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ORIGINAL ARTICLE

Tide impacts the dispersion of eDNA from nearshore net pens in a dynamic high-latitude marine environment

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Abstract

Environmental DNA (eDNA) is increasingly used to detect animals in aquatic habitats, but uncertainty remains about the relationship between the present location of an animal relative to eDNA detections. In marine environments, physical characteristics—such as tides and currents—can influence the distribution of eDNA. In this study, we make use of hatchery net pens containing >46 million juvenile chum salmon (*Oncorhynchus keta*) in nearshore Southeast Alaska to test for dispersion of eDNA and the effects of tide. Initially, we collected and filtered surface water every 80 m along a 2 km transect to test eDNA attenuation over surface distance during incoming and outgoing tides on a single day. The following year, we sampled at three depths (0 m, 5 m, and 10 m) every 500 m along the same transect as well as along a perpendicular transect, to understand dispersion by depth and in additional directions. Chum salmon eDNA was quantified using species-specific qPCR. We found that surface samples showed a consistent signal of decreasing chum salmon eDNA across the 2 km transect ($R^2 = 0.665$), with the majority of eDNA detections within 1.5 km of the net pens. Tide had a significant effect, resulting in higher concentrations of chum DNA throughout the transect during incoming tide and a steeper decline in eDNA over distance during outgoing tide ($R^2 = 0.759$). Depth affected chum salmon DNA concentration, with the majority of eDNA at the surface and a decreasing amount of DNA with increasing depth. This study addresses one of the critical knowledge gaps in applying eDNA to marine fisheries management by providing empirical evidence of eDNA dispersion and demonstrating that most eDNA detections are likely from nearby individuals that are either currently or recently present. Yet even at close proximity, eDNA signal strength fluctuates and depends on the physical environmental variables during a given sampling event.

KEYWORDS
coastal, environmental DNA, marine, qPCR, salmon, transport

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1 | INTRODUCTION

Environmental DNA (eDNA) has been rapidly adopted for detecting species across diverse habitats. Despite the popularity of this approach and enthusiasm for integrating eDNA into fisheries management (Gilbey et al., 2021; Hansen et al., 2018; Lacoursière-Roussel, Côté, et al., 2016), interpreting and contextualizing species detections requires understanding the mechanisms of eDNA transport, degradation, and fate, as well as the way in which different environments impact these processes (Fukaya et al., 2021; Hansen et al., 2018). In the ocean, physical variables including temperature, depth, salinity, currents, and tides have been the subject of eDNA studies, primarily using metabarcoding (Jensen et al., 2022; Jeunen et al., 2019; Kelly et al., 2018), with few examples using quantitative PCR (Collins et al., 2018; Murakami et al., 2019; Shea et al., 2022). While metabarcoding can provide information about dozens of species present, qPCR and digital droplet PCR (ddPCR) are used for quantifying a smaller number of species with higher precision. Thus, studies of eDNA fate and transport for a single species benefit from these quantitative approaches.

Many studies have explored community composition across discrete habitats and/or environmental gradients using metabarcoding. Most of these studies found that distinct habitats—even in close proximity—typically harbor some separate species that are readily identified by eDNA (Larson et al., 2022; Monuki et al., 2021; Port et al., 2016). Based on these results, eDNA is thought to be most abundant closest to its point source, despite the potential for rapid and diffuse transport, especially along open coastlines and in marine environments with substantial water movement or tidal exchange (Andruszkiewicz et al., 2019). Logically, eDNA released into the environment through shedding of cells and biological material would continually replenish a localized signal; however, longer-distance transport of those cells is almost certainly also occurring, but swift dilution diminishes or eliminates the signal.

Different assay characteristics of metabarcoding or qPCR impact the capacity to measure eDNA transport. Because metabarcoding data is compositional and composition affects the probability of detection (Shelton et al., 2016), metabarcoding is poorly suited for quantifying small amounts of eDNA far from its point-of-origin. Other organisms are typically contributing to eDNA in a more significant way at this new location, thereby limiting the use of metabarcoding data to effectively study dispersal. Most useful for studying dispersal of marine eDNA are the few studies that use a point source with known position and biomass (Murakami et al., 2019; Shea et al., 2022) and use species-specific qPCR to identify dispersal distance that could otherwise be masked by changes in species composition with metabarcoding.

eDNA signal attenuation is also influenced by degradation of the cellular and extracellular material, which directly impacts the amount of DNA available for transport (Harrison et al., 2019). Several studies have documented rapid degradation over hours to days in temperate water samples (Andruszkiewicz et al., 2017; Ely et al., 2021; Sigsgaard et al., 2017; Strickler et al., 2015; Yamamoto et al., 2016), with higher temperatures increasing decay rates (Lamb et al., 2022). Such rapid degradation also contributes to the localized eDNA signature and bolsters the general assumption that sampling aquatic environments provides a contemporary picture of species at a given site.

Overwhelmingly, experiments to understand eDNA transport have focused on freshwater and rivers. Estimated eDNA transport distance varied across freshwater study systems, with detectable levels of DNA within ~250 m regardless of flow (Jane et al., 2015), within 400 m at low flows and 100 m at high flows (Wood et al., 2021), within 12.3 km for two species of invertebrates (Deiner & Altermatt, 2014), at 5 km downstream (Laporte et al., 2020), and as far as 1 km, but with the majority of detections within 200 m (Spence et al., 2021). In rivers, most studies only sample downstream of the eDNA source, and no target eDNA was identified upstream when it was sampled (Laporte et al., 2020).

Freshwater has different transport mechanisms and decay rates than marine eDNA (Lamb et al., 2022), but the logistical challenges of designing a transport experiment in the marine environment likely contributes to a paucity of empirical data about the fate and transport of marine eDNA. Consequently, data have been generated in mesocosms (Jo et al., 2019; Sassoubre et al., 2016) or modeled (Allan et al., 2021; Andruszkiewicz et al., 2019). The limited number of experimental studies in the ocean contribute to uncertainty around how eDNA transport operates under different physical and environmental conditions, and only a small number of these studies have integrated hydrodynamic models with marine eDNA data (Fukaya et al., 2021; Shea et al., 2022).

In this study, we leverage an existing point source to study the dispersion of eDNA in a coastal marine environment subject to large tidal swings (13.74 feet mean tidal range) and characterized by strong currents and significant freshwater input. We evaluated the dispersion of eDNA from hatchery net pens containing >46 million juvenile chum salmon (*Oncorhynchus keta*) in nearshore Southeast Alaska. At this high latitude, water temperatures are cold (<8°C) and eDNA degradation should be minimal. Marine eDNA can persist in nearshore waters for up to 48 hours (Collins et al., 2018), which we expect should be enough time for eDNA to disperse from the net pens throughout the study area. Specifically, we evaluated the effect that distance and tide had on eDNA transport measured with species-specific qPCR. This study provides empirical evidence for the attenuation of eDNA from a large point source and the impact of water movement caused by tides and contributes data for accurately interpreting eDNA detections for marine fisheries applications.

2 | METHODS

2.1 | Experimental design

Amalga Harbor is a small natural harbor (~2.5 km wide) located 39 km north of Juneau, Alaska, USA (at 58.4947° N, 134.7933° W). Amalga Harbor is located on the east side of Favorite Channel, a natural feature that runs approximately North/Northwest-to-South/Southeast in the inside waters of southeast Alaska (Figure 1). Hatchery net

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pens containing >46 million juvenile chum salmon (*Oncorhynchus keta*) are present in Amalga Harbor from February–June, after which fish are released and pens disassembled and removed. Net pens are 12.2×12.2 meters horizontally and extend vertically in the water column from the surface to 6 m depth. ROV footage has shown salmon vertically distributed throughout the pens. No natural runs of chum salmon return to Amalga Harbor in early May, when eDNA samples were collected, although other species of salmonids (*O. mykiss*, *O. nerka*, *O. kisutch*, *O. gorbuscha*, and *O. tshawytscha*) may be present in small numbers. The closest natural run of chum salmon is ~25 km away.

To study dispersion of eDNA in the nearshore marine environment, we used the hatchery net pens as a point source and plotted a 2 km transect, beginning at the pens, perpendicular to Favorite Channel. Bottom depth across the transect ranged from 36 m at the net pens to 185 m at the deepest point. In 2021, we collected surface samples along this perpendicular transect (Figure 1c) at both outgoing and incoming tides on a single day (10-May). Preliminary results suggested that tidal cycle could be confounded with wind-driven surface flow and/or current, although no current data or hydrodynamic models are available for the Amalga Harbor area at sufficiently high spatial resolution to be useful for this study. In order to better evaluate the variables potentially involved in eDNA transport, in 2022, we conducted a second set of field collections. We plotted a second transect parallel to the shore and perpendicular to the original transect (Figure 1c) to study

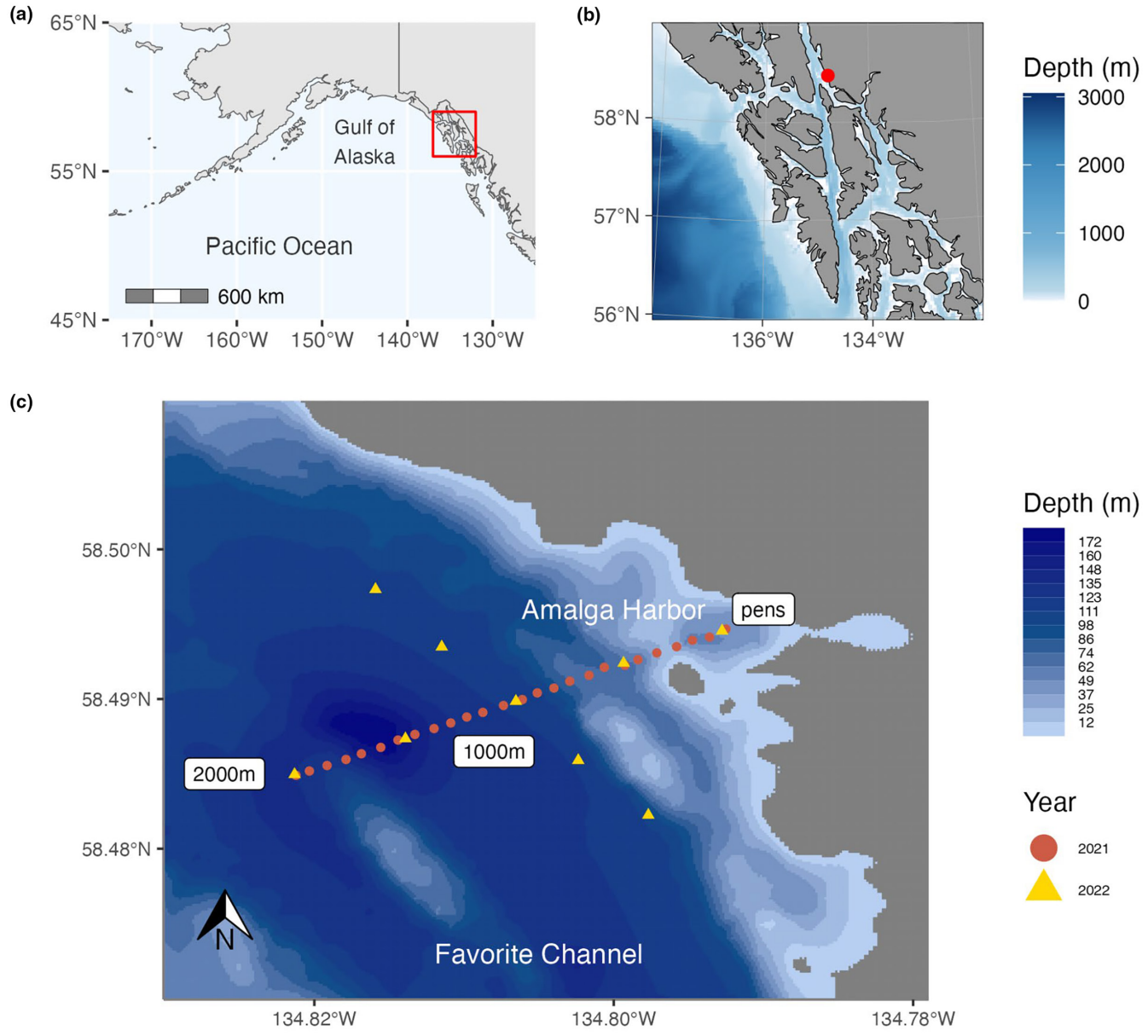

FIGURE 1 Study site of experimental transect from chum salmon hatchery net pens in nearshore Southeast Alaska (a). Amalga Harbor is located within a network of fjords on the inside waters of Southeast Alaska (b). Sampling occurred every 80 m from the net pens, perpendicular to the channel, in 2021. In 2022, sampling included the same perpendicular transect with 500 m between sampling sites, as well as a parallel transect (c).

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dispersion in multiple directions and added vertical depth sampling to both transects to evaluate eDNA stratification.

2.2 | Sample collection

Water samples were collected from the NOAA vessel Sashin during May 2021 and 2022. In 2021, three 1-L surface samples were collected by hand in sterile 1.2 L Whirl-Pak bags every 80 m along a 2 km transect beginning from the net pens (Figure 1c). Sampling took place on 10-May and began in the morning, during the incoming tide, with the entire 2 km transect sampled prior to slack tide (Figure S1a). Afternoon sampling began after the tidal cycle switched to outgoing and was completed prior to slack tide. Temperature, salinity, and depth measurements were collected at each sampling location using a CastAway-CTD instrument (SonTek; Table 1).

In 2022, water samples were collected from the surface, 5 m and 10 m depths along both perpendicular and parallel transects (Table 1; Figure 1) with distance between sampling locations increased to 500 m. Depth samples were collected using a single 8-L Niskin bottle deployed manually, once to 5 m and a second time to 10 m depth. All samples were collected on a single day (5-May) with sampling beginning in the morning, during the outgoing tide (Figure S1b). Afternoon sampling began after the tidal cycle switched to incoming and was completed prior to slack tide. Additionally, background samples, over five kilometer from Amalga Harbor, were collected at all three depths to determine whether chum salmon eDNA was present in the environment, but unrelated to the net pens.

As in 2021, three replicate 1-L surface water samples were collected in sterile Whirl-Pak bags from the same location and stored in a cooler until filtering (within 18 h). All water samples were filtered through a 47 mm 0.45 μm cellulose nitrate filter (Nalgene) using a vacuum pump with a three-sample manifold. Filters were stored in 5 mL of Longmire's buffer (Renshaw et al., 2015) in a 15 mL conical tube at room temperature until DNA extraction. Field negative controls consisted of Whirl-Pak bags containing deionized water brought into the field, opened, and then filtered alongside field samples, with one negative control per collection day/tide.

2.3 | DNA extractions

DNA was extracted using the Qiagen DNeasy Blood and Tissue kit modified for eDNA filters stored in Longmire's buffer. Briefly, modifications included the following: samples (filters in buffer) were vortexed and 400 μL of the Longmire's buffer was added to a 1.5 mL tube before adding 40 μL of proteinase K and 400 μL of Buffer AL (following Menning et al., 2020). Samples were incubated at 56°C for 2 h and following incubation, 400 μL of 100% ethanol was added. DNA was eluted with a final volume of 100 μL. Laboratory-grade water was used for extraction blanks and incorporated approximately every 48 samples. Extracted DNA was stored frozen at −20°C. Extractions occurred in a UV-sterilized hood in a PCR-free laboratory to minimize contamination.

2.4 | Quantitative PCR

Samples were analyzed for chum salmon DNA using qPCR following the protocol from Homel et al. (2021). Each 15 μL reaction included 7.5 μL TaqMan Environmental Master Mix, 300 nM forward primer, 900 nM reverse primer, 250 nM probe, 2 μL DNA extract, and an internal positive control (IPC) with forward and reverse primers at 300 nM and probe at 200 nM. The IPC was designed based on the extinct broad-billed moa (*Euryapteryx curtus*) sequence in Ramón-Laca et al. (2021), and 1000 copies of the IPC were added to each sample along with 1.2 μL of PCR-grade water to bring the total reaction volume to 15 μL. For the standard curve, seven dilutions (10^6 to 10^0) of a gBlock standard (IDT) for both the chum salmon locus and IPC locus were combined and run in triplicate. Three replicates were run for each sample (for a total of nine qPCR replicates per location/tide), and three no-template-controls (negatives) were included on each 96-well plate. Samples were run on a QuantStudio 12 K Flex (Applied Biosystems) in 96-well plates. Thermocycling conditions were 95°C for 10 min, and then 45 cycles of 95°C for 15 s, 60°C for 1 min.

Samples were considered inhibited if the IPC cycle number shifted >2 cycling threshold (CT) values. Inhibited samples from the 2021 sampling event were diluted 1:10 with PCR-grade water and

TABLE 1 Samples collected from experimental transects in 2021 and 2022.

Year	Tide	Depth (m)	Samples	Temperature °C	Salinity (PSU)	Time-of-day
2021	Incoming	0	78	5.98 (4.53–7.26)	28.86 (17.64–31.38)	AM
2021	Outgoing	0	78	6.07 (4.38–7.97)	28.39 (21.69–31.57)	PM
2022	Incoming	0	27	6.07 (5.64–6.63)	29.88 (27.97–30.60)	PM
2022	Outgoing	0	27	5.36 (5.07–5.81)	30.03 (28.96–30.64)	AM
2022	Incoming	5	27	5.15 (5.14–5.36)	30.60 (30.51–30.63)	PM
2022	Outgoing	5	27	5.23 (5.03–5.31)	30.58 (30.16–30.68)	AM
2022	Incoming	10	27	5.22 (5.13–5.40)	30.62 (30.61–30.64)	PM
2022	Outgoing	10	27	5.14 (5.09–5.26)	30.64 (30.60–30.69)	AM

Note: Temperature and salinity are mean values across the transect and from within 0.2 m of the depth indicated. The minimum and maximum values are indicated in parentheses. Note that multiple depths were sampled in 2022, but only surface samples were collected in 2021.

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re-run using the same qPCR conditions described above. All samples from 2022 were diluted 1:10 prior to qPCR to mitigate inhibition.

The limit of detection (LOD) and limit of quantification (LOQ) were calculated based on 24 replicates of each gBlock standard (10^6–10^0) using the procedure described in Klymus et al. (2020). LOD is the lowest standard with a minimum of 95% positive replicates, and LOQ is the lowest standard quantified with a coefficient of variation (CV) below 35%. DNA copy numbers are provided for samples above the LOQ, while detections or non-detections are reported for values below the LOQ and above the LOD.

DNA copies per liter were calculated based on the volume of DNA extract added to the qPCR reaction (2 μL), the original 1 L of filtered seawater, and the 400 uL of Longmire's buffer used for the extraction with an elution volume of 100 μL. Each qPCR reaction represented 1.6 mL of the original seawater sample, while each 10x diluted qPCR reaction represented 0.16 mL of the original sample.

2.5 | Statistical analyses and models of dispersion

For analyses, we omitted qPCR non-detections, and then eDNA concentration was log-transformed (log10) to improve the homogeneity of variance and data were tested for normality using the Shapiro–Wilk's method. For the initial question about eDNA dispersion from the net pens across the perpendicular transect (data from 2021), we generated linear models using distance and distance + tide, and then compared the two models using an ANOVA. For testing whether eDNA was dispersed equally at depth, we used the data from 2022 that was collected at three depths (0, 5, and 10 m) at the edge of the net pens (0 m distance) and used a nested ANOVA with tide and depth. All analyses were performed in R (v 4.2.0).

3 | RESULTS

In 2021, we collected 78 surface water samples on both incoming and outgoing tide, plus one field blank per tidal cycle. In 2022, we collected 27 water samples at each tide and depth, plus field blanks and three replicate water samples per depth for background samples (Table 1). Background samples collected from >5 km away from the net pens had no amplification of chum salmon, indicating that chum salmon in the environment would be sporadic if at all present. None of the field blanks or qPCR non-template controls produced positive detections for chum salmon.

3.1 | qPCR

Based on the gBlock standards for the qPCR data, the LOD was 10 copies/reaction and the LOQ was 38 copies/reaction. Using these thresholds, there were 240 sample replicates above the LOD for 2021 and 52 for 2022 (48% and 10%, respectively; Figure S2). Of these, 83% were above the LOQ in 2021, while 40% were above the LOQ in 2022. All observations above the LOQ in 2022 were within 1000 m of the net pens, whereas 17% of detections above the LOQ in 2021 were between 1000 and 2000 m (83% were between 0 and 1000 m). The dataset for 2021 also included more detections below the LOD (41), all of which were between 720 and 1920 m from the pens. Given that there was no amplification in the extraction blanks and non-template controls, although these samples fell below the experimental LOD, they were likely true detections.

3.2 | Inhibition

For the 2021 dataset, 63 of the 166 samples were inhibited (IPC shift >2 cycles). After diluting samples 1:10, four samples remained inhibited, but in all four samples, the IPC was less than 1 CT value greater than the expected IPC range (within <3 CT values) and so these samples were included without further dilution. Inhibited samples were primarily from the outgoing tide (40/63; 63.5%) within 750 m of the net pens (26/40; 65%; Figure 2a). Most of these samples were collected from within the freshwater lens of a nearby creek emptying into Amalga Harbor (Figure S3).

Based on inhibition data from 2021, all samples from 2022 were diluted 1:10 prior to qPCR analysis. Eighteen samples remained inhibited, even with the 1:10 dilution; however, no spatial or temporal pattern was apparent in these samples and 72% (13/18) were within less than 1 CT value of the expected IPC range.

3.3 | Models of dispersion

Using just the 2021 dataset, the proportion of replicate samples with positive detections and DNA copy number decreased with increasing distance from the net pens (Figures 2b, c). While the proportion of detections was generally high until ~1200 m on incoming tide, on outgoing tide, the proportion of detections showed more variation beginning at ~500 m (Figure 2b). Of those samples with positive detections, the DNA copy number was negatively correlated with distance from the net pens (Figure 2c) with increasing variance. The linear model using both tide and distance from net pens ($F = 423.6$, $p < 0.001$, adjusted $R^2 = 0.759$) outperformed the model using just distance ($F = 532.7$, $p < 0.001$, adjusted $R^2 = 0.665$; AIC = 87.93, Table S1). The rate at which the concentration of chum salmon eDNA decreased was more rapid during the outgoing tide compared to the incoming tide.

The parallel transect sampled in 2022 produced relatively few positive eDNA detections of chum salmon (Figure 3), which precluded quantitative analysis or modeling to compare locations and tidal influence. There were only 14 positive detections across the three depths along the parallel transect at 1000 m from the net pens (~5% of samples), with 50% of those at the surface and 86% (6/7) of those surface samples collected during incoming tide. The distribution of eDNA detections at depth was more similar during

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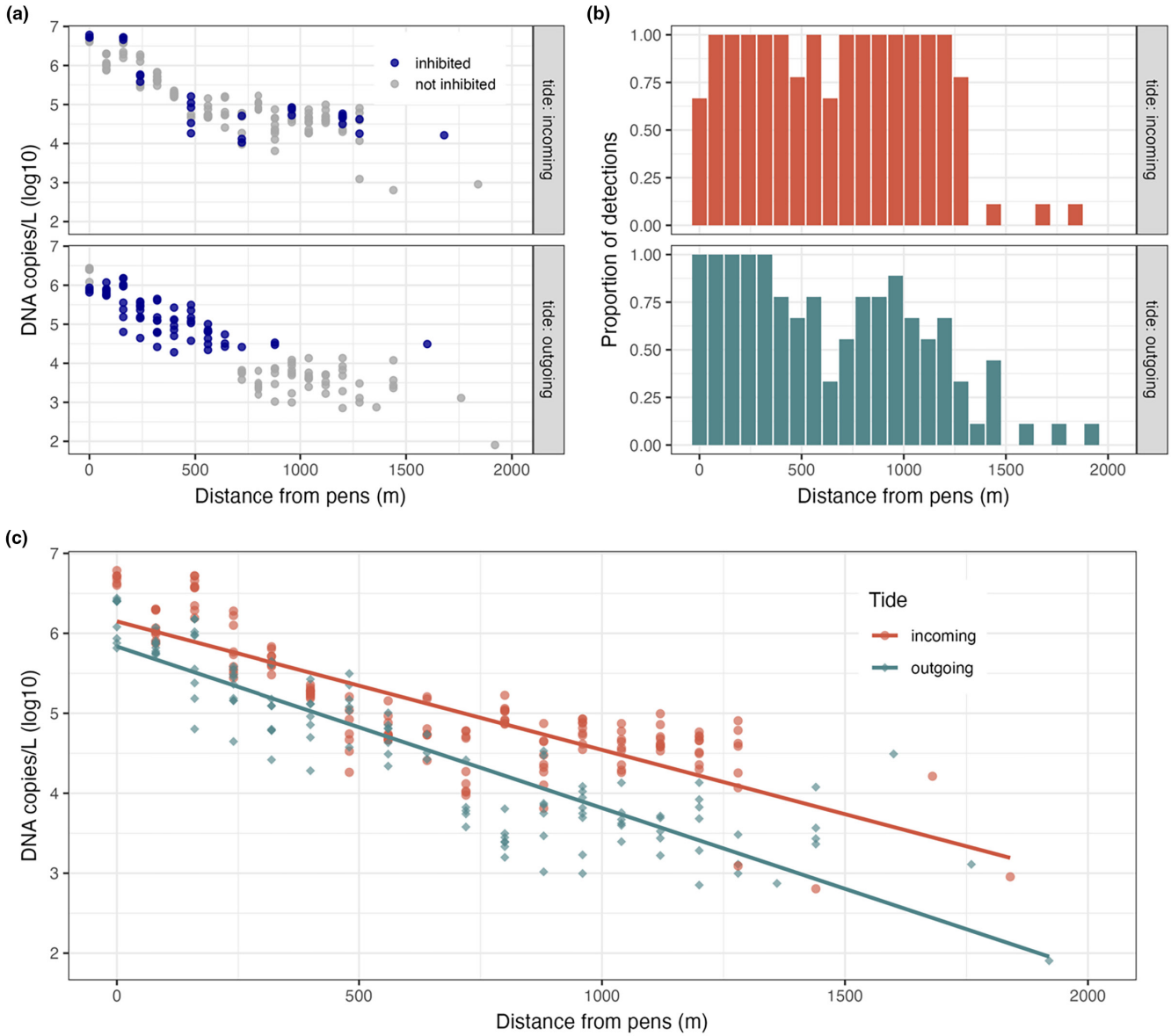

FIGURE 2 PCR inhibition (a), proportion of eDNA detections for chum salmon (b), and DNA quantity (c) over the 2 km transect distance from the hatchery pens sampled in 2021. Each point represents one qPCR replicate and each distance includes three field samples and three qPCR replicates (nine replicates at each distance/tide). Non-detections are not displayed. Inhibited samples exhibited a shift of >2 cycles of the internal positive control (IPC) in the initial qPCR reaction. One field sample at 0 m from the pens on incoming tide and its three replicate qPCR samples produced no detectable amplification.

outgoing tide, with one detection at the surface, four detections at 5 m, and two detections at 10 m. For both the incoming and outgoing tides, positive detections occurred both NW and SE of the original transect, although more detections occurred at 500 m to the SE during incoming tide. All samples with DNA concentration above the LOQ were at the surface and 0 m from the net pens, with the exception of one sample collected at 500 m to the SE on incoming tide. The average DNA concentration was over 3x greater on outgoing tide vs. incoming tide for samples collected at the surface at 0 m from the net pens (outgoing = 1.6×10^5 copies/L, incoming = 4.7×10^4 copies/L [values not log-scaled]).

3.4 | Depth

Although samples from the 2022 dataset produced relatively few positive detections, these data allowed us to examine the distribution of eDNA throughout the upper part of the water column (0–10 m). The highest concentration of DNA and largest number of positive detections occurred in surface samples (63.5%), with decreasing concentrations and detections with increasing depth (25% of detections at 5 m and 11.5% at 10 m; Figure 3). At 0 m from the net pens, depth impacted eDNA detections, with a smaller proportion of detections with increasing depth (Figure 4).

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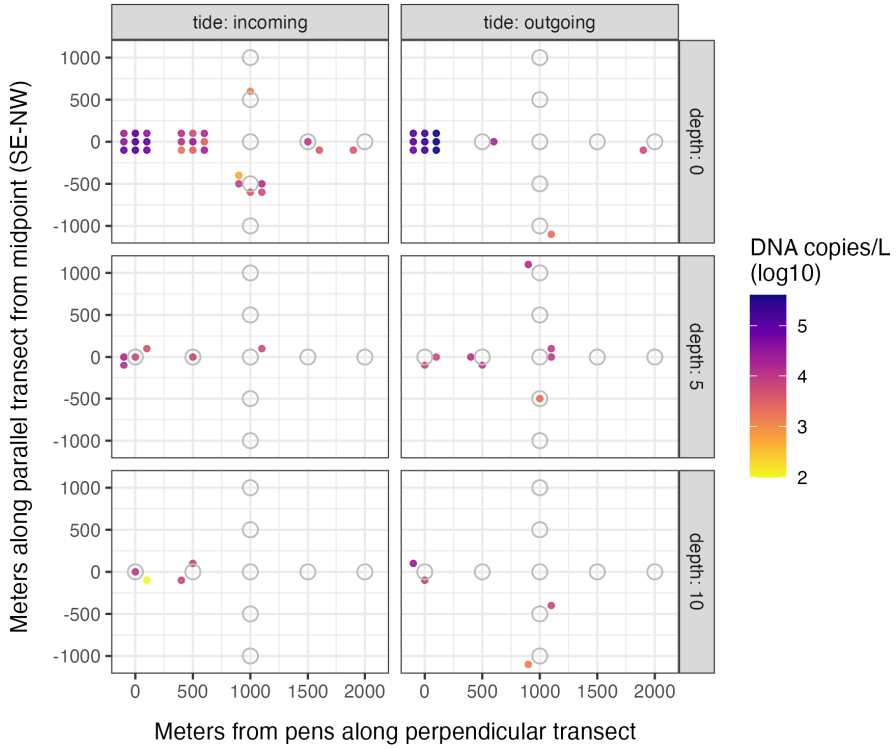

FIGURE 3 Depth distribution of eDNA from surface to 10 meters across both perpendicular and parallel transects relative to the hatchery net pens. The pens are located at 0 m on both the x- and y-axes. Three biological replicates were sampled from three depths (surface, 5 m, and 10 m; displayed in columns), and three technical replicates (qPCR) were performed for each of the samples (displayed in rows; total of nine replicates per location/tide). Any sampling location with one or more non-detections is indicated with an open circle.

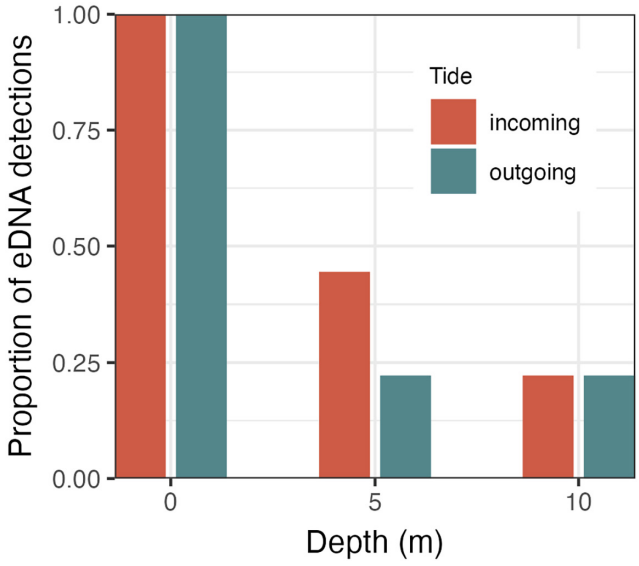

FIGURE 4 eDNA detections across samples from three depths collected at 0 m from the net pens in 2022. The proportion of positive detections decreased as depth increased on both incoming and outgoing tides. There are nine technical replicates per depth/tide. Surface samples are designated as 0 m depth.

4 | DISCUSSION

Understanding the dispersion of DNA in the marine environment is a critical factor for accurate interpretation of species detections from eDNA. In this study, we measure the attenuation of eDNA from salmon hatchery net pens across a perpendicular surface transect, an orthogonal transect horizontally from the midpoint of the perpendicular transect, and at up to 10 meters depth. The majority of DNA detections were within 1.5 km of the pens and in samples collected at the surface. DNA concentrations decreased with increasing distance from the point source and with increasing depth, and tide had a strong and significant effect in both of these dimensions. Tide also dramatically impacted the distribution of PCR inhibitors in samples. The interaction between tide and PCR inhibition represents an unexpected source of temporal and environmental variation impacting eDNA detection and reinforcing the value of experimental studies to characterize marine eDNA.

Although only a small number of studies have used qPCR to track the dispersion of marine eDNA from a known, stationary point source (Murakami et al., 2019; Shea et al., 2022), these studies both measured higher DNA concentrations at closer proximity to the point source and more non-detections with increasing distance, consistent with our findings (Figure 2). Beyond this basic pattern, characteristics of each experiment influence the actual dispersal distance, DNA concentration, and presence of eDNA at depth. Fish biomass or abundance interacts with multiple environmental variables (Lacoursière-Roussel, Rosabal, & Bernatchez, 2016; Ogonowski et al., 2023) that generally differ among studies and almost certainly impact eDNA fate and transport. For example, eDNA degradation in the Sea of Japan (21.4°C) exceeded the exponential decay predicted by tank experiments with temperatures in a comparable range (18.7 ± 1°C to 22.0 ± 1°C) (Murakami et al., 2019). In our study in Southeast Alaska, temperatures ranged from 6.5–8.2°C at the surface to 4.4–5.2°C at 10 m depth, corresponding to much lower rates of degradation caused by temperature-mediated decay (Tsuji et al., 2017). Given the limited eDNA degradation at these cold temperatures, we expect

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dispersion identified in our study to be primarily influenced by water movement.

4.1 | Influence of tide

For coastal marine environments, tides and currents tend to dominate water movement over short time periods. Empirical studies are particularly important in these areas because particle models often predict longer-distance dispersal than has been observed in nature (Andruszkiewicz et al., 2019) and hydrodynamic models that include coastal processes at the scale of eDNA sampling are only available for a limited number of geographic regions (Fukaya et al., 2021; Shea et al., 2022). Although no high-resolution oceanographic models were available for our study area, sampling experimental transects during both incoming and outgoing tides provided clear data about the impact of tidal water movement. Specifically, tide influenced the relationship between eDNA concentration and distance from the net pens, with a more rapid decrease in eDNA concentration on the outgoing tide (Figure 2).

Unexpectedly, tide also impacted the presence of PCR inhibitors in surface samples, with elevated levels of inhibition during the outgoing tide (Figure 3a). One explanation for this phenomenon could be increased concentrations of tannins in nearshore surface water from Peterson Creek, which empties into Amalga Harbor (Jane et al., 2015); (Figure 1; Figure S4). A freshwater surface lens is evident in the CTD data, and salinity values were lowest in the surface water during outgoing tide (Figure S3; Table 1). The extent of this low-salinity surface water coincides with the pattern of PCR inhibited samples to ~750 m from the hatchery net pens (Figure 2a). Accounting for, and mitigating, inhibition in eDNA samples prevents underestimating DNA concentration (McKee et al., 2015). In our study, inhibited samples primarily occurred on outgoing tide, which would have created a tide-specific bias had we not identified and corrected for the inhibition. This result also highlights the interactions between freshwater and coastal environments that can impact eDNA collections.

Previous studies that examined the impact of tides on nearshore eDNA found little to no evidence of tidal patterns influencing the species community (Kelly et al., 2018; Larson et al., 2022). However, these studies used DNA metabarcoding, which may have masked tidal signatures because of the compositional nature of metabarcoding data. Metabarcoding could obscure changes in the absolute eDNA concentration of one or more taxa—particularly if the overall species community remains relatively consistent, or alternatively, if the community composition changes over short time periods unrelated to tide (Jensen et al., 2022). Our experimental transect in 2021 was well suited to detect differences in chum salmon eDNA because of short sampling intervals; however, the increased distance between sampling sites in 2022 produced fewer positive qPCR detections and an overall more limited dataset for identifying the impact of tide.

Although we treat incoming and outgoing tide as binary in this study, sampling during each of these tides occurred over multiple hours (i.e., Figure S1). Water movement varies across tidal stage and can be enhanced by the complex coastline and narrow straits throughout the study area in SE Alaska. Tide also interacts with existing nontidal currents and can increase or decrease the prevailing current velocity (Haight, 1926). The nontidal current in Favorite Channel, adjacent to Amalga Harbor, is from North-to-South/Southeast (Haight, 1926).Thus, it seems likely that during the slowest periods of tidal water movement, North-to-South would be the dominant flow direction, corresponding to movement perpendicular to our primary transect.

4.2 | eDNA distribution across depth

Our dataset from 2022 provided evidence for significant depth stratification of salmon eDNA at our study site. We found the highest concentration of eDNA in surface samples, with decreasing concentration and detections at both 5 m and 10 m (Figures 3 and 4). This vertical distribution mirrors findings from the mackerel cage experiment in the Sea of Japan (Murakami et al., 2019), yet is counter to results from Atlantic salmon farms in British Columbia, where sampling at 8 m depth corresponded to higher DNA concentrations (Shea et al., 2022). However, the Atlantic salmon farm net pens can be 40–50 m deep—much deeper than the chum salmon pens in our study (which extended to 6 m below the surface) or the mackerel cage, which was ~2 m below the surface (Murakami et al., 2019). Thus, is seems plausible that eDNA associated with larger particles in close proximity to the pens will settle out of the water column quickly, leaving only more neutrally buoyant eDNA corresponding to the relative depth layer and water mass where the organism is present (Allan et al., 2021; Shelton et al., 2022). The substantial difference in eDNA concentration between the surface and 5 m depth in our study could be caused by surface-oriented behavior of chum salmon in net pens (i.e., due to surface feeding) and water stratification in the study area (Figure S3).

Although fundamentally a different sampling technique than qPCR, eDNA metabarcoding studies have also detected vertical stratification, diel migration, and other depth patterns indicating that eDNA does not disperse freely between water masses or depth layers (Easson et al., 2020; Jensen et al., 2022; Jeunen et al., 2019). Consistent with these studies, models indicate that vertical displacement by advection, dispersion, and settling has limited influence on eDNA distribution, and the depth at which eDNA is found is generally within tens of meters of the depth at which the eDNA was originally shed from the organism (Allan et al., 2021).

4.3 | Biomass/abundance and dispersion

Perhaps the most obvious source of variation across experimental studies of eDNA dispersion is fish biomass/abundance. Illustrating this point, this study produced a much stronger eDNA signature (both in DNA concentration and detection distance) from >46 million juvenile chum salmon than a cage with 49 mackerel.

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For reference, at 0 m from the net pens, this study measured between 10^5 and 10^7 DNA copies/L, whereas the study of mackerel measured $<10^4$ copies/L at 0 m from the pens. Similarly, a study of eDNA from four Atlantic salmon farms, raising adult fish, detected eDNA farther than 5 km from the nearest farm—consistent with the substantially larger biomass among the Atlantic salmon farms (Shea et al., 2022). More broadly, the relationship between biomass/abundance and eDNA concentration has been correlated with trawl catches (Kasmi et al., 2023; Maes et al., 2023; Salter et al., 2019), acoustic data (Shelton et al., 2022), beach seines (Shelton et al., 2019), and angling catches (Ogonowski et al., 2023). These studies generally identify a positive relationship between biomass and DNA concentration, presumably due to increased DNA shed by more individuals.

4.4 | Non-detections

Patterns of qPCR non-detections varied such that even samples collected within a short distance of the hatchery net pens did not always yield chum salmon. The same was true in the Sea of Japan cage experiment, where, although 79% of samples collected within 30 m of the cage amplified, the remaining 21% did not, despite close proximity to the DNA source. This phenomenon of stochastic non-detections is likely heightened when there is lower biomass of target species—as noted in the literature linking abundance and/or biomass to eDNA concentration (see above). In the case of our study of chum salmon, we expect the distribution of fish within the hatchery net pens to be more homogeneous than the distribution of 49 mackerel in the experimental cage study. If this is indeed true, we would expect fewer non-detections of chum salmon in close proximity to the net pens. In fact, surface samples collected at the edge of the hatchery net pens amplified consistently, as did samples up to several hundred meters away (Figure 3). However, increasing the sampling distance (500 m intervals) and direction (SE, NW) in the second year (2022) increased the number of non-detections (Figure 3). Unfortunately, no current data or hydrodynamic models are available for Amalga Harbor at relevant spatial resolution, and nearshore oceanography includes complex interactions between tides, wind, freshwater input, and currents. Thus, variation between 2021 and 2022 could be caused by a number of untested environmental conditions that impact the distribution of chum salmon eDNA. Our sampling sites that overlapped between 2021 and 2022 show how eDNA dispersion distance may not be consistent, even in the same location (Figure S5).

4.5 | Applications to fisheries management

Importantly, our data provide some bounds that may be useful for modeling efforts to estimate the distribution and abundance of important fisheries species (Shelton et al., 2022). Many such species—especially in the northeast Pacific—form incredibly large schools that represent biomass on the scale of the >46 million salmon in our net pen experiment. Large schools of fish will produce a strong eDNA signal with DNA concentration decreasing and detections becoming more sporadic, and then absent, as distance increases. Based on studies of marine eDNA transport, this detection radius decreases with smaller biomass. Therefore, eDNA samples from a spatially explicit sampling design could be used to estimate the biomass/proximity of target species. Modeling these types of processes is complex, but this study represents an important step toward accurately parameterizing models that could be integrated into management.

5 | CONCLUSIONS

Patterns of eDNA dispersion in the coastal ocean indicate high fidelity of elevated DNA concentrations near a point source, but with variable detections with increasing distance influenced by fish biomass/abundance and environmental factors. Even with very large sources of eDNA (i.e., rearing pens for hatchery salmon), dispersal distance is within just a few kilometers, and the bulk of eDNA remains much closer. Thus, eDNA detections of marine fishes are likely representative of present or recent proximity of those species, especially in environments with significant water movement (i.e., tidal swings, currents). It is possible that the nearshore represents a more complex system for eDNA dispersal than deeper offshore waters, in which case, hydrodynamic models may be of greater benefit to studies of eDNA transport offshore. Future studies that explicitly test offshore dispersal would add valuable context to eDNA collections geared toward characterizing the distribution of fishery species. Here, we provide empirical data on the transport of eDNA in high-latitude, cold-water marine systems, which often coincide with productive fishery regions where managers are eager to incorporate eDNA into their portfolio of management tools.

AUTHOR CONTRIBUTIONS

D.S.B., P.D.B., and W.A.L. designed the study. D.S.B. and M.R.P. performed laboratory work and generated data. D.S.B. analyzed data and wrote the manuscript with input from all authors. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and analyses are available on GitHub at https://github.com/DianaBaetscher-NOAA/amalga-eDNA.

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REFERENCES

Allan, E. A., DiBenedetto, M. H., Lavery, A. C., Govindarajan, A. F., & Zhang, W. G. (2021). Modeling characterization of the vertical and temporal variability of environmental DNA in the mesopelagic ocean. *Scientific Reports*, *11*(1), 21273. https://doi.org/10.1038/s41598-021-00288-5

Andruszkiewicz, E. A., Koseff, J. R., Fringer, O. B., Ouellette, N. T., Lowe, A. B., Edwards, C. A., & Boehm, A. B. (2019). Modeling environmental DNA transport in the Coastal Ocean using Lagrangian particle tracking. *Frontiers in Marine Science*, *6*, 477. https://www.frontiersin.org/articles/10.3389/fmars.2019.00477

Andruszkiewicz, E. A., Sassoubre, L. M., & Boehm, A. B. (2017). Persistence of marine fish environmental DNA and the influence of sunlight. *PLoS One*, *12*(9), e0185043. https://doi.org/10.1371/journal.pone.0185043

Collins, R. A., Wangensteen, O. S., O'Gorman, E. J., Mariani, S., Sims, D. W., & Genner, M. J. (2018). Persistence of environmental DNA in marine systems. *Communications Biology*, *1*(1), 185. https://doi.org/10.1038/s42003-018-0192-6

Deiner, K., & Altermatt, F. (2014). Transport distance of invertebrate environmental DNA in a Natural River. *PLoS One*, *9*(2), e88786. https://doi.org/10.1371/journal.pone.0088786

Easson, C. G., Boswell, K. M., Tucker, N., Warren, J. D., & Lopez, J. V. (2020). Combined eDNA and acoustic analysis reflects diel vertical migration of mixed consortia in the Gulf of Mexico. *Frontiers in Marine Science*, *7*, 552. https://doi.org/10.3389/fmars.2020.00552

Ely, T., Barber, P. H., Man, L., & Gold, Z. (2021). Short-lived detection of an introduced vertebrate eDNA signal in a nearshore rocky reef environment. *PLoS One*, *16*(6), e0245314. https://doi.org/10.1371/journal.pone.0245314

Fukaya, K., Murakami, H., Yoon, S., Minami, K., Osada, Y., Yamamoto, S., Masuda, R., Kasai, A., Miyashita, K., Minamoto, T., & Kondoh, M. (2021). Estimating fish population abundance by integrating quantitative data on environmental DNA and hydrodynamic modelling. *Molecular Ecology*, *30*(13), 3057–3067. https://doi.org/10.1111/mec.15530

Gilbey, J., Carvalho, G., Castilho, R., Coscia, I., Coulson, M. W., Dahle, G., Derycke, S., Francisco, S. M., Helyar, S. J., Johansen, T., Junge, C., Layton, K. K. S., Martinsohn, J., Matejusova, I., Robalo, J. I., Rodríguez-Ezpeleta, N., Silva, G., Strammer, I., Vasemägi, A., & Volckaert, F. A. M. (2021). Life in a drop: Sampling environmental DNA for marine fishery management and ecosystem monitoring. *Marine Policy*, *124*, 104331. https://doi.org/10.1016/j.marpol.2020.104331

Haight, F. J. (1926). Nontidal currents in southeastern Alaska. *Geographical Review*, *16*(4), 642–646. https://doi.org/10.2307/208391

Hansen, B. K., Bekkevold, D., Clausen, L. W., & Nielsen, E. E. (2018). The sceptical optimist: Challenges and perspectives for the application of environmental DNA in marine fisheries. *Fish and Fisheries*, *19*(5), 751–768. https://doi.org/10.1111/faf.12286

Harrison, J. B., Sunday, J. M., & Rogers, S. M. (2019). Predicting the fate of eDNA in the environment and implications for studying biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1915), 20191409. https://doi.org/10.1098/rspb.2019.1409

Homel, K. M., Franklin, T. W., Carim, K. J., McKelvey, K. S., Dysthe, J. C., & Young, M. K. (2021). Detecting spawning of threatened chum salmon Oncorhynchus keta over a large spatial extent using eDNA sampling: Opportunities and considerations for monitoring recovery. *Environmental DNA*, *3*(3), 631–642. https://doi.org/10.1002/edn3.159

Jane, S. F., Wilcox, T. M., McKelvey, K. S., Young, M. K., Schwartz, M. K., Lowe, W. H., Letcher, B. H., & Whiteley, A. R. (2015). Distance, flow and PCR inhibition: eDNA dynamics in two headwater streams. *Molecular Ecology Resources*, *15*(1), 216–227. https://doi.org/10.1111/1755-0998.12285

Jensen, M. R., Sigsgaard, E. E., Ávila, M. D. P., Agersnap, S., Brenner-Larsen, W., Sengupta, M. E., Xing, Y., Krag, M. A., Knudsen, S. W., Carl, H., Møller, P. R., & Thomsen, P. F. (2022). Short-term temporal variation of coastal marine eDNA. *Environmental DNA*, *4*(4), 747–762. https://doi.org/10.1002/edn3.285

Jeunen, G.-J., Knapp, M., Spencer, H. G., Lamare, M. D., Taylor, H. R., Stat, M., Bunce, M., & Gemmell, N. J. (2019). Environmental DNA (eDNA) metabarcoding reveals strong discrimination among diverse marine habitats connected by water movement. *Molecular Ecology Resources*, *19*(2), 426–438. https://doi.org/10.1111/1755-0998.12982

Jo, T., Murakami, H., Yamamoto, S., Masuda, R., & Minamoto, T. (2019). Effect of water temperature and fish biomass on environmental DNA shedding, degradation, and size distribution. *Ecology and Evolution*, *9*(3), 1135–1146. https://doi.org/10.1002/ece3.4802

Kasmi, Y., Blancke, T., Eschbach, E., Möckel, B., Casas, L., Bernreuther, M., Nogueira, P., Delfs, G., Kadhim, S., Meißner, T., Rödiger, M., Eladdadi, A., Stransky, C., & Hanel, R. (2023). Atlantic cod (*Gadus morhua*) assessment approaches in the north and Baltic Sea: A comparison of environmental DNA analysis versus bottom trawl sampling. *Frontiers in Marine Science*, *10*, 1058354. https://doi.org/10.3389/fmars.2023.1058354

Kelly, R. P., Gallego, R., & Jacobs-Palmer, E. (2018). The effect of tides on nearshore environmental DNA. *PeerJ*, *6*, e4521. https://doi.org/10.7717/peerj.4521

Klymus, K. E., Merkes, C. M., Allison, M. J., Goldberg, C. S., Helbing, C. C., Hunter, M. E., Jackson, C. A., Lance, R. F., Mangan, A. M., Monroe, E. M., Piaggio, A. J., Stokdyk, J. P., Wilson, C. C., & Richter, C. A. (2020). Reporting the limits of detection and quantification for environmental DNA assays. *Environmental DNA*, *2*(3), 271–282. https://doi.org/10.1002/edn3.29

Lacoursière-Roussel, A., Côté, G., Leclerc, V., & Bernatchez, L. (2016). Quantifying relative fish abundance with eDNA: A promising tool for fisheries management. *Journal of Applied Ecology*, *53*(4), 1148–1157. https://doi.org/10.1111/1365-2664.12598

Lacoursière-Roussel, A., Rosabal, M., & Bernatchez, L. (2016). Estimating fish abundance and biomass from eDNA concentrations: Variability among capture methods and environmental conditions. *Molecular Ecology Resources*, *16*(6), 1401–1414. https://doi.org/10.1111/1755-0998.12522

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*(7), 2494–2505. https://doi.org/10.1111/1755-0998.13627

Laporte, M., Bougas, B., Côté, G., Champoux, O., Paradis, Y., Morin, J., & Bernatchez, L. (2020). Caged fish experiment and hydrodynamic bi-dimensional modeling highlight the importance to consider 2D dispersion in fluvial environmental DNA studies. *Environmental DNA*, *2*(3), 362–372. https://doi.org/10.1002/edn3.88

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Larson, W. A., Barry, P., Dokai, W., Maselko, J., Olson, J., & Baetscher, D. (2022). Leveraging eDNA metabarcoding to characterize nearshore fish communities in Southeast Alaska: Do habitat and tide matter? *Environmental DNA*, *4*(4), 868–880. https://doi.org/10.1002/edn3.297

Maes, S. M., Desmet, S., Brys, R., Sys, K., Ruttink, T., Maes, S., Hostens, K., Vansteenbrugge, L., & Derycke, S. (2023). Detection and quantification of two commercial flatfishes (Solea solea and Pleuronectes platessa) in the North Sea using environmental DNA. *Environmental DNA*, *1-15*, e426. https://doi.org/10.1002/edn3.426

McKee, A. M., Spear, S. F., & Pierson, T. W. (2015). The effect of dilution and the use of a post-extraction nucleic acid purification column on the accuracy, precision, and inhibition of environmental DNA samples. *Biological Conservation*, *183*, 70–76. https://doi.org/10.1016/j.biocon.2014.11.031

Menning, D., Simmons, T., & Talbot, S. (2020). Using redundant primer sets to detect multiple native Alaskan fish species from environmental DNA. *Conservation Genetics Resources*, *12*(1), 109–123. https://doi.org/10.1007/s12686-018-1071-7

Monuki, K., Barber, P. H., & Gold, Z. (2021). eDNA captures depth partitioning in a kelp forest ecosystem. *PLoS One*, *16*(11), e0253104. https://doi.org/10.1371/journal.pone.0253104

Murakami, H., Yoon, S., Kasai, A., Minamoto, T., Yamamoto, S., Sakata, M. K., Horiuchi, T., Sawada, H., Kondoh, M., Yamashita, Y., & Masuda, R. (2019). Dispersion and degradation of environmental DNA from caged fish in a marine environment. *Fisheries Science*, *85*(2), 327–337. https://doi.org/10.1007/s12562-018-1282-6

Ogonowski, M., Karlsson, E., Vasemägi, A., Sundin, J., Bohman, P., & Sundblad, G. (2023). Temperature moderates eDNA–biomass relationships in northern pike. *Environmental DNA*, *5*(4), 750–765. https://doi.org/10.1002/edn3.440

Port, J. A., O'Donnell, J. L., Romero-Maraccini, O. C., Leary, P. R., Litvin, S. Y., Nickols, K. J., Yamahara, K. M., & Kelly, R. P. (2016). Assessing vertebrate biodiversity in a kelp forest ecosystem using environmental DNA. *Molecular Ecology*, *25*(2), 527–541. https://doi.org/10.1111/mec.13481

Ramón-Laca, A., Wells, A., & Park, L. (2021). A workflow for the relative quantification of multiple fish species from oceanic water samples using environmental DNA (eDNA) to support large-scale fishery surveys. *PLoS One*, *16*(9), e0257773. https://doi.org/10.1371/journal.pone.0257773

Renshaw, M. A., Olds, B. P., Jerde, C. L., McVeigh, M. M., & Lodge, D. M. (2015). The room temperature preservation of filtered environmental DNA samples and assimilation into a phenol–chloroform–isoamyl alcohol DNA extraction. *Molecular Ecology Resources*, *15*(1), 168–176. https://doi.org/10.1111/1755-0998.12281

Salter, I., Joensen, M., Kristiansen, R., Steingrund, P., & Vestergaard, P. (2019). Environmental DNA concentrations are correlated with regional biomass of Atlantic cod in oceanic waters. *Communications Biology*, *2*(1), 461. https://doi.org/10.1038/s42003-019-0696-8

Sassoubre, L. M., Yamahara, K. M., Gardner, L. D., Block, B. A., & Boehm, A. B. (2016). Quantification of environmental DNA (eDNA) shedding and decay rates for three marine fish. *Environmental Science & Technology*, *50*(19), 10456–10464. https://doi.org/10.1021/acs.est.6b03114

Shea, D., Frazer, N., Wadhawan, K., Bateman, A., Li, S., Miller, K. M., Short, S., & Krkošek, M. (2022). Environmental DNA dispersal from Atlantic salmon farms. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(9), 1377–1388. https://doi.org/10.1139/cjfas-2021-0216

Shelton, A. O., Kelly, R. P., O'Donnell, J. L., Park, L., Schwenke, P., Greene, C., Henderson, R. A., & Beamer, E. M. (2019). Environmental DNA provides quantitative estimates of a threatened salmon species. *Biological Conservation*, *237*, 383–391. https://doi.org/10.1016/j.biocon.2019.07.003

Shelton, A. O., O'Donnell, J. L., Samhouri, J. F., Lowell, N., Williams, G. D., & Kelly, R. P. (2016). A framework for inferring biological communities from environmental DNA. *Ecological Applications*, *26*(6), 1645–1659. https://doi.org/10.1890/15-1733.1

Shelton, A. O., Ramón-Laca, A., Wells, A., Clemons, J., Chu, D., Feist, B. E., Kelly, R. P., Parker-Stetter, S. L., Thomas, R., Nichols, K. M., & Park, L. (2022). Environmental DNA provides quantitative estimates of Pacific hake abundance and distribution in the open ocean. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1971), 20212613. https://doi.org/10.1098/rspb.2021.2613

Sigsgaard, E. E., Nielsen, I. B., Carl, H., Krag, M. A., Knudsen, S. W., Xing, Y., Holm-Hansen, T. H., Møller, P. R., & Thomsen, P. F. (2017). Seawater environmental DNA reflects seasonality of a coastal fish community. *Marine Biology*, *164*(6), 128. https://doi.org/10.1007/s00227-017-3147-4

Spence, B. C., Rundio, D. E., Demetras, N. J., & Sedoryk, M. (2021). Efficacy of environmental DNA sampling to detect the occurrence of endangered coho salmon (Oncorhynchus kisutch) in Mediterranean-climate streams of California's central coast. *Environmental DNA*, *3*(4), 727–744. https://doi.org/10.1002/edn3.175

Strickler, K. M., Fremier, A. K., & Goldberg, C. S. (2015). Quantifying effects of UV-B, temperature, and pH on eDNA degradation in aquatic microcosms. *Biological Conservation*, *183*, 85–92. https://doi.org/10.1016/j.biocon.2014.11.038

Tsuji, S., Ushio, M., Sakurai, S., Minamoto, T., & Yamanaka, H. (2017). Water temperature-dependent degradation of environmental DNA and its relation to bacterial abundance. *PLoS One*, *12*(4), e0176608. https://doi.org/10.1371/journal.pone.0176608

Wood, Z. T., Lacoursière-Roussel, A., LeBlanc, F., Trudel, M., Kinnison, M. T., Garry McBrine, C., Pavey, S. A., & Gagné, N. (2021). Spatial heterogeneity of eDNA transport improves stream assessment of threatened Salmon presence, abundance, and location. *Frontiers in Ecology and Evolution*, *9*, 650717. https://doi.org/10.3389/fevo.2021.650717

Yamamoto, S., Minami, K., Fukaya, K., Takahashi, K., Sawada, H., Murakami, H., Tsuji, S., Hashizume, H., Kubonaga, S., Horiuchi, T., Hongo, M., Nishida, J., Okugawa, Y., Fujiwara, A., Fukuda, M., Hidaka, S., Suzuki, K. W., Miya, M., Araki, H., … Kondoh, M. (2016). Environmental DNA as a 'snapshot' of fish distribution: A case study of Japanese Jack mackerel in Maizuru Bay, Sea of Japan. *PLoS One*, *11*(3), e0149786. https://doi.org/10.1371/journal.pone.0149786

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