

¹ Quantitative, Multispecies Monitoring at a Continental Scale

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⁸ **Author Contributions**

⁹ AOS, KMN, RPK, MS, and KP designed the research;

¹⁰ MRS, AR-L and AW did the laboratory work;

¹¹ PB, RPK, and GG did the bioinformatics;

¹² GG, OL, RPK, and AOS analyzed the data;

¹³ GG, OL, RPK, and AOS interpreted the results;

¹⁴ All authors provided edits to the manuscript

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¹⁶ **Author Declaration**

¹⁷ The authors declare no competing interest.

¹⁸ **Keywords**

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³⁰ **Abstract**

³¹ Molecular data from environmental samples can reflect the abundance of species' DNA, an index immediately
³² relevant to natural-resources management at a broad geographic scale. These data commonly derive from
³³ assays designed and targeted for specific species (e.g., using qPCR or dPCR), or metabarcoding assays from
³⁴ more general PCR primers that amplify many species simultaneously. Multispecies analyses make efficient
³⁵ use of field samples and laboratory time, and speak to inherently multispecies questions of management
³⁶ and ecological interest. However, unlike single-species techniques, metabarcoding by itself can reflect only
³⁷ the proportions of target-species DNA present, not their absolute quantities. Here, we combine qPCR and
³⁸ metabarcoding data derived from the same samples to map quantities of many fish species along the US
³⁹ West Coast in three dimensions, demonstrating a technique of practical importance for both management and
⁴⁰ ecology. We derive spatially explicit estimates of eDNA abundance for 12 common species of ecological and
⁴¹ management importance and point the way to quantitative surveys of wild species using molecules alone.
⁴² We find that species distribution maps derived from eDNA effectively capture species niches and spatial
⁴³ distributions. Notably, our analyses identified biodiversity hotspots that align with previously documented
⁴⁴ regions of ecological significance, such as the Columbia River plume and the Heceta Bank.

45 Introduction

46 Environmental DNA (eDNA, residual genetic material sampled from water, soil, or air) is an increasingly
47 common tool for non-invasively sampling marine and aquatic ecological communities, valuable for estimating
48 species occurrence [72], biodiversity (i.e., Richness, [46]), and genetic structure [4]. However, eDNA has
49 not been widely used for quantitative abundance estimation, upon which many practical management and
50 conservation applications rely (but see [59, 20, 64]). The use of eDNA for quantification is supported both
51 conceptually – where there is more of a species, more cells are shed in the environment, and thus there
52 is more DNA – and empirically (e.g. there are strong linkages between single-species eDNA measures of
53 in aquaria [27, 37], rivers and streams [50], estuaries and nearshore habitats [14, 6], and coastal oceans
54 [41, 58]). However, uses of quantitative eDNA observations in management applications have significantly
55 lagged behind their use in occurrence and biodiversity applications.

56 Quantitative estimates of DNA are more common with species-specific assays (e.g. qPCR and ddPCR)
57 because these approaches directly measure DNA concentration. In contrast, multispecies analysis (metabarcoding)
58 reflects information on many species of interest simultaneously, but at the costs of producing compositional
59 estimates of proportional abundance [18, 43] that may require statistical correction for species-specific
60 biases due to PCR amplification [57]. Consequently, metabarcoding data alone cannot yield information
61 about the abundance of DNA from environmental samples (e.g. [20]).

62 Surveys of marine environments play a fundamental role in supporting fisheries and conservation of pro-
63 tected species but are often difficult and expensive endeavors. While trawling, acoustics, or other traditional
64 sampling methods have long been used to directly measure species abundance and biomass, they can be
65 impractical for species inhabiting inaccessible habitats, occurring at low densities, or for fragile species easily
66 injured during capture. By contrast, eDNA sampling captures information on a broader range of taxa, in-
67 cluding those that are difficult or impossible to study with traditional gear. As such, eDNA can meaningfully
68 complement traditional stock assessment methods for commercially important species while at the same time
69 revealing the abundance and distribution of elusive or understudied species.

70 Here, we develop quantitative estimates of eDNA abundance for a diverse group of fish species spanning
71 different depth niches across 10 degrees of latitude along the US West Coast entirely from eDNA. We inte-
72 grate single- and multi-species (using MiFish-U universal primers [44]) techniques to create three-dimensional
73 distribution maps, leveraging models established in previous studies [59, 20, 57, 2]. By calibrating metabar-
74 coding data – correcting raw species observations to their initial proportions using a mock community [57]
75 – and using the absolute eDNA quantity of a reference species (here Pacific Hake (*Merluccius productus*)),
76 we expand initial estimated proportions into absolute estimates of the abundance of each species' eDNA

77 [20]. We subsequently smooth the estimated eDNA quantities to generate species distribution maps [39]. We
78 present quantitative results for 12 fish species using eDNA, comparing them with literature-based species
79 distributions to illustrate the approach, but note that it immediately generalizes to any ecological community
80 of interest.

81 The eDNA-derived estimates we provide here speak directly to the requirements of natural-resources
82 management at large scales. For example, indices of abundance have a central role in determining stock
83 status for fisheries applications (i.e., stock assessments in the U.S. under the Magnuson-Stevens Act) as
84 well as informing conservation status (e.g., under the U.S. Endangered Species Act). Thus eDNA-derived
85 abundance indices can fill a variety of existing requirements for management. While these indices are still
86 in their infancy and will require additional technical developments to ensure their proper usage, they are
87 conceptually and practically little different from abundance estimates derived from more traditional ocean
88 survey methods (i.e., net-based or acoustic surveys). Indeed, eDNA methods may provide some notable
89 improvements because single- and multi-species eDNA approaches avoid tradeoffs involved with physically
90 capturing many species simultaneously using a single net. Molecular surveys capture many species with
91 the same “gear” using methods that are easily replicated in space and time. As U.S. agencies begin to
92 implement the new National Aquatic eDNA Strategy [31] – the first goal of which is to fold eDNA data into
93 federal decisionmaking – this and other large-scale examples point the way to maximizing the benefit of this
94 information-rich datastream for natural-resources management at a continental scale.

95 Methods

96 Sample Collection, Processing, and Quantitative PCR (qPCR)

97 We used samples collected in 10L Niskin bottles deployed on a CTD rosette at six depths (0, 50, 150, 300,
98 500 m) from stations along the West Coast of the US aboard the ship *Bell M. Shimada* during Summer 2019
99 on the Joint U.S.–Canada Integrated Ecosystem and Pacific Hake Acoustic-Trawl Survey [12]. 2.5L water
100 samples were collected from each Niskin and filtered immediately on 47 mm diameter mixed cellulose-ester
101 sterile filters with a 1 μ m pore size, subsequently extracted using a phase-lock phenol-chloroform protocol,
102 and analyzed in triplicate using a qPCR assay, multiplexed for Pacific hake, sea lamprey, and eulachon, as
103 described in [53] and [59]. A subset of the samples ($n = 554$) collected in [59], was used for metabarcoding
104 analysis this study in addition to qPCR samples already published for hake quantification [59] ($n = 1,794$).

105 **Metabarcoding: Environmental Samples and Mock Community**

106 In total, 554 environmental samples were randomized and divided into 7 sequencing libraries for an Illumina
107 MiSeq (v3 600 cycle kit). Total PCR reactions including PCR blanks ($n = 7$) and positive controls ($n =$
108 7), were amplified using MiFish-U universal primers [44] (see SI Appendix Extended Methods for details
109 on metabarcoding methods). Importantly, we only analyzed one water sample collected from each sampling
110 station using metabarcoding.

111 Sequences were de-multiplexed and the adapters removed by Illumina sequencing. Primers were removed
112 with Cutadapt v4.9 [42]. We then used DADA2 (default parameters, [10]) to denoise sequences, remove
113 chimeras, and generate amplicon sequence variants (ASVs). The sequences were then BLASTed against
114 the NCBI nucleotide (nt) database (access: August 2024) using BLASTn algorithm with a cut off at 97%
115 identity, assigning the least common ancestor of the top hit, resulting in species, genus, family, or higher
116 rank classifications. Samples with fewer total number of reads than 1000 were filtered as an indicator of poor
117 reliability. Of the initial environmental samples, 535 passed the quality filtering and and 371 were selected
118 for downstream analysis (see SI Appendix, Fig. S4) due to presence detection of Pacific hake in both qPCR
119 and metabarcoding data streams (see SI Appendix Extended Methods). Details on bioinformatic pipeline
120 are available in SI Appendix Extended Methods.

121 To calibrate metabarcoding observations and account for amplification bias [57, 19], we generated multi-
122 ple mock communities comprising a total of 39 fish species. Vouchered DNA extracts or tissues were obtained
123 from either the University of Washington Fish Collection at the Burke Museum or the NOAA Northwest
124 Fisheries Science Center collections. After quantifying the concentration of mitochondrial DNA template in
125 each DNA extract, we constructed a total of eight mock communities of varying species compositions (see SI
126 Appendix, Table S1). We selected 12 species (additional to Pacific hake) of commercial and ecological impor-
127 tance that co-occurred in the environmental samples and in the mock community for downstream analysis:
128 Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), northern smoothtongue (*Leuroglos-*
129 *sus stilbius*), Dover sole (*Microstomus pacificus*), Pacific sardine (*Sardinops sagax*), Pacific chub mackerel
130 (*Scomber japonicus*), widow rockfish (*Sebastodes entomelas*), northern lampfish (*Stenobrachius leucopsarus*),
131 California barracudina (*Tactostoma macropus*), plainfin midshipman (*Tarletonbeania crenularis*), eulachon
132 (*Thaleichthys pacificus*), Pacific jack mackerel (*Trachurus symmetricus*). After amplification and sequenc-
133 ing using the protocols outlined above, we used the mock communities (which were run in the same PCR
134 conditions as the environmental samples) to estimate species-specific amplification efficiencies and correct
135 for amplification bias following [57].

136 **Statistical analysis**

137 To generate estimates of DNA concentration, we constructed a joint statistical model for qPCR and Mi-
138 fish metabarcoding observations from the same samples. This model is based on the QM R package
139 (www.github.com/gledguri/QM), with some modifications and advancements. The full statistical details
140 are described in SI Appendix Extended Methods, with an overview of the approach (Fig. 1). We used
141 qPCR observations of hake DNA concentration for all water samples available (1,794 unique water samples
142 were assayed and using a total of 5,394 qPCR reactions). This model takes observations of the PCR cycle
143 at which amplification was detected in each field sample and estimates a hake DNA concentration for each
144 water bottle collected at each sampling station-depth combination (Fig. 1). This statistical model accounts
145 for sample-specific effects (e.g., dilution of the sample before PCR amplification), the effect of replicate
146 water samples (a random effect), to provide estimates of hake DNA concentration in from each water sam-
147 ple collected at each location and depth (Fig. 1). This qPCR component of the joint model provides a
148 quantification of DNA concentration for one species (Pacific hake) that can be connected to the multispecies
149 proportions provided by DNA metabarcoding (Fig. 1).

150 Unlike single-species observation methods, metabarcoding data is compositional data. This means that
151 each sample only provides information about relative species abundances rather than absolute DNA concen-
152 trations. Furthermore, metabarcoding does not yield a consistent, species-specific detection probability (i.e.,
153 sensitivity). Instead, the likelihood of detecting a particular species depends heavily on its competition with
154 other sequences during PCR amplification [57], as well as on the total sequencing depth for that sample [32].
155 Greater sequencing depth generally increases the probability of identifying rarer species, conditional on their
156 DNA being collected and it being amplifiable with the chosen PCR primers.

157 We follow [57] and construct a compositional model for the metabarcoding data from 371 of the water
158 samples (after quality filtering) analyzed for Pacific hake qPCR. We use the metabarcoding observations of
159 the 8 mock communities to calibrate the relative amplification efficiency of the 12 focal species (plus hake,
160 a 13th species). In the absence of qPCR data, this model would produce estimates of proportional DNA
161 contributions for each water sample. But for each sample in which we have non-zero estimates of hake DNA
162 concentration from qPCR, and non-zero estimate of hake proportional contribution from metabarcoding
163 (SI Appendix Fig. S4), we can expand from the DNA concentration of hake to provide an estimate of
164 the DNA concentration of the 12 remaining focal species [2]. Our model generates estimates of DNA
165 concentration (copies/L) for each species. Thus hake is a lynchpin that allows us to provide estimates of
166 DNA concentration for all other species. Hake was present in 86.7% of samples via qPCR, and 67.7% of
167 samples via metabarcoding, making it an appropriate and important reference species. To enhance sample

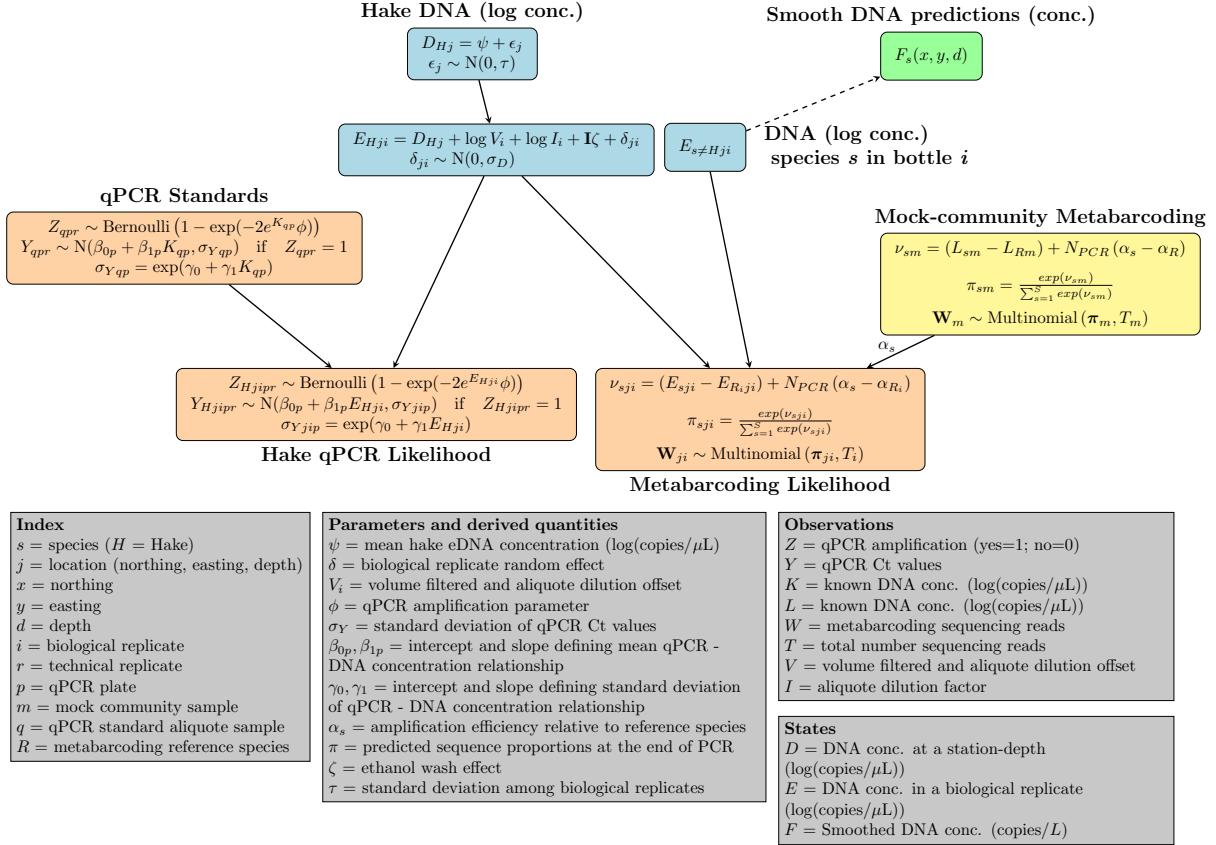


Figure 1: Schematic for the statistical models to produce species distributions. Three sets of observations (orange) were used simultaneously to provide estimates of eDNA concentration for twelve fish species (blue) from which we derive smoothed predictions of DNA concentration (green). Mock communities for metabarcoding (yellow) were estimated externally and provided estimated α_s that were used in the joint model. Notation for parameters, subscripts, and observations are indicated in gray.

168 coverage – by increasing the number of non-zero estimates of link species – and improve model accuracy,
169 multiple single-species qPCR assays can be integrated as additional sources of DNA concentration. However,
170 this approach must be applied thoughtfully, ensuring that selected qPCR targeted species have minimal co-
171 occurrence, like Pacific sardine or northern anchovy in our case (SI Appendix Fig. S5). Nevertheless, samples
172 lacking hake detections here were sporadically distributed across the study area (SI Appendix Fig. S4), and
173 deserve further attention in future work.

174 We focused on species that were relatively common in the raw dataset – those well above the lower de-
175 tection limits under our sampling and sequencing conditions – ensuring greater confidence in their consistent
176 detectability. Although many more species were detected in the raw data, the majority were much rarer and
177 thus less reliably observed.

178 The above statistical model (Fig. 1) provides predictions of species-specific DNA concentrations at each
179 location and depth sampled ($d = 0, 50, 150, 300$, or 500 m). We used the sdmTMB package [3] to generate
180 smooth maps of DNA concentration for each species independently (Fig. 1, green box). As Pacific hake
181 (*Merluccius productus*) has been examined elsewhere using qPCR [59], we did not include the spatial patterns
182 of that species in our analysis.

183 Analyses, figure preparation, and data curation were performed in R [52] and the joint statistical model
184 for qPCR and metabarcoding was coded in stan [62]. For a simplified version of this model, the QM R
185 package can be utilized (www.github.com/gledguri/QM).

186 Results

187 Previous eDNA work has tended to feature more qualitative multispecies results, or else quantitative analysis
188 of single species at small spatial scales. Here, we create a rigorous quantitative framework and use hundreds of
189 water samples to make ecological inferences at the scale of management. In this study, we find spatial patterns
190 of DNA concentrations reflect the distributions of commercially important coastal-pelagic fish species in
191 three dimensions and across ten degrees of latitude in a single year of sampling in 2019 (Fig. 2: Northern
192 Anchovy, Pacific Sardine; SI Appendix, Fig. S1, Pacific Herring and Jack Mackerel). For other high-biomass
193 species otherwise lacking well-described distributions, we provide the first species distribution models (Fig.
194 2, SI Appendix, Fig. S1). We find that the estimated eDNA concentrations are correlated among species
195 with similar traits and habitat preferences (Fig. 3). Emergent patterns of species richness and estimated
196 eDNA aggregation correspond with known ecological drivers, evidence that eDNA traces can reliably capture
197 ecologically meaningful patterns (Fig. 4). Particularly for forage fish species – which are critical high-biomass
198 links in marine food webs, but difficult to survey with traditional methods [49] – molecular methods offer

199 tractable and quantitative index of abundance over large spatial scales.

200 Below we highlight results for six species (Fig. 2) representing a range of habitat associations and general
201 species information; distribution maps for all the remaining species are presented in SI Appendix, Fig. S1. In
202 particular, our analyses present detailed, depth-specific information on abundance that is difficult to obtain
203 with traditional sampling methods.

204 **Surface species**

205 Northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*) are the two iconic coastal
206 pelagic species of the eastern North Pacific [63] and play a vital ecological role linking lower and upper
207 trophic levels (e.g., Chinook salmon diets, sea lions, [28]); historically these supported large commercial
208 fisheries particularly in California. While larvae and juveniles typically occupy the upper 50m, adults move
209 to 100m during the day to avoid predators. Our eDNA estimates consistently reflect the expected three-
210 dimensional distributions of known surface dwelling species, with high concentrations in surface waters for
211 both species[38, 48], and an accumulation pocket near the Columbia River outflow (46.2°N; Fig. 2). Sardine
212 favors slightly warmer temperatures and more southerly waters than anchovy (SST range from literature:
213 13–24°C for sardine vs. 10–14°C for anchovy). eDNA patterns tracked these differences with sardine eDNA
214 in greatest abundance at 41°N (range 40°–45°), while anchovy eDNA abundance was greatest at 43.5°N
215 (range 42°–48°; Fig. 5) such that eDNA captured subtle yet meaningful differences in habitat preferences.
216 When comparing the magnitude difference between the two species, eDNA abundance patterns suggest a
217 2.5-fold higher abundance for anchovy than sardine which agree in direction with stock assessments for
218 anchovy and sardine (an approximately 35-fold difference; [35, 34]). However, due to differences in stock
219 definitions and survey areas (the anchovy stock assessment includes southern California waters (32.5°–36°N)
220 not covered by the eDNA survey) these magnitudes are not directly comparable.

221 **Midwater species**

222 Widow rockfish (*Sebastodes entomelas*) is common between 100-350m between northern Baja California and
223 southern Alaska, with pelagic larvae and juveniles generally detected in shallower habitats (< 150m depth)
224 [54, 8] including in nearshore kelp forests [51, 36]. Moreover, because it is a common bycatch species in
225 the Pacific hake (*Merluccius productus*) fishery, concerns about bycatch of widow rockfish can also influence
226 the much larger hake fishery (i.e., it is a “choke” species for hake; [61]). Despite its commercial importance,
227 no targeted survey effort exists for widow rockfish, in part because bottom trawls do not sample its pelagic
228 habitat well. We find widow rockfish eDNA strongly and nearly exclusively associated with 50m sample

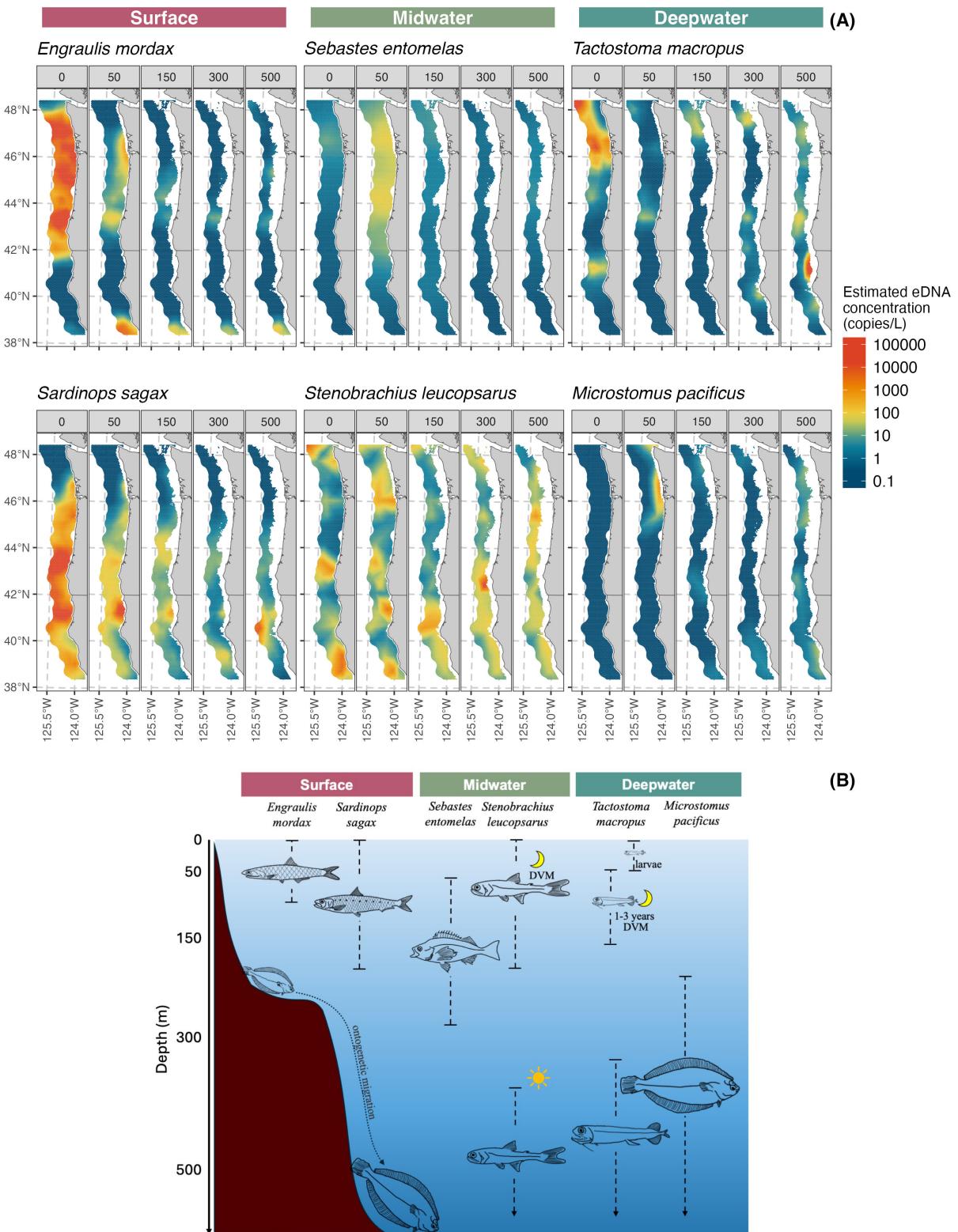


Figure 2: Estimated species eDNA concentration (A) across 0, 50, 150, 300, and 500m depth samples and known depth distribution of those species from literature (B).

229 depths (Fig. 2 and 5), consistent with the pelagic larvae and juveniles reported in the literature and
230 somewhat shallower than adults [54, 8, 51], potentially reflecting the species' nocturnal feeding schooling
231 behavior [54, 8].

232 The eDNA patterns for northern lampfish (*Stenobrachius leucopsarus*) – an abundant myctophid that
233 migrates from 400-700m up to 20-200m at night [45, 67] – are again consistent with the ecology of the species,
234 having notably lower concentrations in surface samples. Owing to the diel vertical migration of the northern
235 lampfish, the signal of eDNA for this species is observed across depths.

236 Deepwater species

237 Among deeper-water fishes, eDNA revealed spatial and potentially ontogenetic migration patterns for species
238 that are common, yet under studied, such as the dragonfish (*Tactostoma macropus*). Available literature
239 suggests dragonfish occur roughly between 40°N-50°N (adults at 300-900m, larvae at 0-60m in summer) [29]
240 and perform diel vertical migrations to around 100 meters [29, 74]. The eDNA concentrations appeared
241 to reflect this activity (Fig. 5), with the predominant surface signal at northern latitudes likely reflecting
242 larvae and juveniles (Fig. 2; near Columbia River discharge), and two deeper hotspots at 300m and 500m
243 separated by about eight degrees of latitude. However, no other quantitative estimates of abundance or
244 detailed distribution patterns for dragonfish exist in the current literature.

245 Also consistent with known habitats are commercially caught flatfish such as Dover sole (*Microstomus*
246 *pacificus*), which lives at 200m to 1200m along the Pacific coast [15, 9, 16]; individuals move progressively
247 deeper as they grow [73, 25]. The eDNA concentration estimates are consistent with this pattern, showing
248 high concentrations mostly in water samples collected close to the seabed (Fig. 2) [47].

249 Species Associations

250 Pairwise correlations of DNA concentration showed meaningful patterns among species associated with depth
251 (Fig. 3). Surface-associated species were nearly all positively correlated with each other, with some cor-
252 relations particularly large (Pearson's $\rho > 0.50$; Fig. 3). Correlations were weak among the six midwater
253 and deepwater species (all $\rho < |0.40|$; Fig. 3). Within the surface species, further subdivision was also
254 apparent, with chub mackerel (*Scomber japonicus*) and sardine (*Sardinops sagax*) showing very high cor-
255 relation ($\rho = 0.76$; Fig. 3) with both more common in the more southern (and somewhat warmer) waters
256 (Fig. 2 and Fig. 5). Concentrations of the remaining surface-dwelling species (Northern anchovy, eulachon,
257 jack mackerel, and Pacific herring) had modest correlations with midwater species (Fig. 3) consistent with
258 more northerly distribution (Fig. 5). Together these findings suggest that eDNA is capturing both depth

259 and latitudinal habitat associations. Deep-water species are distinct (Fig. 2 and Fig. 5) and not strongly
 260 correlated with those from other zones (Fig. 3). Deeper water tends to feature lower and more diffuse fish
 261 eDNA concentrations (Fig. 2 and Fig. 5). Lower overall eDNA concentrations and fewer deep water samples
 262 may make similarities among species distributions more difficult to detect at 300m and deeper.

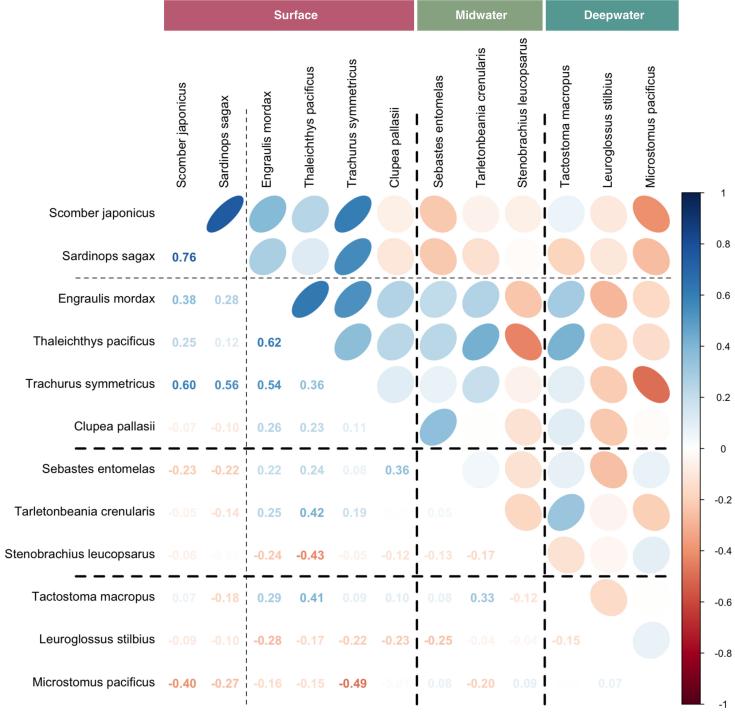


Figure 3: Correlation plot describing species co-abundance and co-occurrence. Spearman's ρ correlation coefficient are expressed in numbers and colors ranging from -1 (red) negatively correlated to 1 (blue) positively correlated. Species are ordered in known ecological groups (surface, midwater, and deepwater) to visually indicate the gradual change of species co-occurrence.

263 Species richness and total eDNA accumulation

264 In addition to providing species-specific patterns, eDNA metrics of abundance from individual species can
 265 be combined to reveal important aggregate ecological patterns. For the 12 species considered here, we show
 266 how species richness (see SI Appendix Fig. S3 for defining species presence) from eDNA varied substantially
 267 and predictably with depth, with the highest richness observed at the surface (Fig. 4A). In part, this pattern
 268 is likely to be an artifact of the focal species included in this study – chosen for their relevance to fisheries
 269 management as well as for their frequency in the observations (see Methods) – but the richness-depth gradient
 270 also reflects the expectation that habitat and nutrient availability is greatest near the surface [60, 22]. Surface
 271 waters also host the eggs, larvae, and juvenile stages of many meso- and bathypelagic species [48], some of

272 which we have included here, and hence we both expect and observe higher richness in the upper layer of
273 the water column [33].

274 Species richness also corresponds strongly with the influence of Columbia River plume (Fig. 4A), which
275 extends well beyond the coastline [24]. The nitrate-rich river water interacts with ocean currents and inten-
276 sifies coastal upwelling, enhancing both primary and secondary productivity [23] and likely influencing the
277 patterns of species richness we observe (Fig. 4A) [70]. The total fish eDNA accumulation (Fig. 4B) sug-
278 gests the highest aggregation of forage fish DNA near Heceta Bank (44 degrees N; overlapping anchovy and
279 sardine distributions are the two largest contributors to the observed peak of accumulated eDNA concentra-
280 tion) in addition to other commercialy important mesopelagic fish (*Sebastes entomelas* and *Tarletonbeania*
281 *crenularis*) a center of abundance for commercial fisheries [8, 69], and elsewhere nearshore in areas of coastal
282 upwelling.

283 Discussion

284 We report species-specific DNA concentrations smoothed over ten degrees of latitude and across the conti-
285 nental shelf to 500m. We reveal distributional patterns for 12 species ranging from the iconic coastal pelagic
286 species of the northeast Pacific to understudied-but-abundant deepwater species, and our results suggest
287 clear pathways for the broader use of eDNA in both fisheries and ecosystem management.

288 eDNA as Management Tool

289 By mapping three-dimensional spatial patterns, eDNA provides information on species distributions, habitat
290 preferences, and ecological processes that is often otherwise unavailable. A single water sample can yield
291 quantitative information on tens to hundreds of species – including for species for which traditional fish-
292 eries surveys are not currently conducted – without the need to develop species-specific assays. We find
293 species-level eDNA concentrations align closely with the preferred habitats' physiological constraints (e.g.,
294 temperature tolerance or food availability) described for each species in the available literature. The ob-
295 served latitudinal differences of eDNA concentration among species – such as those between anchovy and
296 sardine – highlights species' thermal ranges and largely coincide with other surveys [75]; moreover, eDNA
297 patterns appear to reflect diel vertical migrations as observed in myctophids, where eDNA concentrations
298 are consistent with the species' ontogenetic movement between surface and mid- to deep-water habitats.
299 We also identify aggregations of richness and total eDNA near high-productivity regions of ecological and
300 commercial value.

301 For well-studied taxa, existing information helps contextualize eDNA signals, providing insights into

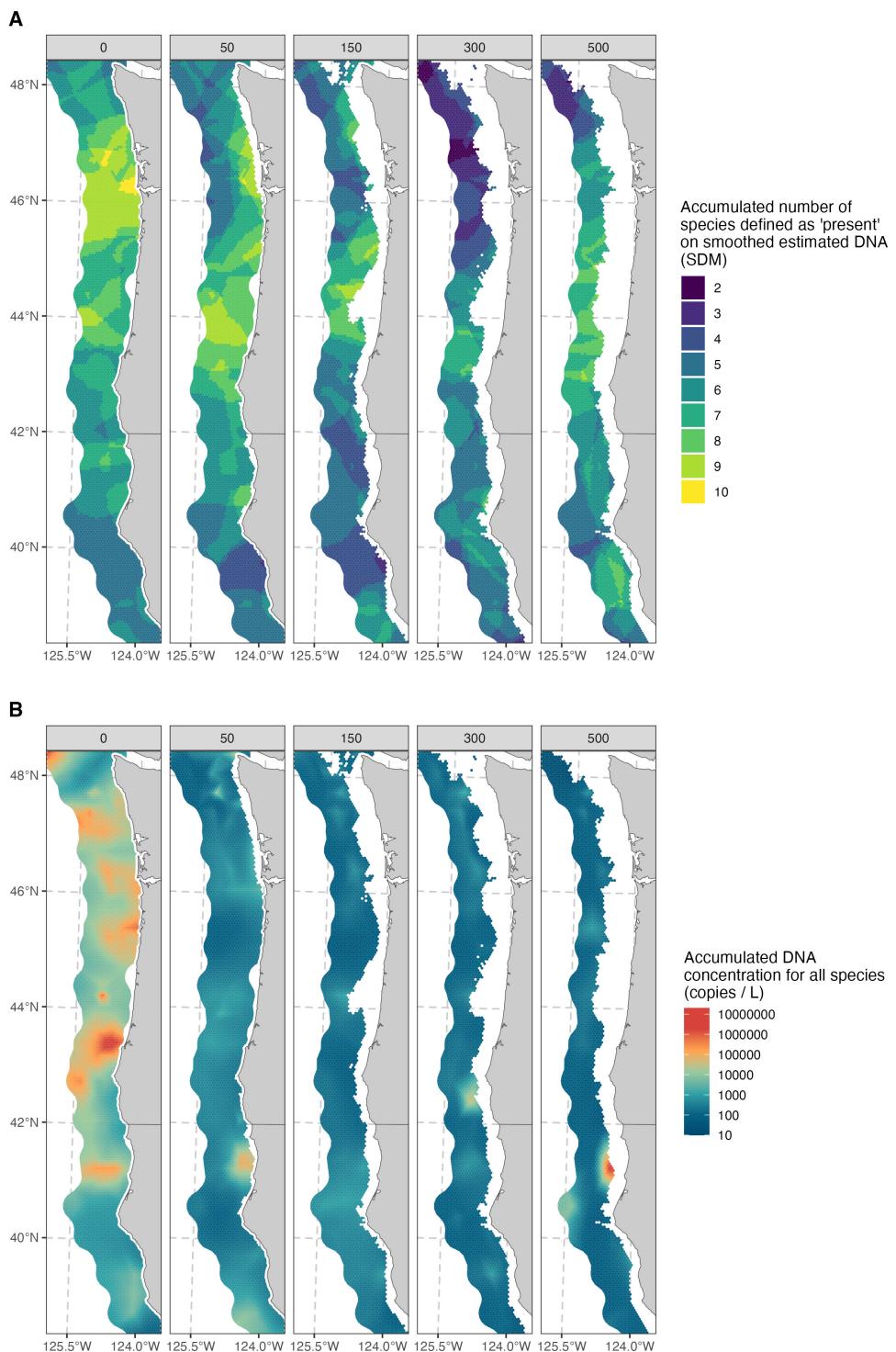


Figure 4: Spatial and vertical distribution of species richness (A) and environmental DNA (B) concentration across depths (0, 50, 150, 300, and 500 m). (B) Species richness represented as the cumulative number of species present (species with higher than 1.5 copies/L (see Fig. 5 for defining presence) on smoothed estimated eDNA concentrations) and accumulated eDNA concentration representing the cumulative sum of eDNA (copies/L) across all species.

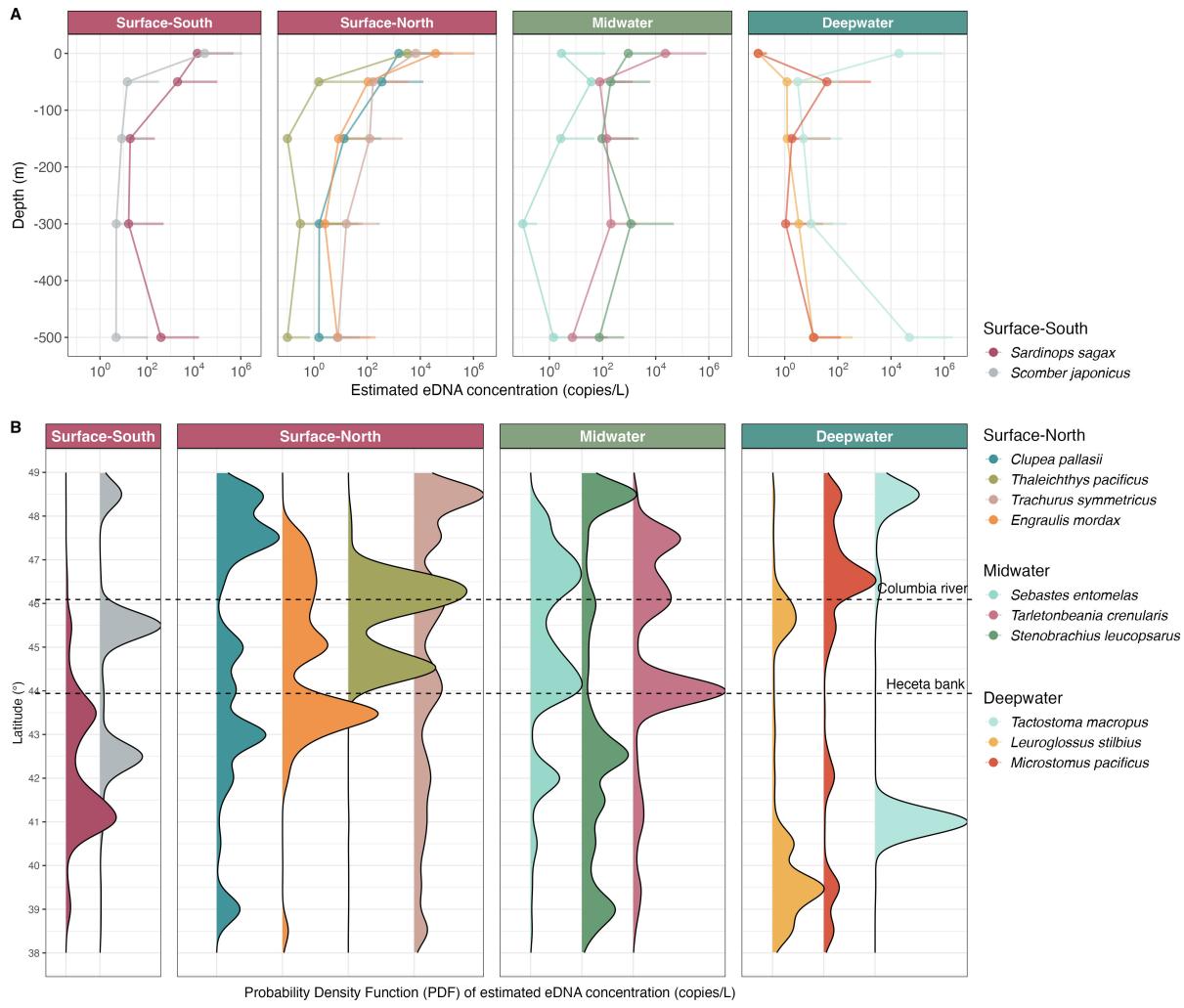


Figure 5: Vertical (A) and latitudinal (B) distribution of eDNA concentrations grouped in ecological groups (surface south, surface north, midwater, and deepwater). Mean eDNA concentration of vertical distribution is shown with dots and 99% upper quantile with ticks (A). Probability density functions (PDF) of estimated eDNA concentrations across latitudinal gradients (B; square root transformed of x-axis to enhance low concentration peaks). Key geographic features, such as the Columbia River and Heceta Bank, are marked to indicate alignment of species distributions.

302 habitat preferences, seasonal patterns, or temperature tolerances. For poorly studied species, eDNA serves as
303 an exploratory tool, detecting elusive taxa and revealing unexpected habitats. Widow rockfish, for example,
304 appear almost exclusively in pelagic habitats around 50m deep, which are sampled poorly by traditional
305 bottom-trawl surveys [30]. This species has been of special interest, as its targeted commercial harvest
306 resumed in the late 2010s after a decade of closure (harvest was less than 500 mt annually between 2003
307 and 2013 but has exceeded 10,000 mt annually since 2018) and no existing survey adequately captures its
308 patterns of abundance [1].

309 Environmental Smoothing

310 Our findings illustrate the power of eDNA as a transformative tool for fisheries management, biodiversity
311 conservation, and the study of environmental change. However, the observable eDNA signal at any given
312 location and time is an integrated product of DNA production and loss across time and space [19]: the
313 vast majority of DNA detectable in a given sample is of recent origin (within the previous hours to days
314 [66, 11, 40]), and it may be subject to a degree of physical transport within its window of detectability.
315 Accordingly, the vast majority of DNA will be relatively proximate to its source in both space and time, and
316 the distribution of DNA from a given species at any given time will be smoother and more extensive when
317 compared to the distribution of discrete source individuals. We refer to this as environmental smoothing of
318 eDNA signal relative to the source organisms themselves.

319 The majority of eDNA shed into the environment dissipates from surface waters within hours [5]. Thus,
320 the horizontal scale of environmental smoothing in our dataset likely spans several kilometers at most [6].
321 Given that our sampling area spans more than 1,200 km north to south and tens of km east to west, the
322 spatial patterns we report are likely to reflect genuine differences in fish communities rather than artifacts
323 of eDNA transport dynamics [21]. Vertical smoothing of eDNA signals appears minimal, with patterns at
324 the scale of meters: shallow-water species (sardine, anchovy, herring) occur largely at the surface and 50m
325 depth bins; Widow rockfish occurs almost exclusively at the 50m depth; species found throughout the water
326 column are either diel vertical migrators or species occupying different depths at various life-history stages
327 (Fig. 4B); and bottom-dwelling fishes are detected primarily at the deepest point sampled on any station.

328 Notably, the comparison between sample-specific eDNA estimation (SI Appendix, Fig. S6) and spatially
329 smoothed maps (Fig. 2 and SI Appendix, Fig. S1) revealed minimal differences. Large-scale sampling com-
330 bined with statistical smoothing mitigates many challenges associated with eDNA transport and degradation
331 – which decouple the eDNA observations from their particular source organisms – allowing reliable detection
332 of broad patterns in species distributions. Further methodological improvements may incorporate informa-

333 tion about the ecology of eDNA itself, such as the degree to which observations of eDNA concentrations
334 depend upon water temperature or other covariates [27].

335 **Integrating DNA with traditional surveys**

336 Effective management of natural resources at large scales requires that we maximize the information content
337 of existing sampling regimes. Here, we follow [59], leveraging the same water samples to provide information
338 on an additional 12 species of ecosystem and management importance. Elsewhere, a subset of these samples
339 has yielded information on the distribution of marine mammals [71]. The repeated use of a single set of
340 samples highlights an important strength of eDNA samples; they allow researchers to revisit and re-sequence
341 the genetic material in archived samples as new research questions arise or attention shifts to different taxa.
342 The use of these samples, from a targeted fisheries survey for hake, highlights the efficiency for which eDNA
343 can effectively provide survey data for tens or hundreds of additional species for which traditional surveys
344 do not exist.

345 This capacity for retrospective analysis allows historical samples to be re-examined at any point, insofar as
346 the sample is not exhausted, thereby offering opportunities to address emerging priorities and to reconstruct
347 past ecological conditions. For example, the ability to retrospectively pinpoint the origins and pathways of
348 invasive species can inform targeted interventions, helping managers understand not only where an incursion
349 began but also how it spread [17]. Similarly, the capacity to trace the initial onset of harmful algal blooms or
350 the earliest presence of pathogenic microbes enables researchers and policymakers to identify the underlying
351 drivers of these events and mitigate future outbreaks [56].

352 Moreover, integrating retrospective eDNA analyses a changing climate can enrich predictive frameworks
353 by providing historically grounded baselines of community composition, thereby enhancing our understanding
354 of ecosystem responses to environmental shifts. For example, [13] demonstrated how archived samples
355 could be leveraged to reconstruct past fish communities using eDNA, thereby complementing traditional
356 monitoring methods and further extending the utility of archived material. Such retrospective applications
357 deepen and extend the value of every research expedition, ensuring that once-collected samples continue
358 to yield valuable ecological insights over time. We therefore see eDNA as an important datastream that
359 maximizes the information value of existing research cruises, rather than a means of replacing those cruises
360 themselves.

361 We have shown an example of the potential value of multi-species eDNA analysis for fisheries and other
362 natural-resource management questions [37, 65], however, molecular patterns alone are unlikely to drive
363 quantitative natural-resources decisions, in part because eDNA generally does not provide auxiliary infor-

364 mation important for managing populations (e.g., information on size- or age structure, fecundity, sex, or
365 disease). Relating observed eDNA concentrations to species mass requires data external to the eDNA sig-
366 nal [20], and in particular, requires that we understand proportionalities between eDNA concentration and
367 biomass that may vary among species. We therefore see eDNA analysis as strengthening and extending
368 existing surveys, with different data streams complementing one another.

369 Conventional fish surveys, such as trawling or mark-recapture methods, typically rely on a closure as-
370 sumption assuming that fish populations are static during the sampling period [7], ignoring the reality of
371 fish movement within the study area thus introducing potential bias into abundance estimates [55]. By con-
372 trast, eDNA analysis leverages the continuous shedding of DNA by fish, which decays over time with higher
373 concentrations remaining fresh while older DNA persists at lower levels [68, 26]. This cumulative, time-
374 integrated signal allows eDNA surveys to circumvent the closure assumption and provide a more accurate
375 representation of fish presence and activity.

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