, except at eight sites at which weight was estimated from length-weight regressions obtained from the same stream or a nearby stream in the same basin.

Brook trout eDNA concentration from environmental samples was quantified using a species-specific qPCR assay (Wilcox et al., 2013). For details on sample extraction, qPCR components and sample preparation, cycling conditions, and standard curve preparation, see (Wilcox et al., 2013,2016). Final eDNA concentrations derived from qPCR were converted to a flow-corrected estimate (sensu Levi et al., 2019) by multiplying estimated sample eDNA concentration (copies/L) by discharge rate (L/s):

\[ \text{eDNA flow rate} = \frac{\text{Copies}}{s} \times \text{eDNA conc.} \times \frac{\text{Copies}}{L} \times \text{Discharge} \times \frac{L}{s} \]

which produces an estimate of the eDNA flow rate (copies/s) at a sampling location.

2.2 | Allometrically scaled mass

Allometrically scaled mass was calculated according to the following formula:
### TABLE 1  Characteristics for the 27 stream reaches ("Site") analyzed from Wilcox et al., 2016

| Stream       | Latitude (N) | Longitude (W) | Site     | Captures | $N_c$ | Mean Individual Mass (g) | Reach Length (m) | Discharge (L/s) | % Slope | Flow-Corrected eDNA Copies |
|--------------|--------------|---------------|---------|----------|-------|--------------------------|------------------|-----------------|---------|----------------------------|
| Buck         | 46.17775     | 110.38330     | Buck-000 | 6        | 9     | 22.3                     | 100              | 70.8            | 0.031   | 3,327                      |
| Deep         |              |               | Deep-000 | 25       | 63    | 29.9                     | 100              | 104.7           | 0.019   | 126,268                    |
|              |              |               | Deep-100 | 40       | 53    | 19.0                     | 100              | 104.7           | 0.019   | 115,902                    |
|              |              |               | Deep-200 | 133      | 155   | 15.3                     | 100              | 104.7           | 0.030   | 136,214                    |
|              |              |               | Deep-300 | 31       | 78    | 18.9                     | 100              | 104.7           | 0.030   | 116,321                    |
|              |              |               | Deep-400 | 39       | 51    | 32.5                     | 100              | 104.7           | 0.030   | 83,027                     |
|              |              |               | Deep-500 | 25       | 43    | 21.7                     | 100              | 104.7           | 0.030   | 83,236                     |
|              |              |               | Deep-600 | 29       | 73    | 35.3                     | 100              | 104.7           | 0.030   | 43,869                     |
|              |              |               | Deep-700 | 29       | 38    | 23.7                     | 100              | 104.7           | 0.026   | 77,059                     |
|              |              |               | Deep-800 | 50       | 66    | 20.9                     | 100              | 104.7           | 0.026   | 105,537                    |
|              | 46.16245     | 110.43764     | Deep-900 | 39       | 51    | 55.3                     | 100              | 104.7           | 0.028   | 49,732                     |
| Dugout       | 46.18554     | 110.37901     | Dugout-1 | 17       | 21    | 14.2                     | 103              | 56.6            | 0.028   | 53,826                     |
|              | 46.18628     | 110.37804     | Dugout-2 | 47       | 48    | 21.4                     | 100              | 56.6            | 0.028   | 35,771                     |
|              | 46.18723     | 110.37628     | Dugout-3 | 13       | 16    | 17.6                     | 100              | 56.6            | 0.029   | 39,337                     |
|              | 46.19266     | 110.37039     | Dugout-3.5 | 17     | 21    | 25.9                     | 120              | 45.3            | 0.028   | 23,284                     |
|              | 46.18979     | 110.37347     | Dugout-4 | 15       | 18    | 34.6                     | 95               | 50.9            | 0.015   | 32,626                     |
|              | 46.19632     | 110.36652     | Dugout-4.5 | 11     | 14    | 15.2                     | 125              | 62.3            | 0.017   | 37,753                     |
|              | 46.19682     | 110.36569     | Dugout-5 | 17       | 21    | 21.5                     | 103              | 70.8            | 0.017   | 20,319                     |
|              | 46.19927     | 110.36117     | Dugout-6 | 5       | 5     | 8.2                      | 100              | 76.4            | 0.022   | 2,444                      |
| Marshall     | 47.28065     | 113.66119     | Marshall | 50       | 55    | 26.3                     | 100              | 133.0           | 0.011   | 150,955                    |
| Horn         | 47.17455     | 113.65846     | Horn     | 27       | 41    | 27.9                     | 100              | 104.7           | 0.024   | 74,651                     |
| Placid       | 47.17980     | 113.67796     | Placid   | 50       | 80    | 15.0                     | 100              | 25.5            | 0.006   | 11,016                     |
| Shields      | 46.18509     | 110.38397     | Shields  | 6        | 8     | 14.2                     | 330              | 161.3           | 0.01    | 23,388                     |
| Smith        | 46.22832     | 110.52792     | Smith    | 47       | 62    | 15.8                     | 100              | 17.0            | 0.019   | 32,980                     |
| Unnamed-1    | 46.19230     | 110.38380     | Unnamed-1 | 17     | 17    | 21.7                     | 112              | 11.3            | 0.035   | 2,802                      |
| Unnamed-2    | 46.19158     | 110.38459     | Unnamed-2 | 8     | 8     | 40.4                     | 120              | 11.3            | 0.044   | 259                         |
| Clearwater   | 47.30331     | 113.60398     | Clearwater | 17     | 17    | 26.9                     | 100              | 121.7           | 0.016   | 44,663                     |

Note: Captures = the number of fish captured during electrofishing surveys, $N_c$ = abundance of brook trout estimated from multiple capture passes.
FIGURE 1 Brook trout mass distributions (g) obtained from electrofishing surveys conducted on 27 stream reach study sites in Wilcox et al. (2016)

\[
\text{ASM} = \frac{\sum_{i=1}^{N_{\text{cap}}} (\text{mass}_{i\text{cap}}^b)}{N_{\text{cap}}} \hat{N}
\]

where \(\sum_{i=1}^{N_{\text{cap}}} \text{mass}_{i\text{cap}}^b\) is the sum of the masses captured during electrofishing surveys, \(b\) is the value of the allometric scaling coefficient, \(N_{\text{cap}}\) is the number of fish captured during electrofishing surveys, and \(\hat{N}\) is the estimated abundance of brook trout \(\geq 75\) mm. Reaches in one stream reach were sampled continuously every 100 m for 1 km. The number of fish caught per reach varied substantially (0–133 individuals). The primary focus of this study is to estimate the effect of population size structure on total eDNA production—sites where no fish were captured from electrofishing efforts were therefore excluded from the analysis because no population size structure could be estimated (12 sites total). Similarly, sites where three or fewer fish were captured were also excluded from the analysis due to sample size (8 sites total), as the calculation of ASM requires a representative sample of individuals to estimate population size structure. ASM values were calculated for the remaining stream reaches (5–133 individuals captured), resulting in data from 27 sites (across 11 streams) for our analysis (Table 1). These stream reaches were 95–330 m long, so brook trout population estimates were standardized to the number of fish per 100 m. Reaches in one stream (Deep) were sampled continuously every 100 m for 1 km.

To estimate the optimal scaling coefficient for these data, we iteratively estimated ASM using scaling coefficients ranging from 0.00 to 1.00 (by intervals of 0.01) and modeled observed eDNA concentration as a function of these ASM values using linear regressions. For each scaling coefficient value, model fit was then evaluated using AIC (Akaike, 1974). The distribution of AIC values was compared for the optimal scaling coefficient model, the density model \((b = 0)\) and biomass model \((b = 1)\). All analyses were performed in base R (R Development Core Team, 2017).

3 RESULTS

Density estimates ranged from 2 to 155 individuals/100 m and biomass estimates ranged from 0.03 to 2.81 kg/100 m. Mean individual brook trout mass at each site ranged from 8.2 to 55.3 g, and mean total length ranged from 104 to 158 mm (Figure 1).
Both biomass and density exhibited a significant and positive relationship with flow-corrected eDNA particle concentration (Table 2, Figure 2). The distribution of AIC values calculated for eDNA × ASM regressions for scaling coefficients ranging from 0.00 to 1.00 exhibited an approximately upward parabola shape, with the best-fit value of the scaling coefficient equal to 0.36 (ASM$^{0.36}$, Figure 3). Models with scaling coefficients between 0.00 and 0.73 generated ΔAIC values $<2$. While ASM$^{0.36}$ represented substantial improvement as a predictor for flow-corrected eDNA concentration relative to biomass (ΔAIC = 5.19), it exhibited only marginal improvement relative to density (ΔAIC = 1.25); $r^2$ values for density and ASM$^{0.36}$ exhibited similar explanatory power (Table 2).

4 | DISCUSSION

We found that eDNA production scaled allometrically for brook trout in headwater mountain stream systems in the U.S. Midwest, with a scaling coefficient of 0.36 associated with the lowest AIC value. These findings were consistent with Yates et al. (2020), although the scaling coefficient was substantially lower than that found for this species in mountain lakes in the Canadian Rockies (0.72). Additionally, the optimal model for brook trout in streams in this study accounted for approximately half of the variation in eDNA concentrations relative to the lake-based model ($r^2 = 0.78$; Yates et al., 2020). The low values for allometric scaling coefficients observed in this study imply a weak effect of individual biomass on eDNA production—in other words, fish in the stream sites appeared to produce similar quantities of eDNA among individuals, with a tendency to produce slightly more eDNA as individual biomass increased. Further, although ASM$^{0.36}$ produced better fitting models than did biomass, model fit was similar to that of simple individual density (ΔAIC = 1.25, $r^2 = 0.43$ vs. 0.40 for ASM$^{0.36}$ and individual density models, respectively). Notably, physiological processes that scale with individual density represent a form of strong allometric scaling because “density” (individuals/area) is equivalent to Σ(individual biomass)/area. Models with scaling coefficients of 0.00 or 0.36 both provided significantly improved model fit relative to biomass; our results provide evidence that eDNA production in wild brook trout exhibits an allometric relationship with biomass.

The low value of $b$ estimated for the stream sites could be due to the 75 mm cutoff for inclusion in brook trout counts. Sites with smaller mean size distributions could, on average, have a larger abundance of fish $<$75 mm that were not formally counted during the stream surveys. Sites with smaller fish, on average, may therefore have more “uncounted” individuals and, as a result, overestimate the apparent eDNA particle contribution of fish $>75$ mm. The influence of juvenile fish on eDNA concentrations is likely to be more important in streams when compared to lakes because they constitute the typical spawning and rearing habitat for brook trout (Josephson & Youngs, 1996). Future work should be conducted to evaluate the relative contribution of juveniles to eDNA particle production because they are expected to be particularly metabolically active per unit of biomass (Maruyama et al., 2014).

The population size structure of brook trout also differed between streams and lakes. Mean book trout mass ranged from 14 to 55 g between the 27 sampling sites within and among the 11 headwater streams. In the nine lakes in Yates et al. (2020), fish were often substantially larger; mean individual masses ranging from 43 to 405 g. In small cold headwater stream systems, the opportunity for growth can often be relatively limited for brook trout (Hazzard, 1932; Hutchings, 1993). Accounting for size structure might therefore be most important when the magnitude and variation in population size structure is large.

Finally, differences in collection methodology could account for discrepancies between the two study. A myriad of differences between the studies, including (but not limited to) different filter pore sizes, filter preservation methods, DNA extraction methods, qPCR protocols, and timing of sample collection, could have caused unknown biases in results. Future research to optimize eDNA collection, extraction, and analysis is crucial to better standardize and compare results across eDNA studies (Hinlo et al., 2017; Tsuji et al., 2019).

Overall, explanatory power of the stream model was less than in the lake model, regardless of whether allometry was incorporated. Although it should be noted that the lake model was based on a smaller sample size ($n = 9$ compared to $n = 27$ sampling sites across 11 streams), we suspect that the discrepancy in model explanatory power observed is due to characteristics of the systems affecting eDNA deposition and retention. Environmental DNA deposition is likely slower and less complex or variable in lentic systems; horizontal transport tends to be limited as eDNA particles largely diffuse downwards as they slowly settle (Ghosal et al., 2018; Goldberg et al., 2018). By contrast, in lotic systems eDNA deposition is an extremely complex process that depends on multiple environmental variables such as discharge, water velocity, eDNA input from individuals upstream, width, depth, and channel roughness (Robinson et al., 2019; Shogren et al., 2017; Wilcox et al., 2016). This complexity likely contributed substantially to the increased variability in eDNA particle concentrations observed across the stream study sites. While flow-corrected estimates of eDNA production (Levi et al., 2019) can account for some of this variability, eDNA particle transport and deposition are ultimately much more complex in lotic systems relative to lentic systems. Predictive models of organism abundance based on observed eDNA particle concentrations may therefore be more precise in lentic systems compared to lotic

| Model          | $F$   | $p$    | $r^2$ | AIC  | ΔAIC |
|----------------|-------|--------|-------|------|------|
| Density        | 18.38 | <.001  | 0.40  | 644.84 | 1.25 |
| Biomass        | 12.49 | .002   | 0.31  | 648.78 | 5.19 |
| ASM$^{0.36}$   | 20.44 | <.001  | 0.43  | 643.59 | -    |

TABLE 2 Model results for regressions between eDNA concentration and density (fish/reach), biomass (kg/reach), and allometrically scaled mass (ASM$^{0.36}$/reach)
environments. Future work could potentially address this complexity by incorporating the impact of site environmental characteristics as covariates on eDNA detection and concentration (Mackenzie et al., 2002; Wilcox et al., 2016).

As shown here, there are likely ample opportunities to test for allometric scaling in eDNA production using existing datasets. Many studies have examined the relationship between organism abundance and the concentration of eDNA in a natural environment, typically quantifying abundance using density and biomass (e.g., Doi et al., 2017; Erickson et al., 2016; Nevers et al., 2018; Pilliod et al., 2013). As long as both density and individual biomass data have been recorded, it would be possible to explore the extent to which allometric scaling coefficients improve the correlation between eDNA particle concentration and abundance. To this end, we also recommend that future studies examining the relationship between abundance and eDNA concentration record individual biomass data to ensure that allometry in eDNA production can be accounted for. Nevertheless, our findings contribute to a growing number of studies demonstrating that individual eDNA production likely does not scale linearly with individual biomass (Maruyama et al., 2014; Takeuchi et al., 2019; Yates et al., 2020).

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AUTHOR CONTRIBUTIONS

TMW, KSM, MKY, and MKS collected eDNA samples and abundance data. MCY conducted statistical analyses and wrote the first draft of the manuscript, and all authors contributed substantially to subsequent drafts.

DATA AVAILABILITY STATEMENT

eDNA, population size structure, and site habitat data are deposited in the Dryad Digital repository at: Yates, Matthew et al. (2020), Data from: Allometric scaling of eDNA production in stream-dwelling brook trout (Salvelinus fontinalis) inferred from population, size structure, Dryad Digital Repository, https://doi.org/10.5061/dryad.bvq83bk6v

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