1

2

3 **Scoping the Line Up: A Comparison of Biomonitoring Methodologies for Surf Zone Fish**

4 **Communities**

5

6 Zachary Gold[1] [¶*], McKenzie Q. Koch[1¶], Nicholas K. Schooler[2], Kyle A. Emery[2], Jenifer E.

7 Dugan[2], Robert J. Miller[2], Henry M. Page[2], Donna M. Schroeder[3], David M. Hubbard[2], Jessica

8 R. Madden[2], Stephen G. Whitaker[2,4], and Paul H. Barber[1]

9

10 [1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, CA,
11 USA
12
13 [2]Marine Science Institute, University of California Santa Barbara, CA, USA
14
15 [3]Bureau of Ocean Energy Management, Camarillo, CA, USA
16
17 [4]Channel Islands National Park, Ventura, CA, USA
18

19

20 * Corresponding Author

21 Email: zjgold@ucla.edu

22 Phone: +1(310)-795-0020

23

24

25

26 ¶ These authors contributed equally to this work.

27

Abstract

Surf zones are highly dynamic marine ecosystems that are subject to increasing anthropogenic and climatic pressures, posing multiple challenges for biomonitoring. Traditional methods such as seines and hook and line surveys are often labor intensive, taxonomically biased, and can be physically hazardous. Emerging techniques, such as baited remote underwater video (BRUV) and environmental DNA (eDNA) are promising nondestructive tools for assessing marine biodiversity in surf zones of sandy beaches. Here we compare the relative performance of beach seines, BRUV, and eDNA in characterizing community composition of bony (teleost) and cartilaginous (elasmobranch) fishes of surf zones at 18 open coast sandy beaches in southern California. Seine and BRUV surveys captured overlapping, but distinct fish communities with 50% (18/36) of detected species shared. BRUV surveys more frequently detected larger species (e.g. sharks and rays) while seines more frequently detected one of the most abundant species, barred surfperch (*Amphistichus argenteus*). In contrast, eDNA metabarcoding captured 83.3% (30/36) of all fishes observed in seine and BRUV surveys plus 59 additional species, including 13 that frequent surf zone habitats. eDNA approaches showed significantly higher sensitivity than seine and BRUV methods and more consistently detected 29 of the 30 (96.7%) jointly observed species across beaches. The six species detected by BRUV/seines, but not eDNA either lacked reference sequences, were only resolved at higher taxonomic ranks (e.g. *Embiotocidae* surfperches), or were detected below occupancy thresholds. Low site-species overlap between methods limited comparisons of richness and abundance estimates, highlighting the challenge of comparing biomonitoring approaches. Despite potential for improvement, results overall demonstrate that eDNA can provide a cost-effective tool for long-term surf zone monitoring that

50   complements data from seine and BRUV surveys, allowing more comprehensive surveys of

51   vertebrate diversity in surf zone habitats.

52

Introduction

54   Sandy beaches and their adjacent surf zones comprise ~30% of the world's ice-free shoreline

55   [1,2]. Surf zones provide critical ecosystem services, supporting local marine biodiversity

56   through the provisioning of forage habitat, refuge from predators, spawning sites, and nurseries

57   for commercially and recreationally important fish species [2–5]. Furthermore, sandy beaches

58   and surf zones are important areas for recreation and tourism [3,6,7]. In California alone, the

59   value of sandy beach ecosystem services in 2017 was estimated at $25.9 billion annually [6,8,9].

60   Despite their tremendous societal and ecological value, our understanding of the status,

61   and spatial and temporal dynamics of surf zone fish communities in southern California and

62   around the world is lacking [1], and sandy beaches and surf zones are rarely included in

63   conservation management plans [10]. Sandy beaches and associated surf zone biological

64   communities face both local and global anthropogenic stressors that threaten their biodiversity

65   and ecosystem function [11]. Sea-level rise coupled with coastal armoring is contributing to

66   coastal squeeze, compressing or eliminating sandy beaches and altering surf zone habitats [12–

67   15]. Coastal urban development and engineering are increasing erosion along shorelines,

68   increasing turbidity and altering surf zone characteristics [16–18]. Compounding these stressors,

69   pollutants from stormwater, sewage, oil spills, and agricultural runoff often spill directly into surf

70   zone habitats [11]. As urban development and climate change continues to impact these

71   important coastal ecosystems, our ability to effectively manage sandy beaches hinges on accurate

72   assessments and monitoring of the species and communities that depend on them [11,19].

3

73   Traditional methods for monitoring surf zone ecosystems are based on surveys using

74   nets, such as seines or bottom trawls, or hook and line fishing to capture surf zone fish [1,3,20].

75   Net, and hook and line surveys are advantageous as they can provide detailed information on

76   size, sex, and age structure of fish populations, and are not influenced by poor underwater

77   visibility. However, these capture surveys have known biases that limit their reliability and

78   repeatability. Hook and line fishing surveys are often species-specific due to the choice of tackle

79   and bait, and observer skill affects capture rates [21]. Wave and weather conditions can affect

80   seine surveys by reducing the capture efficiency of nets and creating hazards to researchers in

81   heavy surf (Table 1). Seines are also sensitive to slight variation in mesh size, width of opening,

82   and speed of implementation, impacting repeatability and comparability of results [10,22].

83   Seines are also less effective for sampling large, fast-moving species [23,24] as well as small

84   benthic fishes, such as flatfish (Families Pleuronectidae and Paralichthyidae), that pass through

85   or under the nets. In addition, both these techniques are highly labor-intensive, and can be

86   destructive, often injuring or killing captured specimens [25] (Table 1).

87   **Table 1. Comparisons of Survey Methods**

Metric	Beach Seine	BRUV	eDNA
Team size needed	4-6	2	2
Set up and Field time	20 minutes per seine, 20-85 minutes to measure & release	1.5 to 2.0 hours	20 minutes
Field Gear required	Seine, poles, lines	Weighted video rigs, bait	Sampling bags, filters, ice chest
Field Sample processing	Minimal, gear clean up and repair	Minimal, gear clean up and repair	~1.5 hours for gravity filtering and preserving samples
Post-Field Sample Processing	None	1.5-3.0 hours per video	12-24 hours per sample (DNA extraction, PCR, Library preparation, sequencing), but can be automated and

			optimized for high throughput
Sample Archiving	No – fish released	Yes – video record	Yes – DNA extractions archived & sequence record
Abundance	Relative	Relative	Relative (needs ground truthing)
Size and age distribution	Yes	No	No
Injury/mortality of fish	A small percentage of catch	No	No
Effect of sea conditions	Significant- affects net behavior and safety	Significant- affects visibility	Wider tolerance but unknown effects on spatial and temporal variability

88

89   Alternative surf zone biomonitoring approaches rely on visual surveys, either via SCUBA

90   or snorkel transects or baited remote underwater video (BRUV) units [1,26,27]. BRUVs are

91   increasingly used to overcome diver avoidance behavior [20,28–30], instead employing baited

92   video cameras that record fish passing through the field of view, allowing for non-invasive

93   measurements of fish diversity, abundance, and behavior. However, BRUV surveys also have

94   biases that limit their reliability and repeatability (Table 1). Large waves, inclement weather,

95   light conditions, and drifting macrophytes, can all reduce visibility and impair species

96   identification and detection [31,32]. BRUV methods are also sensitive to bait choice, length and

97   location of deployment [10,22], may not attract planktotrophic and herbivorous fish that are not

98   attracted to the bait, and are poor at detecting cryptic species [22]. Moreover, they are

99   challenging to deploy by kayak or swimming in the surf zone, and can require processing of

100   hundreds of hours of underwater video [27]. Together, these limitations affect the reliably and

101   effectiveness of visual monitoring approaches of surf zone fish communities, highlighting the

102   need for new approaches.

103   A promising new approach for surveying the diversity of coastal marine ecosystems is

104   environmental DNA (eDNA) metabarcoding [33,34]. eDNA refers to the collection, capture,

105   sequencing, and identification of DNA from recently dissociated cells of organisms inhabiting a

106   particular ecosystem [35,36]. Studies indicate that eDNA metabarcoding is highly sensitive and

107   provides an accurate, practical, and cost-effective method of monitoring marine biodiversity [37–

108   41].

109   Studies of eDNA highlight some key advantages relative to seining and BRUVs (Table

110   1). In particular, eDNA identifies a broad diversity of marine life, frequently detecting more

111   species than other methods [42–45], including cryptic, rare, invasive, and endangered species

112   [46–50], and is effective across a variety of marine ecosystems, including coral reefs [51,52],

113   kelp forests [53], estuaries [31,54], and coastal oceans [37,55,56]. eDNA is largely independent

114   of developmental stage, allowing for the detection of larval and juvenile life stages, identifying

115   potential nursery grounds [34]. In addition, eDNA samples are simple to collect, encouraging

116   citizen and community science, and are also cost effective, permitting increased sampling efforts

117   across both time and space [34,57–59].

118   Yet eDNA also has limitations. For example, the need for molecular expertise and

119   laboratory space to process samples may limit some research groups and monitoring agencies

120   where such resources are not already available [41]. Additionally, eDNA does not provide key

121   information needed for fishery and stock assessments (e.g., size, age, sex), and it is unclear

122   whether eDNA results accurately reflect the relative abundance of marine species [31,40,60,61].

123   There are also unresolved questions about the fate and transport of eDNA, particularly in

124   highly dynamic coastal marine ecosystems. For example, previous students report spatial

125   resolution of eDNA in nearshore marine environments is on the scale of 50-1000 m [53,62–65]

6

126   and temporal resolution is on the scale of hours to days [66–68], complicating the ecological

127   interpretation of detected community assemblages [62,68–73]. However, these studies were not

128   conducted in surf zone ecosystems which are strongly affected by wave driven longshore

129   transport and nearshore currents with higher velocities (e.g., rip currents) and tides compared to

130   the subtidal ecosystems previously studied, potentially integrating ecological signatures over

131   greater space and time, and mixing species detections across ecosystems [1].

132   Although eDNA and BRUV surveys hold promise for monitoring surf zone habitats,

133   evaluating how well these methods perform compared to traditional seine surveys and each other

134   is a crucial information gap [27,74,75]; to date, only two studies [73,76] employed eDNA to

135   assess fish biodiversity in surf zones habitats. To address this gap, we compared the ability of

136   seine, BRUV, and eDNA methods to describe surf zone fish communities using a series of

137   surveys where we simultaneously employed all three methodologies at 18 open coast surf zones

138   associated with beaches in southern California. We compared these results to assess how the

139   different survey methods performed in surf zone habitats, information critical to resource

140   managers charged with monitoring these important coastal ecosystems.

141

Methods

Study Sites

144   To compare the effectiveness of seine, BRUV, and eDNA survey techniques for monitoring surf

145   zone bony (teleost) and cartilaginous (elasmobranch) fish communities, we deployed the three

146   survey techniques contemporaneously at 18 sandy beach sites across southern California, USA

147   (Figure 1;Table S1); 14 on the California Channel Islands and 4 on the mainland. These

148   represent novel fish community surveys for all but three of the mainland sites, providing

149   important baseline data for fish assemblages. To maximize comparability, we surveyed surf

150   zones using all three methods at each location on the same day using the methods described

151   below. All surveys were conducted between August 15, 2018 and November 2, 2018. At one

152   site, Soledad beach, on Santa Rosa Island, we were unable to conduct the BRUV surveys due to

153   hazardous surf conditions.

154   **Fig 1. Site Map. A) The entire study region. B) Northern Channel Islands. C)**
155   **Catalina Island**
156   Map of the (A) study region showing mainland sites, (B) Northern Channel Islands sites,
157   (C) Catalina Island sites on the coast of southern California, USA. Black dots and
158   numbers correspond to site names. 1– Dangermond, 2 – R Beach, 3 – Santa Claus, 4 –
159   Santa Monica, 5 – Cuyler Harbor, 6 – Sandy Point, 7 – Soledad, 8 – Bechers Bay, 9 –
160   Water Canyon, 10 – Southeast Anchorage, 11 – Ford Point, 12 – China Camp, 13 –
161   Forney Cove, 14 – Christy Beach, 15 – Coches Prietos, 16 – Emerald Bay, 17 – Little
162   Harbor, 18 – Ben Weston.
163

164   *Beach seine surveys*

165   Beach seine surveys were employed using methods modified from the California Department of

166   Fish and Wildlife (Monterey, CA, USA) [20] using a 15.3 m (50 ft) x 1.8 m (6 ft) seine net (10

167   mm knotless nylon mesh, 2 m poles, 20 m leader ropes) with a bag, floats, and weighted lead

168   line. At each site, we conducted seine hauls in the surf zone at four locations spaced haphazardly

169   along the beach. For each seine haul, two researchers opened the beach seine parallel to shore in

170   approximately 1.5 m of water. Keeping the weighted line flush with the bottom, we dragged the

171   seine perpendicular to the shoreline until reaching the beach. Fish were then immediately

172   removed from the seine, placed in aerated 1 m x 0.5 m x 0.5 m live wells, identified, enumerated,

173   measured (total and standard length) on glazed (smooth) fish boards, and released alive at the site

174   of capture in accordance University of California Santa Barbara's Institutional Animal Care and

175   Use (IACUC) protocol #943. Any fish that appear to be severely injured, moribund, or that did

176   not recover from the stress of trapping were euthanized using Tricaine methanosulfonate (MS-

8

177   222), a non-inhaled agents approved in the "AVMA Guidelines for the Euthanasia of Animals:

178   2013 Edition" for finfish [77].

179

180   *Baited remote underwater video (BRUV) surveys*

181   We conducted BRUV surveys following methods modified from Vargas-Fonseca et al. [78] and

182   Borland et al. [26]. Each BRUV consisted of a GoPro Hero2 camera (GoPro Inc., San Mateo,

183   California, USA, 2020) mounted on a five kg weight with a line and float attached for ease of

184   retrieval. We then attached a bait bag containing ~152 g of frozen squid (*Loligo* sp.) to the

185   weight with a PVC pipe, positioning it one meter in front of the camera. Snorkelers deployed

186   three haphazardly spaced BRUV units along the outer edge of the surf zone at a depth of greater

187   than two meters within two hours of low tide after conducting sein hauls, except for at sites

188   where sufficient personnel allowed for concurrent sampling. We deployed each BRUV for one

189   hour, producing three hours of video per beach. We reviewed videos to determine fish

190   abundance, species richness, and community composition, using the *MaxN* statistic, the

191   maximum number of individuals of one species in one frame during the hour-long footage [79].

192

193   *Environmental DNA (eDNA) surveys*

194   We collected three replicate 0.5 L samples of seawater (herein referred to as sample replicates)

195   using sterile collapsible enteral feeding bags. We then gravity filtered samples through 0.2 μm

196   Sterivex filters following the methods of Gold et al. [80] (See Supplement for detailed

197   description), storing filters at -20˚C prior to extraction via a modified Qiagen DNAeasy Blood

198   and Tissue kit (Qiagen Inc., Gernmantown, MD, USA) [81]. We amplified eDNA samples in

199   triplicate using both *12S* MiFish Universal teleost (MiFish-U) and elasmobranch (MiFish-E)

9

200   primer sets [82], and then prepared sequencing libraries preparation followed Gold et al. [80]

201   using Nextera Unique Dual Indices (Illumina, San Diego, CA, USA). We pooled all samples in

202   equimolar concentrations by primer set, resulting in a MiFish-U and a MiFish-E library which

203   were separately sequenced on NextSeq PE 2 x 150 bp mid-output at the Technology Center for

204   Genomics & Bioinformatics at the University of California – Los Angeles (UCLA) with 20%

205   PhiX added to both sequencing runs.

206

207   *eDNA bioinformatics*

208   We processed the resulting eDNA metabarcoding sequences using the *Anacapa Toolkit* (version

209   1) [83], conducting quality control, amplicon sequence variant (ASV) parsing, and taxonomic

210   assignment. Taxonomy was assigned using a curated reference database composed of fishes from

211   the California Current Large Marine Ecosystem following Gold et al. [80] (See detailed

212   description in Supplement). The resulting taxonomic tables were transferred into *R* for further

213   processing [84]. We employed a multifaceted decontamination approach developed by Kelly et

214   al. (2018) to remove field contamination, lab contamination, and index hopping [71,85–87]. We

215   then summed the total reads of ASVs by assigned taxonomy including multiple ASVs from the

216   two MiFish markers employed. From these processes, we obtained decontaminated eDNA

217   species-by-sample community tables with counts of total sequence reads.

218   We transformed the eDNA read counts into eDNA index scores according to Kelly et al.

219   [71], which normalizes the read count per technical PCR replicate per species. This index was

220   computed by first calculating the relative abundance of each species in each technical PCR

221   replicate. The relative abundance was then divided by the maximum relative abundance for a

222   given species across all samples, yielding the eDNA index score, which ranges from 0 to 1 and

223   allows for comparisons of relative abundance for specific taxa across samples.

224

225

226   *Data analysis*

227   To explore the relative efficacy of seines, BRUV, and eDNA surveys for characterizing surf zone

228   fish communities, we compared the total number of teleost and elasmobranch species identified

229   by each method using the *phyloseq* (version 1.28.0) and *vegan* packages (version 2.5-7) [88,89]

230   in *R* (version 3.6.1, R Core Team 2020). Comparisons were made in two ways: 1) all detected

231   fish taxa and 2) only surf zone fish taxa. Surf zone taxa were determined using habitat

232   descriptions from FishBase.org and the literature [3,90,91] (Table S2). We determined and

233   visualized the overlapping and unique fish species detected by each survey method across all 18

234   sites using the *VennDiagram* package (version 1.6.20) [92], comparing species richness of each

235   method using Analysis of Variance (ANOVA) and post-hoc Tukey tests using the *vegan* package

236   [89].

237   To examine survey method performance on a site-by-site basis, we calculated and

238   compared the overlap of presence/absence site-species detections [84,93,94]. Here, we define a

239   site-species detection as the detection of a species at a given site (e.g., Top smelt detected at

240   Bechers Bay). Comparisons of site-species detections were conducted for both the surf zone

241   fishes and all fishes, observed by seine, BRUV, and eDNA, respectively. We estimated sample

242   coverage, the fraction of the total incidence probabilities of the discovered species for a set of

243   sampling units, from rarefaction and extrapolation models for species richness (Hill number q=0)

244   for each method using the *iNext* package (version 2.0.20) [95].

11

245   To determine whether the presence or absence of a species is a true reflection of

246   biological reality or due to issues in the sampling process [96,97], we also conducted a site-

247   occupancy analysis of species detections at each site following the methods of Chambert et al.

248   [87] as implemented by Kelly et al. [98]. The binomial model yields the likelihood that a taxon

249   detected is truly present in the sample. The model, implemented in Stan for *R* (version 2.2.12;

250   [100]), depends upon three parameters: 1) the commonness of a taxon in the dataset (denoted

251   P_{si}), 2) the probability of a detection given that the taxon is truly present (true positive detection;

252   denoted P_{11}), and 3) the probability of a detection given that the taxon was not truly present

253   (false positive; denoted P_{10}). The probability of occurrence function used was the following:

254     $$Probability\ of\ Occurrence = \frac{p_{si} * p_{11}^{N} * (1 - p_{11})^{K-N}}{p_{si} * p_{11}^{N} * (1 - p_{11})^{K-N} + (1 - p_{si}) * p_{10}^{N} * (1 - p_{10})^{K-N}}$$

255   Where K is the number of samples taken within a site and N is the number of species

256   detections within a site (See Supplemental methods for detailed description). For each species we

257   calculated the number of detections out of the number of replicate surveys taken at each site. The

258   occurrence of either a single sequence or single individual for one species in a given replicate

259   was treated as a detection at that site.

260   In addition to probability of occurrence we also calculated the mean sensitivity, the

261   proportion of true positive detections correctly identified as positive using the following equation

262   for each species:

263     $$Sensitivity = \frac{p_{11}}{p_{11} + p_{10}}$$

264   We also calculated the mean specificity, the proportion of true negative detections correctly

265   identified as negative, using the following equation for each species:

12

266
$$Specificity = \frac{1 - p_{10}}{(1 - p_{10}) + (1 - p_{11})}$$

267   We then compared the probability of occupancy, mean sensitivity, and mean specificity

268 of each method across all species detected [101]. We further compared differences in the eDNA-

269 derived probability of occurrence of surf zone and non-surf zone associated species to test if

270 occupancy rates are a potential function of transport dynamics.

271   To analyze differences in the composition of surf zone fish detected among methods and

272 across sites, we conducted a PERMANOVA and companion multivariate homogeneity of group

273 dispersions on Jaccard-Binary dissimilarity indices based on presence/absence data using the

274 *adonis* and *betadisper* functions in the *vegan* package [89]. The PERMANOVA was conducted

275 using the following model:

276   *Detection ~ Survey Method + Site.*

277 We excluded the Soledad site on Santa Rosa Island given the lack of a BRUV survey. We further

278 visualized community beta diversity among sampling methods using a constrained canonical

279 analysis of principal components (CAP) through the *vegan* package [84,88].

280   Lastly, to assess the ability of eDNA to capture relative abundance, we compared mean

281 eDNA index scores to both the average catch counts per seine as well as average *MaxN* counts

282 per BRUV station using species-specific linear regressions. Similarly, we compared BRUV-

283 derived average *MaxN* counts against average seine counts. We focused our analyses on species

284 detected jointly by each method at three or more sites.

285

286 **Results**

287 Our beach seine surveys captured a total of 1,359 individuals in 72 hauls across all sites (4 hauls

288 per site). Seven of the 72 hauls produced 0 individuals. In total, seining detected 24 species of

13

289   fish from 24 genera, 13 families, and two classes (Table S3). On average, we captured 4.0

290   species (± 2.5 standard deviation, range 0-9), and 75.5 ± 82.8 individuals per site (range 0-325

291   individual fishes).

292   Our BRUV surveys detected a total of 1,114 individual fishes in 51 BRUV deployments

293   (3 replicate deployments per site). In total, BRUV surveys detected 30 species, 30 genera, 21

294   families, and two classes (Table S4). An average of 6.3 ± 3.2 species (range 2-16 species) and

295   65.5 ± 65.5 total individuals (range 13-236 individuals) were recorded per site.

296   Sequencing of the 54 eDNA samples yielded a total of 4,839,336 MiFish elasmobranch

297   reads and 16,835,503 MiFish teleost reads that passed the initial NextSeq quality controls across

298   all samples. After decontamination and site occupancy modeling, we retained 3,638,292 reads

299   and 908 ASVs from MiFish Elasmobranch primer set and 12,953,877 reads and 1,877 ASVs

300   from MiFish Teleost primer set, representing 89 species of fish from 79 genera, 48 families, and

301   two classes across sites. On average we observed 34.4 ± 12.3 SD species per site (range 11-59

302   species) (Figure S1).

303

304   *Species assemblages characterized by each method*

305   We found variable agreement in the assemblages of species captured by each survey method

306   across all 18 sites (Figures 2 & S2). Seine and BRUV captured distinct, but overlapping surf

307   zone fish assemblages, sharing only 50% (18/36) of fishes species. Seine surveys detected 6

308   species of fishes not observed in BRUV surveys, including 2 species of croakers (Family

309   Sciaenidae), 2 species of surfperches (Family Embiotocidae), and two planktotrophic coastal-

310   pelagic species (families Clupeidae and Atherinidae). In contrast, BRUV surveys detected 12

14

311   fish species not observed in seines, including 3 species of elasmobranchs, 6 species of rocky reef

312   associated species, and 2 coastal-pelagic predator species.

313   **Fig 2. Venn Diagram of eDNA, Seine, and BRUV Species Detections.**
314   Environmental DNA methods captured the majority (30/36) of fish species detected by
315   both BRUV and seine surveys, only failing to identify six fish species found in the other
316   two survey methods. In addition eDNA identified 59 additional fish species missed by
317   seine and BRUV methods. In contrast, BRUV and seine surveys only captured 50% of
318   species detected by both methods, showing strong difference in the species detected by
319   each method. This was largely driven by the unique detection of elasmobranchs as well
320   as nearshore pelagic and rocky reef carnivorous fishes in BRUV surveys compared to the
321   unique detection of surfperches (Family Embiotocidae), grunts (Family Sciaenidae), and
322   planktivorous nearshore pelagic species in seine surveys.
323
324

325   In contrast, eDNA detected the majority (83.3%, 30 out of 36) of species found in seine

326   and BRUV surveys (Figure 2). Similarly, when only focusing on surf zone fish (Table S2),

327   eDNA detected 83.3% (25 out of 30) of species detected in seine and BRUV surveys (Figure

328   S2). eDNA methods failed to detect six species found in the seine and BRUV surveys including

329   three species of surfperch, the most abundant and widespread family (*Embiotocidae*) detected in

330   the seine surveys. Undetected species include the walleye surfperch *(Hyperprosopon*

331   *argenteum),* silver surfperch *(Hyperprosopon ellipticum),* barred surfperch (*Amphistichus*

332   *argenteus*), white seabass *(Atractoscion nobilis)*, kelp pipefish *(Syngnathus californiensis),* and

333   the soupfin shark (*Galeorhinus galeus)*. However, eDNA surveys detected 59 fish species not

334   detected in seine or BRUV surveys (Table S5 & S6), including 13 surf-zone associated species

335   and 46 species more typically associated with reef and pelagic habitats (Table S2). Thus, eDNA

336   had high overlap with both BRUV and seine surveys in addition to capturing additional surf zone

337   and nearshore marine fishes.

338   Composition of detected taxa varied significantly among survey methods (Figures 3 and

339   S3; CAP ANOVA $p < 0.001$) driven by biases in detection of specific taxa. Seines and BRUVs

15

340   commonly detected barred surfperch (*Amphistichus argenteus*), whereas eDNA only could not

341   resolve surfperches below family level. Similarly, eDNA and BRUV surveys more frequently

342   detected leopard shark (*T. semifasciata*)*,* California bat ray (*M. californica*), and kelp bass

343   (*Paralabrax clathratus*) compared to seine surveys. In contrast, eDNA detected many more

344   species than BRUVs or seines, including opaleye (*Girella nigricans*)*,* Pacific sardine (*Sardinops*

345   *sagax*)*,* northern anchovy (*Engraulis mordax*)*,* giant kelpfish (*Heterostichus rostratus*),

346   California grunion (*Leuresthes tenuis*), dwarf perch (*Micrometrus minimus*), and black surfperch

347   (*Embiotica jacksoni*) (Figure 3).

348   **Fig 3. Constrained Analysis of Principal Components**
349   Constrained Analysis of Principal Components (CAP) analysis was conducted on Jaccard
350   binary dissimilarities of fish assemblages of all species detected across surveys. Survey
351   method explained 41.5% of the total variation observed in the composition of detected
352   taxa while site explained an additional 28.8% (PERMANOVA p <0.0001). We found no
353   significant difference in homogeneity of dispersions across sites (betadisper > 0.05).
354   BRUV and eDNA approaches more frequently detected leopard sharks (*Triakis*
355   *semifasciata*) and California bat ray (*Myliobatis californica*) compared to seine surveys.
356   Both seine and BRUV surveys detected Barred surfperch (*Amphistichs argenteus*) while
357   eDNA methods could only achieve family level resolution for this taxon. eDNA
358   approaches more consistently detected opaleye (*Girella nigricans*)*,* northern anchovy
359   (*Engraulis mordax*)*,* giant kelpfish (*Heterostichus rostratus*), and dwarf perch
360   (*Micrometrus minimus*).
361

362   In total, survey method explained 41.5% of the total variation observed in the

363   composition of detected taxa, while site explained an additional 28.8% (PERMANOVA p

364   <0.0001). We found no significant difference in homogeneity of dispersions across methods or

365   sites (betadisper > 0.05) (Table S7). We also found similar differences in fish communities

366   between survey methods when we limited our comparisons to only taxa observed by both visual

367   and eDNA methods. Survey method explained 33.1% of the total variation observed in the

368   composition of detected taxa, while site explained an additional 33.6% (PERMANOVA , p<

369   0.001). However, eDNA had significantly lower dispersion than seines across all sites

370   (homogeneity of dispersions p= 0.002) (Table S8).

371

372   *Detection rates of species across methods*

373   Detection rates of species also differed significantly among survey methods (Figure 4 & S4-S7)

374   with eDNA having a significantly higher sensitivity (98.5%) than both seine (96.7%) and BRUV

375   (96.2%) surveys across all taxa (ANOVA, p< 0.0001). Likewise, eDNA had significantly higher

376   probability of occupancy (45.8%) at the site level than both seine (24.9%) and BRUV (28.6%)

377   surveys (ANOVA, p< 0.0001) as well as having significantly higher specificity (71.0%) than

378   seines (66.4%) (ANOVA, p = 0.01). However, we observed no difference in specificity between

379   BRUV (69.1%) and eDNA or seine surveys at the site level (ANOVA, p >0.5) (Figure 5).

380   Furthermore, we found that eDNA methods had significantly higher probability of occupancy for

381   species known to inhabit surf zone habitats (52.7%) than non-surf zone associated species

382   (40.2%) (ANOVA, p=0.011) (Figure S8).

383   **Fig 4. Heatmap of surf zone fishes jointly detected between surveys**
384   Teleost species in black font and elasmobranch species in blue font. Environmental DNA
385   approaches more frequently detected 24 of 25 species detected by either BRUV or seine
386   surveys. Only Leopard shark *Triakis semifasciata* was more frequently detected by
387   BRUV surveys.
388
389   **Fig 5. Probability of Occupancy, Specificity, and Sensitivity of eDNA, Seine, and**
390   **BRUV surveys**
391   Environmental DNA surveys had higher probability of occupancy and sensitivity than
392   BRUV and seine surveys. eDNA had significantly higher specificity than seine surveys.
393   We found no difference in specificities between BRUV and eDNA and seine surveys.
394   Probability of occurrence is a measure of how likely a species is present at a site as a
395   function of the commonness of the species as well as the true positive and false positive
396   detection rates of the method surveyed. Sensitivity is the proportion of true positive
397   species detections correctly identified as true positive detections. Specificity is the
398   proportion of true negative species detections identified as negative detections.
399

400 The three methods yielded different levels of detection both overall and of individual

401 species of surf zone fish. Our eDNA samples more consistently detected 96.7% (29/30) of all

402 species jointly observed by either BRUV or seines. However, seine surveys more frequently

403 detected barred surfperch (*Amphistichus argenteus*) and walleye surfperch (*Hyperprosopon*

404 *argenteum*) than eDNA and BRUV surveys. Seine surveys also more frequently detected

405 California corbina (*Menticirrhus undulatus*), northern anchovy (*Engraulis mordax*), giant

406 kelpfish (*Heterostichus rostratus*), and kelp pipefish (*Syngnathus californiensis*) than BRUV

407 surveys, but not for eDNA surveys. Our BRUV surveys detected elasmobranchs and flatfishes

408 (Families Pleuronectidae and Paralichthyidae) more frequently than seine surveys. Leopard shark

409 (*Triakis semifasciata*) was the only species more frequently detected with BRUV (15/18) than

410 eDNA methods (14/18). In total, eDNA only failed to detect five species observed in seine

411 surveys at a single site: round stingray (*Urobatis helleri*), California grunion (*Leuresthes tenuis*),

412 black surfperch (*Embiotoca jacksoni*), dwarf perch (*Micrometrus minimus*), and giant kelpfish

413 (*Heterostichus rostratus*). Likewise, eDNA only failed to detect three species observed with

414 BRUV: leopard shark (*Triakis semifasciata)* and speckled sanddab (*Citharichthys stigmaeus*) at

415 two sites and California bat ray (*Myliobatis californica*) at one site.

416 Across all sites, eDNA had higher sample coverage estimates (98.9%) than both BRUV

417 (89.6%) and seine (85.2%) surveys (Figure 6). From species rarefaction curves of all species

418 surveyed at the site level, we estimate that both BRUV and seine surveys would have to be

419 conducted at more than 100 sites to achieve similar sample coverage estimates as eDNA at the

420 18 sites surveyed here. However, within each site surveyed, we found no significant differences

421 in sample coverage estimates between methods (seine mean = 92%, BRUV mean = 91.6%,

422 eDNA mean = 90.3%; ANOVA, $p > 0.05$, Table S9).

18

423 **Fig 6. Sample Coverage Estimates of eDNA, Seine, and BRUV surveys**
424 Across all sites, environmental DNA surveys had an estimate sample coverage of 98.9%,
425 higher than the sample coverage of BRUV (89.6%) and seine (85.2%) surveys. Shaded
426 area represents 95% confidence intervals. Sample rarefaction curves across sites suggest
427 BRUV and seine surveys would have to be conducted at more than 100 sites to achieve
428 similar sample coverage estimates to eDNA surveys conducted at the 18 sites surveyed
429 here.
430
431 *Comparisons of relative abundance among survey methods*

432 Estimates of relative abundance varied significantly among the three survey methods and were

433 generally not correlated. We found a significant positive relationship between BRUV *MaxN*

434 values and seine counts ($R^2 = 0.31$, p = 0.032, Table S10, Figure S9) for only one species,

435 topsmelt (*Atherniops affinis*). Likewise, there was a significant positive relationship between

436 seine counts and eDNA index scores for only two species, topsmelt, $R^2 = 0.32$, p = 0.014, Table

437 S11, Figure S10)*,* and California corbina, *Menticirrhus undulatus* ($R^2 = 0.82$, p < 0.001, Table

438 S11). Similarly, there was a significant positive relationship between BRUV *MaxN* and eDNA

439 index for only three species (kelp bass, *Paralbrax clathratus*, shovelnose guitarfish, *Psuedobatos*

440 *productus*, and round stingray *Urobatis halleri*) (respective R^2: 0.45, 0.41, and 0.94, p < 0.005,

441 Table S12, Figure S11).

442

443 **Discussion**

444 Despite extreme methodological differences, seine, BRUV, and eDNA surveys captured largely

445 overlapping, but distinct fish assemblages in surf zone habitats with notable taxonomic biases.

446 Seines more consistently detected surfperches, including the most abundant fished species,

447 barred surfperch (*Amphistichus argenteus*) while BRUV surveys efficiently revealed larger

448 predatory species, particularly elasmobranchs as previously documented [102]. eDNA captured

449 the highest species richness of all three methods, including the majority of species detected by

19

450 seine and BRUV surveys (30/36). The mismatch in fish assemblages sampled by each method

451 made comparisons of relative abundance difficult, highlighting a key challenge of comparing

452 survey methods [44].

453 Importantly, similar to other studies (see Bakker et al. 2017a, Boussarie et al. 2018, Stat

454 et al. 2019, Cole et al. 2021, Fediajevaite et al. 2021, Mirimin et al. 2021), we found that eDNA

455 analysis had higher sensitivity than the two traditional methods, and more frequently detected

456 nearly all jointly observed species at a given site. Our results suggest that seine, BRUV, and

457 eDNA approaches are complementary and their use in tandem provides the most accurate

458 characterization of surf zone fish communities. Recent studies using two of these three methods

459 reached similar conclusions [102,106].

460

461 *Species assemblages characterized by each method*

462 Only half of fish species detected by seine and/or BRUV surveys overlapped (18/36) indicating

463 that these methods target different species assemblages. Compared to BRUV surveys, seine

464 surveys captured additional surfperches and croakers associated with surf zone habitats as well

465 as planktivorous coastal pelagic species. In contrast, BRUV surveys detected a greater number of

466 elasmobranch and rocky reef species, particularly carnivores and scavengers, suggesting that fish

467 are attracted from adjacent habitats to the bait, or our current understanding of species' surf zone

468 habitat utilization is limited. Combined, our results align well with previous findings from

469 tropical shorelines indicating that BRUV and seines capture distinct, but overlapping fish

470 assemblages in surf zone habitats [102].

471 Our finding that eDNA approaches detected 83% (30 out of 36) of fish species observed

472 using seine and BRUV methods, with higher overlap in detected fish assemblages. Importantly,

20

473   eDNA approaches also captured an additional 13 surf zone species not observed by our seine or

474   BRUV methods, including the federally listed northern tidewater goby (*Eucyclogobius*

475   *newberryi*) and commercially-fished species of management concern, such as the flathead grey

476   mullet (*Mugil cephalus*), black croaker (*Cheilotrema saturnum*), white croaker (*Genyonemus*

477   *lineatus*)*,* and Pacific sanddab (*Citharichthys sordidus)* (Allen & Pondella, 2006). Furthermore,

478   eDNA detected a wide array of elasmobranchs that are typically underrepresented in most

479   traditional sampling approaches [103,109–111] including angel shark (*Squatina californica*),

480   horn shark (*Heterodontus francisci)*, California butterfly ray (*Gymnura marmorata*), and

481   broadnose sevengill shark (*Notorynchus cepedianus*). As such, eDNA should be viewed as a

482   valuable complement both seine and BRUV surveys.

483   The failure of eDNA to detect six common species captured by seine and BRUV surveys

484   was predominantly due to the limitations of the 12S MiFish-U primers, particularly for the

485   surfperches, and associated reference databases [80]. Specifically, *Embiotocidae* is a diverse,

486   recent radiation [112] and the MiFish-U primers perform poorly in such cases, such as rockfish

487   in the genus *Sebastes* [113]. Failure to detect three of six surfperch species is likely a result of

488   insufficient genetic variation within the 12S gene region bounded by the MiFish 12S primer set,

489   leading to many surfperches only being resolved at higher taxonomic ranks (e.g. *Embiotocidae*)

490   [80]. Importantly, we note all three species had corresponding 12S reference barcodes [80]

491   which were nearly identical. In contrast, White seabass (*Atractoscion nobilis*) lacks a MiFish-U

492   barcode and thus could not be resolved given incomplete reference databases [80].

493   However, two of the six species, soupfin shark (*Galeorhinus galeus*) and kelp pipefish

494   (*Syngnathus californiensis*), were detected with eDNA approaches but below the occupancy

495   thresholds required to be considered a positive detection. We note that these species were

21

496   detected in the seine and BRUV surveys, but very rarely (soupfin shark BRUV n=1; kelp

497   pipefish BRUV n=1, seine n=5 individuals). Likewise, eDNA methods only detected 790 total

498   reads of soupfin shark species across all sites. However, we at most observed 56 reads in one

499   technical replicate where it was observed in BRUV footage - below our occupancy threshold of

500   detection at a given site. Likewise, kelp pipefish was detected by eDNA, but again below our

501   occupancy threshold. These low-threshold detections, corroborated here by more traditional

502   methods, may justify adopting different threshold values for eDNA occupancy than employed

503   here, particularly for species that are shown to shed small amounts of DNA or that have high

504   eDNA degradation rates.

505   eDNA captured a strong signature of surf zone fish assemblages including an additional

506   13 species of surf zone fishes not observed by seine and BRUV approaches, highlighting the

507   utility of eDNA biomonitoring to improve estimates of total fish diversity in coastal monitoring

508   surveys. eDNA also detected an additional 43 native coastal marine fishes not detected by our

509   seine and BRUV surveys (Tables S5-6). Although many of these species are unlikely to inhabit

510   surf zone habitats directly [114], our study beaches were adjacent to rocky reef kelp forests,

511   rocky intertidal habitats, and estuaries. Our detections of additional native fish species highlight

512   the capacity for movement of both fish and eDNA across pelagic and inshore habitats [62].

513   Given the potential for transport on the scale of tens to thousands of meters, the detection of

514   fishes from adjacent habitats in eDNA samples is to be expected [70], thus highlighting a

515   potential shortcoming of eDNA approaches, and the need for better understanding of spatial and

516   temporal variability in the dispersal of eDNA within and across ecosystems. Despite the need to

517   better characterize the fate and transport of eDNA, our results still demonstrate that such eDNA

518   approaches can be highly informative of surf zone communities as previously demonstrated [73],

22

519   particularly on longer open coast beaches that are not located adjacent to rocky subtidal or

520   intertidal habitats.

521

522   *Detection rates of species across methods*

523   In addition to the differences in fish assemblages captured by each method, we found substantial

524   differences in the detection frequency of jointly observed species across sites between these

525   methods. Overall, we found that eDNA had higher frequency of detection of nearly all species

526   (29/30) jointly detected by either of the seine and BRUV methods (Tables S5-6). This higher

527   rate of detection also resulted in eDNA having significantly higher sensitivity than both seines

528   and BRUV surveys. Furthermore, results from species rarefaction curves suggest that eDNA

529   surveys capture a larger proportion of the total fish diversity across sites than seine and BRUV

530   surveys, but that each method was deployed with sufficient replication within each site to capture

531   the majority of fish diversity present. Importantly, our results strongly suggest that additional

532   BRUV and seine surveys should be deployed across more sandy beach sites rather than

533   additional deployments at the same site to maximize fish diversity across the region. In contrast,

534   our results suggest that the current eDNA deployment of three sample replicates with three

535   technical replicates was sufficient to adequately capture diversity across the region, providing a

536   baseline sampling regime for future eDNA deployments for monitoring fish diversity in surf

537   zone ecosystems.

538   One possible explanation for the differences in site-species detection frequency across

539   methods is poor taxonomic resolution or erroneous assignment across methods. The *Anacapa*

540   *Toolkit* provides confidence scores around each taxonomic rank of assignment, providing

541   information on the accuracy of eDNA identifications [83]. However, such confidence scores are

23

542   not readily available for data from seine and BRUV surveys, where taxonomic identification

543   depends on the presence of easily observed morphological characteristics and the resolution of

544   video still captures. For example, topsmelt (*Atherinops affinis*) and California grunion (*Leurethes*

545   *tenuis*) are morphologically very similar, with the potential for misidentification, particularly

546   under low visibility conditions for BRUV surveys.

547   The variation in temporal and spatial scales sampled by each of the three survey methods

548   may also drive differences in site-species detections [27,62,66–68,102,111]. Beach seines survey

549   a small spatial area (here 15.3 m x 1.8 m x 2m) at 0 to 1.5 m depth at a single instantaneous

550   snapshot of sampling [3,31]. In contrast, BRUV units were deployed for an hour at 2-3 m depth

551   and likely attracted species across tens to hundreds of square meters [27,102,105,111]. Although

552   the spatial and temporal scales of eDNA methods in marine systems are still an active area of

553   research, previous studies have found that eDNA integrates across spatial scales from 50 – 1,000

554   meters and degrades *in situ* between 2 and 12 hours, although laboratory experiments suggest

555   degradation rates on the order of days [53,62,67,68,73,115]. Thus the ecological integration time

556   of each of these surveys is substantially different and likely contributes to the differences we

557   observed in species detections [44,73].

558   Differences in species detection among methods are also likely driven by the dynamics of

559   eDNA. eDNA shedding rates can vary among [116] and within species [117], driven by

560   differences in physiology and behavior. Increased shedding rates result in higher eDNA

561   detection probabilities, thus biasing which species are successfully detected within surf zone

562   ecosystems. For example, eDNA methods have the potential to be biased during spawning events

563   when high DNA concentrations are released [118]. Likewise, the interaction between high water

24

564   transport within and potentially variable degradation rates across species or environmental

565   conditions (temperature, UV, etc.) could influence detection probabilities [66,69,119].

566   We found that eDNA captured a wide variety of species not typically associated with surf

567   zone habitats, suggesting transport of eDNA from offshore and other intertidal habitats and some

568   level of spatial integration of eDNA measurements. However, our finding that species known to

569   inhabit surf zone habitats had significantly higher probability of occupancy than species known

570   to associate with further offshore habitats, strongly suggests that detection is biased towards

571   species recently inhabiting the surveyed surf zone habitat. This corroborates previous work

572   finding that eDNA signatures were able to distinguish surf zone and adjacent subtidal kelp forest

573   ecosystems from differences in fish assemblage composition as well as relative abundance

574   estimates [73]. However, additional research on modeling eDNA dispersal and its dependence on

575   transport and degradation in a range of habitats could allow modeled adjustment of eDNA data

576   to account for these processes.

577

578   *Relative abundance*

579   Given the observed low site-species overlap among survey methods, assessing the capability of

580   eDNA approaches to estimate relative abundance was challenging, particularly since eDNA

581   surveys frequently detected a species at multiple sites where seine and BRUV surveys did not

582   detect that species at all. This presents a core challenge of comparing eDNA to capture and

583   visual surveys when the true abundance of species is unknown (Table 1) [44]. However, recent

584   work from studies with greater survey overlap show promise for estimating relative abundance

585   using eDNA approaches [31,40,60].

586   Given that the ability to estimate relative abundance is a function of the ability to detect a

587   given species, our results suggest that eDNA approaches are more sensitive and better suited

588   than capture and visual survey methods to estimate abundance [87,96,97]. This result, however,

589   is highly dependent on the ability of eDNA approaches to resolve a given taxa. Here eDNA

590   approaches using the MiFish-U primer set failed to resolve the most abundant surf zone species

591   from both seine and BRUV surveys, the surfperches (Family Embiotocidae). Future work is

592   needed using controlled mesocosm studies in which the true abundance of species is known, as

593   well as field studies on tagged and intensively monitored populations to further determine the

594   effectiveness of abundance estimation from eDNA metabarcoding [60]. Importantly, such studies

595   should account for transport, residence time, and variation in species specific shedding and

596   degradation rates of eDNA [119] as well as the role of amplification efficiency for biasing

597   metabarcoding results [120,121].

598

599   *Choosing a survey method*

600   All survey methods have biases, and the more a particular survey method is used allows the

601   determination of such biases. For example diver avoidance behavior is a well-established bias of

602   visual SCUBA surveys [20,28–30]. Likewise, results of this study showed that each method had

603   distinct advantages and disadvantages. BRUVs are more likely to capture large mobile species

604   than seines, and eDNA captured more total diversity than BRUVs or seines. As such, method

605   selection will largely be a function of the goals of a study, and whether detection of specific taxa

606   or total diversity is a priority.

607   However, an important consideration when employing eDNA or BRUV data compared to

608   seine surveys (without photographic documentation of hauls) is that the DNA sequences and

26

609   ASV tables generated by eDNA and the video footage produced by BRUVs are a permanent

610   records of what was present at a particular time [34] (Table 1). For eDNA in particular, as

611   reference databases are improved, eDNA sequence data can be reanalyzed to test for the

612   presence of previously missed or poorly resolved taxa, e.g. surfperch. In addition, bio-archived

613   eDNA samples or extractions can be revisited for future resequencing and management and

614   biomonitoring applications (e.g., species invasions) [122]. The ability for future analyses of a

615   given ecosystem at a specific time highlights the advantages of applying multiple approaches,

616   where eDNA can provide robust and accurate taxonomic information that can be updated over

617   time while carefully deployed stereo-video approaches (not deployed here given challenging surf

618   conditions) and seine hauls can provide size structure and biomass estimates with demonstrated

619   utility [27,102].

620

Conclusion

622   There is a growing need to survey threatened surf zone and beach ecosystems in the face of

623   global change [11]. Our results suggest that seine, BRUV, and eDNA approaches are

624   complementary techniques for surveying fish diversity in open coast surf zone habitats. eDNA is

625   a relatively quick, effective, and nondestructive approach to surveying marine wildlife, compared

626   to capture and visual surveys of dynamic surf zone habitat (Table 1). Given the cost effectiveness

627   and ability to automate collection and processing, eDNA methods could provide an approach to

628   increase the scope and scale of surf zone ecosystem monitoring across time and space [33,41].

629   The ease of sample collection in this challenging habitat could allow researchers, marine

630   resource managers, and community scientists to conduct surveys more frequently and in more

631   places, better characterizing surf zone biodiversity and dynamics [25,57,58,123]. Furthermore,

632   the ability to archive eDNA samples for future use provides an important resource for

633   comparative analyses of ecosystem change [34,122] and for making use of advances in reference

634   libraries.

635   Although we demonstrated that eDNA provides more robust species detections in surf

636   zone habitats, eDNA cannot provide information on sex ratios or population size structure that

637   can be obtained from seine and BRUV surveys, information critical to resource management

638   [1,3]. Thus, eDNA cannot be viewed as a wholesale replacement for other survey methods, but

639   instead as a complementary tool for biomonitoring surf zone ecosystems [106]. Nevertheless,

640   adding eDNA surveys to traditional monitoring programs or conducting them on their own when

641   and where other methods are untenable has the potential to greatly enhance our knowledge of

642   surf zone fish communities, providing a new source of comprehensive and detailed information

643   needed for management and preservation of these vital coastal ecosystems in the face of global

644   change.

645

Acknowledgements

653

Data reporting

654

655 All data, accession numbers, and code used to conduct analyses will be made publicly available

656 on Dryad, NCBI, and GitHub upon acceptance of the manuscript.

657

668

References

669

670 1.   Olds AD, Vargas-Fonseca E, Connolly RM, Gilby BL, Huijbers CM, Hyndes GA, et al.

671   The ecology of fish in the surf zones of ocean beaches: A global review. Fish Fish.

672   2018;19: 78–89.

673 2.   Luijendijk A, Hagenaars G, Ranasinghe R, Baart F, Donchyts G, Aarninkhof S. The state

674   of the world's beaches. Sci Rep. 2018;8: 1–11.

675 3.   Allen LG, Pondella II DJ. Surf zone, coastal pelagic zone, and harbors. Ecol Mar fishes

676   Calif Adjac waters Univ Calif Press Berkeley. 2006; 149–166.

677   4.   Klein YL, Osleeb JP, Viola MR. Tourism-generated earnings in the coastal zone: a

678   regional analysis. J Coast Res. 2004;20: 1080–1088.

679   5.   McLachlan A, Defeo O, Jaramillo E, Short AD. Sandy beach conservation and recreation:

680   guidelines for optimising management strategies for multi-purpose use. Ocean Coast

681   Manag. 2013;71: 256–268.

682   6.   Dugan JE, Hubbard DM, Nielsen KJ, Altstatt J, Bursek J. Baseline Characterization of

683   Sandy Beach Ecosystems Along the South Coast of California - Final Report. 2015.

684   Available: https://caseagrant.ucsd.edu/sites/default/files/SCMPA-24-Final-Report_0.pdf

685   7.   Schlacher TA, Dugan J, Schoeman DS, Lastra M, Jones A, Scapini F, et al. Sandy beaches

686   at the brink. Divers Distrib. 2007;13: 556–560.

687   8.   NMFS. Fisheries economics of the United States, 2015. NOAA Technical Memorandum;

688   2017.

689   9.   Dugan JE, Hubbard DM, Martin DL, Engle JM, Richards DM, Davis GE, et al.

690   Macrofauna communities of exposed sandy beaches on the Southern California mainland

691   and Channel Islands. Proceedings of the Fifth California Islands Symposium Minerals

692   Management Service Publication. 2000. pp. 339–346.

693   10.   Schlacher TA, Schoeman DS, Dugan J, Lastra M, Jones A, Scapini F, et al. Sandy beach

694   ecosystems: key features, sampling issues, management challenges and climate change

695   impacts. Mar Ecol. 2008;29: 70–90.

696   11.   Defeo O, McLachlan A, Schoeman DS, Schlacher TA, Dugan J, Jones A, et al. Threats to

697   sandy beach ecosystems: a review. Estuar Coast Shelf Sci. 2009;81: 1–12.

698   12.   Jaramillo E, Dugan J, Hubbard D, Manzano M, Duarte C. Ranking the ecological effects

699   of coastal armoring on mobile macroinvertebrates across intertidal zones on sandy

30

700   beaches. Sci Total Environ. 2021;755: 142573.

701   13.   Barnard PL, Dugan JE, Page HM, Wood NJ, Hart JAF, Cayan DR, et al. Multiple climate

702   change-driven tipping points for coastal systems. Sci Rep. 2021;11: 1–13.

703   14.   Schooler NK, Dugan JE, Hubbard DM. No lines in the sand: Impacts of intense

704   mechanized maintenance regimes on sandy beach ecosystems span the intertidal zone on

705   urban coasts. Ecol Indic. 2019;106: 105457.

706   15.   Dugan JE, Emery KA, Alber M, Alexander CR, Byers JE, Gehman AM, et al.

707   Generalizing ecological effects of shoreline armoring across soft sediment environments.

708   Estuaries and coasts. 2018;41: 180–196.

709   16.   Manning LM, Peterson CH, Fegley SR. Degradation of surf-fish foraging habitat driven

710   by persistent sedimentological modifications caused by beach nourishment. Bull Mar Sci.

711   2013;89: 83–106.

712   17.   Parkinson RW, Ogurcak DE. Beach nourishment is not a sustainable strategy to mitigate

713   climate change. Estuar Coast Shelf Sci. 2018;212: 203–209.

714   18.   Peterson CH, Bishop MJ, D'Anna LM, Johnson GA. Multi-year persistence of beach

715   habitat degradation from nourishment using coarse shelly sediments. Sci Total Environ.

716   2014;487: 481–492.

717   19.   Allen LG, Horn MH. The ecology of marine fishes: California and adjacent waters. Univ

718   of California Press; 2006.

719   20.   Carlisle JG, Schott JW, Abrahamson NJ. The barred surf perch in Southern California,

720   Calif. Dept Fish Fish Bull. 1960;109.

721   21.   Kuriyama PT, Branch TA, Hicks AC, Harms JH, Hamel OS. Investigating three sources

722   of bias in hook-and-line surveys: survey design, gear saturation, and multispecies

723   interactions. Can J Fish Aquat Sci. 2019;76: 192–207.

724   22.   Andradi-Brown DA, Macaya-Solis C, Exton DA, Gress E, Wright G, Rogers AD.

725   Assessing Caribbean shallow and mesophotic reef fish communities using baited-remote

726   underwater video (BRUV) and diver-operated video (DOV) survey techniques. PLoS One.

727   2016;11: e0168235.

728   23.   Ceni G, Vieira JP. Looking through a dirty glass: how different can the characterization of

729   a fish fauna be when distinct nets are used for sampling? Zool. 2013;30: 499–505.

730   24.   Baker R, Sheaves M. Visual surveys reveal high densities of large piscivores in shallow

731   estuarine nurseries. Mar Ecol Prog Ser. 2006;323: 75–82.

732   25.   Kelly RP, Port J a., Yamahara KM, Martone RG, Lowell N, Thomsen PF, et al.

733   Harnessing DNA to improve environmental management. Science (80-). 2014;344.

734   doi:10.1126/science.1251156

735   26.   Borland HP, Schlacher TA, Gilby BL, Connolly RM, Yabsley NA, Olds AD. Habitat type

736   and beach exposure shape fish assemblages in the surf zones of ocean beaches. Mar Ecol

737   Prog Ser. 2017;570: 203–211.

738   27.   Schramm KD, Harvey ES, Goetze JS, Travers MJ, Warnock B, Saunders BJ. A

739   comparison of stereo-BRUV, diver operated and remote stereo-video transects for

740   assessing reef fish assemblages. J Exp Mar Bio Ecol. 2020;524: 151273.

741   28.   Hodgson G, Maun L, Shuman C. Reef Check Survey Manual. Reef Check, Inst Environ

742   Univ California, Los Angeles, CA. 2004.

743   29.   Kushner DJ, Rassweiler A, McLaughlin JP, Lafferty KD. A multi-decade time series of

744   kelp forest community structure at the California Channel Islands. Ecology. 2013;94:

745   2655. doi:https://doi.org/10.1890/13-0562R.1

746 30. Lindfield SJ, Harvey ES, McIlwain JL, Halford AR. Silent fish surveys: bubble-free

747   diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished

748   areas. Börger L, editor. Methods Ecol Evol. 2014;5: 1061–1069. doi:10.1111/2041-

749   210X.12262

750 31. Shelton AO, Kelly RP, O'Donnell JL, Park L, Schwenke P, Greene C, et al.

751   Environmental DNA provides quantitative estimates of a threatened salmon species. Biol

752   Conserv. 2019;237: 383–391. doi:10.1016/j.biocon.2019.07.003

753 32. Lowry M, Folpp H, Gregson M, Mckenzie R. A comparison of methods for estimating

754   fish assemblages associated with estuarine artificial reefs. Brazilian J Oceanogr. 2011;59:

755   119–131.

756 33. Beng KC, Corlett RT. Applications of environmental DNA (eDNA) in ecology and

757   conservation: opportunities, challenges and prospects. Biodivers Conserv. 2020;29: 2089–

758   2121.

759 34. Deiner K, Bik HM, Mächler E, Seymour M, Lacoursière-Roussel A, Altermatt F, et al.

760   Environmental DNA metabarcoding: Transforming how we survey animal and plant

761   communities. Mol Ecol. 2017;26: 5872–5895. doi:10.1111/mec.14350

762 35. Taberlet P, Bonin A, Zinger L, Coissac E. Environmental DNA: For biodiversity research

763   and monitoring. Oxford University Press; 2018.

764 36. Taberlet P, Coissac E, Hajibabaei M, Rieseberg LH. Environmental DNA. Mol Ecol.

765   2012;21: 1789–1793. doi:10.1111/j.1365-294X.2012.05542.x

766 37. Djurhuus A, Closek CJ, Kelly RP, Pitz KJ, Michisaki RP, Starks HA, et al. Environmental

767   DNA reveals seasonal shifts and potential interactions in a marine community. Nat

768   Commun. 2020;11: 1–9.

33

769   38.   Closek CJ, Santora JA, Starks HA, Schroeder ID, Andruszkiewicz EA, Sakuma KM, et al.

770   Marine vertebrate biodiversity and distribution within the central California Current using

771   environmental DNA (eDNA) metabarcoding and ecosystem surveys. Front Mar Sci.

772   2019;6: 732.

773   39.   Doi H, Inui R, Akamatsu Y, Kanno K, Yamanaka H, Takahara T, et al. Environmental

774   DNA analysis for estimating the abundance and biomass of stream fish. Freshw Biol.

775   2017;62: 30–39.

776   40.   Stoeckle MY, Adolf J, Charlop-Powers Z, Dunton KJ, Hinks G, VanMorter SM. Trawl

777   and eDNA assessment of marine fish diversity, seasonality, and relative abundance in

778   coastal New Jersey, USA. ICES J Mar Sci. 2021;78: 293–304.

779   41.   Bohmann K, Evans A, Gilbert MTP, Carvalho GR, Creer S, Knapp M, et al.

780   Environmental DNA for wildlife biology and biodiversity monitoring. Trends Ecol Evol.

781   2014;29: 358–367. doi:10.1016/j.tree.2014.04.003

782   42.   Thomsen PF, Kielgast J, Iversen LL, Møller PR, Rasmussen M, Willerslev E. Detection of

783   a diverse marine fish fauna using environmental DNA from seawater samples. PLoS One.

784   2012;7: e41732.

785   43.   Valentini A, Taberlet P, Miaud C, Civade R, Herder J, Thomsen PF, et al. Next-generation

786   monitoring of aquatic biodiversity using environmental DNA metabarcoding. Mol Ecol.

787   2015; n/a-n/a. doi:10.1111/mec.13428

788   44.   Kelly RP, Closek CJ, O'Donnell JL, Kralj JE, Shelton AO, Samhouri JF. Genetic and

789   manual survey methods yield different and complementary views of an ecosystem. Front

790   Mar Sci. 2017;3: 283. doi:https://doi.org/10.3389/fmars.2016.00283

791   45.   Gold ZJ. Design and Implementation of Environmental DNA Metabarcoding Methods for

792   Monitoring the Southern California Marine Protected Area Network. UCLA. 2020.

793   doi:ark:/13030/m5j44187

794   46.   Thomas AC, Tank S, Nguyen PL, Ponce J, Sinnesael M, Goldberg CS. A system for rapid

795   eDNA detection of aquatic invasive species. Environ DNA. 2019.

796   47.   LeBlanc F, Belliveau V, Watson E, Coomber C, Simard N, DiBacco C, et al.

797   Environmental DNA (eDNA) detection of marine aquatic invasive species (AIS) in

798   Eastern Canada using a targeted species-specific qPCR approach. Manag Biol Invasions.

799   2020;11: 201.

800   48.   Weltz K, Lyle JM, Ovenden J, Morgan JAT, Moreno DA, Semmens JM. Application of

801   environmental DNA to detect an endangered marine skate species in the wild. PLoS One.

802   2017;12: e0178124.

803   49.   Simpfendorfer C, Kyne P, Noble T, Goldsbury J, Basiita R, Lindsay R, et al.

804   Environmental DNA detects Critically Endangered largetooth sawfish in the wild.

805   Endanger Species Res. 2016;30: 109–116. doi:10.3354/esr00731

806   50.   Lafferty KD, Benesh KC, Mahon AR, Jerde CL, Lowe CG. Detecting southern

807   California's white sharks with environmental DNA. Front Mar Sci. 2018;5: 1–6.

808   51.   West KM, Stat M, Harvey ES, Skepper CL, DiBattista JD, Richards ZT, et al. eDNA

809   metabarcoding survey reveals fine-scale coral reef community variation across a remote,

810   tropical island ecosystem. Mol Ecol. 2020;29: 1069–1086.

811   52.   Stat M, Huggett MJ, Bernasconi R, DiBattista JD, Berry TE, Newman SJ, et al.

812   Ecosystem biomonitoring with eDNA: metabarcoding across the tree of life in a tropical

813   marine environment. Sci Rep. 2017;7: 12240. doi:10.1038/s41598-017-12501-5

814   53.   Port JA, O'Donnell JL, Romero-Maraccini OC, Leary PR, Litvin SY, Nickols KJ, et al.

815   Assessing vertebrate biodiversity in a kelp forest ecosystem using environmental DNA.

816   Mol Ecol. 2015. doi:https://doi.org/10.1111/mec.13481

817 54. Stoeckle MY, Soboleva L, Charlop-Powers Z. Aquatic environmental DNA detects

818   seasonal fish abundance and habitat preference in an urban estuary. PLoS One. 2017;12.

819 55. Andruszkiewicz EA, Starks HA, Chavez FP, Sassoubre LM, Block BA, Boehm AB.

820   Biomonitoring of marine vertebrates in Monterey Bay using eDNA metabarcoding. PLoS

821   One. 2017;12: e0176343.

822 56. Thomsen PF, Møller PR, Sigsgaard EE, Knudsen SW, Jørgensen OA, Willerslev E.

823   Environmental DNA from seawater samples correlate with trawl catches of subarctic,

824   deepwater fishes. PLoS One. 2016;11. doi:10.1371/journal.pone.0165252

825 57. Meyer R, Ramos MM, Lin M, Schweizer TM, Gold Z, Ramos DR, et al. The CALeDNA

826   program: Citizen scientists and researchers inventory California's biodiversity. Calif

827   Agric. 2021;75: 20–32. Available: http://dx.doi.org/10.3733/ca.2021a0001

828 58. Freiwald J, Meyer R, Caselle JE, Blanchette CA, Hovel K, Neilson D, et al. Citizen

829   science monitoring of marine protected areas: Case studies and recommendations for

830   integration into monitoring programs. Mar Ecol. 2018;39: e12470.

831   doi:10.1111/maec.12470

832 59. Biggs J, Ewald N, Valentini A, Gaboriaud C, Dejean T, Griffiths RA, et al. Using eDNA

833   to develop a national citizen science-based monitoring programme for the great crested

834   newt (Triturus cristatus). Biol Conserv. 2014;183: 19–28.

835   doi:10.1016/j.biocon.2014.11.029

836 60. Di Muri C, Handley LL, Bean CW, Li J, Peirson G, Sellers GS, et al. Read counts from

837   environmental DNA (eDNA) metabarcoding reflect fish abundance and biomass in

838   drained ponds. Metabarcoding and Metagenomics. 2020;4: e56959.

839   61.   Ushio M, Murakami H, Masuda R, Sado T, Miya M, Sakurai S, et al. Quantitative

840   monitoring of multispecies fish environmental DNA using high-throughput sequencing.

841   Metabarcoding and Metagenomics. 2018;2: e23297.

842   62.   O'Donnell JL, Kelly RP, Shelton AO, Samhouri JF, Lowell NC, Williams GD. Spatial

843   distribution of environmental DNA in a nearshore marine habitat. PeerJ. 2017;5: e3044.

844   doi:10.7717/peerj.3044

845   63.   West K, Travers MJ, Stat M, Harvey ES, Richards ZT, DiBattista JD, et al. Large-scale

846   eDNA metabarcoding survey reveals marine biogeographic break and transitions over

847   tropical north-western Australia. Divers Distrib. 2021.

848   64.   Gold Z, Sprague J, Kushner DJ, Zerecero E, Barber PH. eDNA metabarcoding as a

849   biomonitoring tool for marine protected areas. bioRxiv. 2020; 2020.08.20.258889.

850   doi:10.1101/2020.08.20.258889

851   65.   Lamy T, Pitz KJ, Chavez FP, Yorke CE, Miller RJ. Environmental DNA reveals the fine-

852   grained and hierarchical spatial structure of kelp forest fish communities. Sci Rep.

853   2021;11: 1–13.

854   66.   Collins RA, Wangensteen OS, O'Gorman EJ, Mariani S, Sims DW, Genner MJ.

855   Persistence of environmental DNA in marine systems. Commun Biol. 2018;1: 1–11.

856   67.   Murakami H, Yoon S, Kasai A, Minamoto T, Yamamoto S, Sakata MK, et al. Dispersion

857   and degradation of environmental DNA from caged fish in a marine environment. Fish

858   Sci. 2019;85: 327–337. doi:https://doi.org/10.1007/s12562-019-01341-z

859   68.   Ely T, Barber PH, Man L, Gold Z. Short-lived detection of an introduced vertebrate

860   eDNA signal in a nearshore rocky reef environment. PLoS One. 2021;16: e0245314.

37

861 69. Shogren AJ, Tank JL, Andruszkiewicz E, Olds B, Mahon AR, Jerde CL, et al. Controls on

862   eDNA movement in streams: Transport, Retention, and Resuspension /704/158/2464

863   /704/242 /45/77 article. Sci Rep. 2017;7. doi:10.1038/s41598-017-05223-1

864 70. Andruszkiewicz EA, Koseff JR, Fringer OB, Ouellette NT, Lowe AB, Edwards CA, et al.

865   Modeling environmental DNA transport in the coastal ocean using Lagrangian particle

866   tracking. Front Mar Sci. 2019;6: 477. doi:10.3389/fmars.2019.00477

867 71. Kelly RP, Gallego R, Jacobs-Palmer E. The effect of tides on nearshore environmental

868   DNA. PeerJ. 2018;6: e4521. doi:https://doi.org/10.7717/peerj.4521

869 72. Yamamoto S, Minami K, Fukaya K, Takahashi K, Sawada H, Murakami H, et al.

870   Environmental DNA as a "snapshot" of fish distribution: A case study of Japanese jack

871   mackerel in Maizuru Bay, Sea of Japan. PLoS One. 2016;11.

872   doi:10.1371/journal.pone.0149786

873 73. Monuki K, Barber PH, Gold Z. eDNA captures depth partitioning in a kelp forest

874   ecosystem. PLoS One. 2021;16: e0253104.

875 74. French B, Wilson S, Holmes T, Kendrick A, Rule M, Ryan N. Comparing five methods

876   for quantifying abundance and diversity of fish assemblages in seagrass habitat. Ecol

877   Indic. 2021;124: 107415.

878 75. Gutiérrez-Martínez M, Muñoz-Lechuga R, Rodríguez-García C, Sanz-Fernández V,

879   Cabrera-Castro R. Spatial-temporal patterns of fish and macroinvertebrate communities in

880   sandy beach surf zones: Short and medium-term variations. J Sea Res. 2021;168: 101993.

881 76. Stoeckle MY, Das Mishu M, Charlop-Powers Z. Improved environmental DNA reference

882   library detects overlooked marine fishes in New Jersey, United States. Front Mar Sci.

883   2020;7: 226.

884   77.   Leary SL, Underwood W, Anthony R, Cartner S, Corey D, Grandin T, et al. AVMA

885   guidelines for the euthanasia of animals: 2013 edition. American Veterinary Medical

886   Association Schaumburg, IL; 2013.

887   78.   Vargas-Fonseca E, Olds AD, Gilby BL, Connolly RM, Schoeman DS, Huijbers CM, et al.

888   Combined effects of urbanization and connectivity on iconic coastal fishes. Divers Distrib.

889   2016;22: 1328–1341.

890   79.   Ellis DM. Evaluation of video camera technique for indexing abundances of juvenile pink

891   snapper Pristipomoides filamentosus, and other Hawaiian insular shelf fishes. Fish Bull.

892   1995;93: 67–77.

893   80.   Gold Z, Curd E, Goodwin K, Choi E, Frable B, Thompson A, et al. Improving

894   Metabarcoding Taxonomic Assignment: A Case Study of Fishes in a Large Marine

895   Ecosystem. 2021.

896   81.   Spens J, Evans AR, Halfmaerten D, Knudsen SW, Sengupta ME, Mak SST, et al.

897   Comparison of capture and storage methods for aqueous macrobial eDNA using an

898   optimized extraction protocol: advantage of enclosed filter. Yu D, editor. Methods Ecol

899   Evol. 2017;8: 635–645. doi:10.1111/2041-210X.12683

900   82.   Miya M, Sato Y, Fukunaga T, Sado T, Poulsen JY, Sato K, et al. MiFish, a set of universal

901   PCR primers for metabarcoding environmental DNA from fishes: detection of more than

902   230 subtropical marine species. R Soc Open Sci. 2015;2: 150088.

903   doi:10.1098/rsos.150088

904   83.   Curd EE, Gold Z, Kandlikar GS, Gomer J, Ogden M, O'Connell T, et al. Anacapa: an

905   environmental DNA toolkit for processing multilocus metabarcode datasets. Methods Ecol

906   Evol. 2019;10: 1469– 1475. doi:https://doi.org/10.1111/2041-210X.13214

39

907   84.   R Core Team. R: A Language and Environment for Statistical Computing. Vienna;

908   Austria; 2020.

909   85.   Costello M, Fleharty M, Abreu J, Farjoun Y, Ferriera S, Holmes L, et al. Characterization

910   and remediation of sample index swaps by non-redundant dual indexing on massively

911   parallel sequencing platforms. BMC Genomics. 2018;19: 332.

912   86.   Goldberg CS, Turner CR, Deiner K, Klymus KE, Thomsen PF, Murphy MA, et al.

913   Critical considerations for the application of environmental DNA methods to detect

914   aquatic species. 2016 [cited 20 Mar 2019]. doi:10.1111/2041-210X.12595

915   87.   Chambert T, Pilliod DS, Goldberg CS, Doi H, Takahara T. An analytical framework for

916   estimating aquatic species density from environmental DNA. Ecol Evol. 2018;8: 3468–

917   3477. doi:10.1002/ece3.3764

918   88.   McMurdie PJ, Holmes S. phyloseq: an R package for reproducible interactive analysis and

919   graphics of microbiome census data. PLoS One. 2013;8: e61217.

920   89.   Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. vegan:

921   Community Ecology Package. 2020.

922   90.   Froese R, Pauly D. FishBase. Fisheries Centre, University of British Columbia; 2010.

923   91.   Kells VA, Rocha LA, Allen LG. A field guide to coastal fishes: from Alaska to California.

924   JHU Press; 2016.

925   92.   Chen H, Boutros PC. VennDiagram: a package for the generation of highly-customizable

926   Venn and Euler diagrams in R. BMC Bioinformatics. 2011;12: 1–7.

927   93.   Wickham H, François R, Henry L, Müller K. dplyr: A Grammar of Data Manipulation.

928   2021.

929   94.   Wickham H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York;

930   2016.

931   95.   Hsieh TC, Ma KH, Chao A. iNEXT: an R package for rarefaction and extrapolation of

932   species diversity (Hill numbers). Methods Ecol Evol. 2016;7: 1451–1456.

933   doi:https://doi.org/10.1111/2041-210X.12613

934   96.   Royle JA, Link WA. Generalized site occupancy models allowing for false positive and

935   false negative errors. Ecology. 2006;87: 835–841.

936   97.   Schmidt BR, Kery M, Ursenbacher S, Hyman OJ, Collins JP. Site occupancy models in

937   the analysis of environmental DNA presence/absence surveys: a case study of an

938   emerging amphibian pathogen. Methods Ecol Evol. 2013;4: 646–653.

939   98.   Gold Z, Wall AR, Curd EE, Kelly RP, Pentcheff ND, Ripma L, et al. eDNA

940   metabarcoding bioassessment of endangered fairy shrimp (Branchinecta spp.). Conserv

941   Genet Resour. 2020;12: 685–690.

942   99.   Team RC. R: A language and environment for statistical computing. Vienna, Austria: R

943   Foundation for Statistical Computing; 2014. 2014.

944   100.   Goodrich B, Gabry J, Ali I, Brilleman S. rstanarm: Bayesian applied regression modeling

945   via Stan. R Packag version. 2018;2: 1758.

946   101.   Parikh R, Mathai A, Parikh S, Sekhar GC, Thomas R. Understanding and using

947   sensitivity, specificity and predictive values. Indian J Ophthalmol. 2008;56: 45.

948   102.   Esmaeili YS, Corte GN, Checon HH, Gomes TRC, Lefcheck JS, Amaral ACZ, et al.

949   Comprehensive assessment of shallow surf zone fish biodiversity requires a combination

950   of sampling methods. Mar Ecol Prog Ser. 2021;667: 131–144.

951   103.   Boussarie G, Bakker J, Wangensteen OS, Mariani S, Bonnin L, Juhel J-B, et al.

952   Environmental DNA illuminates the dark diversity of sharks. Sci Adv. 2018;4: eaap9661.

953   104.   Bakker J, Wangensteen OS, Chapman DD, Boussarie G, Buddo D, Guttridge TL, et al.

954   Environmental DNA reveals tropical shark diversity in contrasting levels of anthropogenic

955   impact. Sci Rep. 2017;7: 1–11.

956   105.   Cole VJ, Harasti D, Lines R, Stat M. Estuarine fishes associated with intertidal oyster

957   reefs characterized using environmental DNA and baited remote underwater video.

958   Environ DNA. 2021.

959   106.   Stat M, John J, DiBattista JD, Newman SJ, Bunce M, Harvey ES. Combined use of eDNA

960   metabarcoding and video surveillance for the assessment of fish biodiversity. Conserv

961   Biol. 2019;33: 196–205.

962   107.   Fediajevaite J, Priestley V, Arnold R, Savolainen V. Meta-analysis shows that

963   environmental DNA outperforms traditional surveys, but warrants better reporting

964   standards. Ecol Evol. 2021.

965   108.   Mirimin L, Desmet S, Romero DL, Fernandez SF, Miller DL, Mynott S, et al. Don't catch

966   me if you can–Using cabled observatories as multidisciplinary platforms for marine fish

967   community monitoring: An in situ case study combining Underwater Video and

968   environmental DNA data. Sci Total Environ. 2021;773: 145351.

969   109.   Bakker J, Wangensteen OS, Chapman DD, Boussarie G, Buddo D, Guttridge TL, et al.

970   Environmental DNA reveals tropical shark diversity in contrasting levels of anthropogenic

971   impact. Sci Rep. 2017;7: 16886. doi:10.1038/s41598-017-17150-2

972   110.   Bassett DK, Montgomery JC. Investigating nocturnal fish populations in situ using baited

973   underwater video: with special reference to their olfactory capabilities. J Exp Mar Bio

974   Ecol. 2011;409: 194–199.

975   111.   Jeunen G-J, Urban L, Lewis R, Knapp M, Lamare M, Rayment W, et al. Marine

976   environmental DNA (eDNA) for biodiversity assessments: a one-to-one comparison

977   between eDNA and baited remote underwater video (BRUV) surveys. Authorea Prepr.

978   2020.

979 112. Longo G, Bernardi G. The evolutionary history of the embiotocid surfperch radiation

980   based on genome-wide RAD sequence data. Mol Phylogenet Evol. 2015;88: 55–63.

981 113. Min MA, Barber PH, Gold Z. MiSebastes: An eDNA metabarcoding primer set for

982   rockfishes (genus Sebastes). Conserv Genet Resour. 2021; 1–10.

983 114. Love MS, Passarelli JK. Miller and Lea's Guide to the Coastal Marine Fishes of

984   California. 2nd. University of California Agriculture and Natural Resources; 2020.

985 115. Yamamoto S, Masuda R, Sato Y, Sado T, Araki H, Kondoh M, et al. Environmental DNA

986   metabarcoding reveals local fish communities in a species-rich coastal sea. Sci Rep.

987   2017;7: 40368.

988 116. Andruszkiewicz Allan E, Zhang WG, C Lavery A, F Govindarajan A. Environmental

989   DNA shedding and decay rates from diverse animal forms and thermal regimes. Environ

990   DNA. 2021;3: 492–514.

991 117. Thalinger B, Rieder A, Teuffenbach A, Pütz Y, Schwerte T, Wanzenboeck J, et al. The

992   effect of activity, energy use, and species identity on environmental DNA shedding of

993   freshwater fish. Front Ecol Evol. 2021;9: 73.

994 118. Tillotson MD, Kelly RP, Duda JJ, Hoy M, Kralj J, Quinn TP. Concentrations of

995   environmental DNA (eDNA) reflect spawning salmon abundance at fine spatial and

996   temporal scales. Biol Conserv. 2018;220: 1–11. doi:10.1016/J.BIOCON.2018.01.030

997 119. Barnes MA, Turner CR. The ecology of environmental DNA and implications for

998   conservation genetics. Conserv Genet. 2016;17: 1–17. doi:10.1007/s10592-015-0775-4

999 120. McLaren MR, Willis AD, Callahan BJ. Consistent and correctable bias in metagenomic

1000   sequencing experiments. Elife. 2019;8: e46923.

1001 121. Kelly RP, Shelton AO, Gallego R. Understanding PCR processes to Draw Meaningful

1002   conclusions from environmental DNA Studies. Sci Rep. 2019;9: 1–14.

1003   doi:https://doi.org/10.1038/s41598-019-48546-x

1004 122. Jarman SN, Berry O, Bunce M. The value of environmental DNA biobanking for long-

1005   term biomonitoring. Nat Ecol Evol. 2018;2: 1192–1193.

1006 123. Goodwin K, Davis J, Strom M, Werner C. NOAA'Omics Strategy: Strategic Application

1007   of Transformational Tools. 2020.

1008
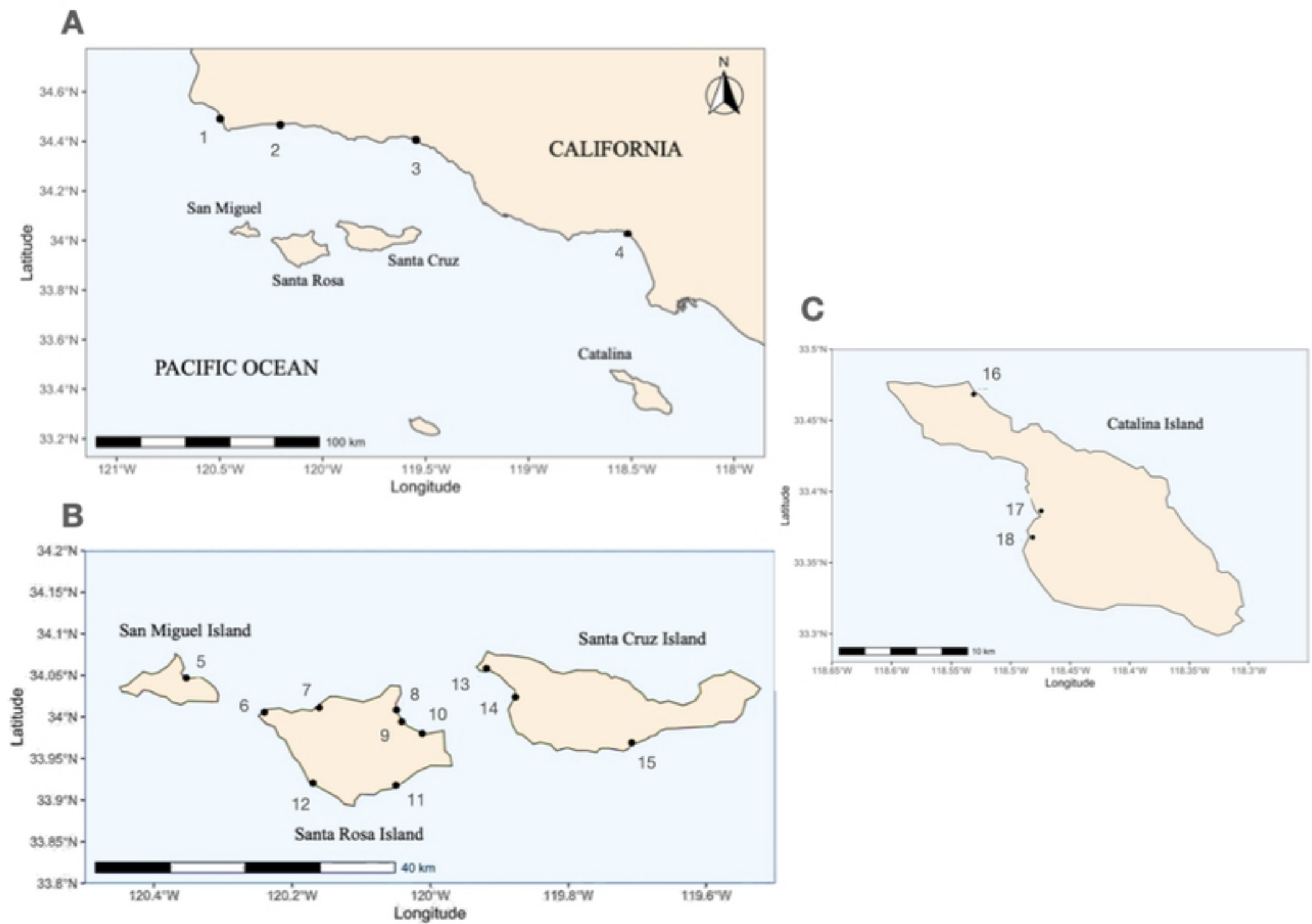
Figure 1
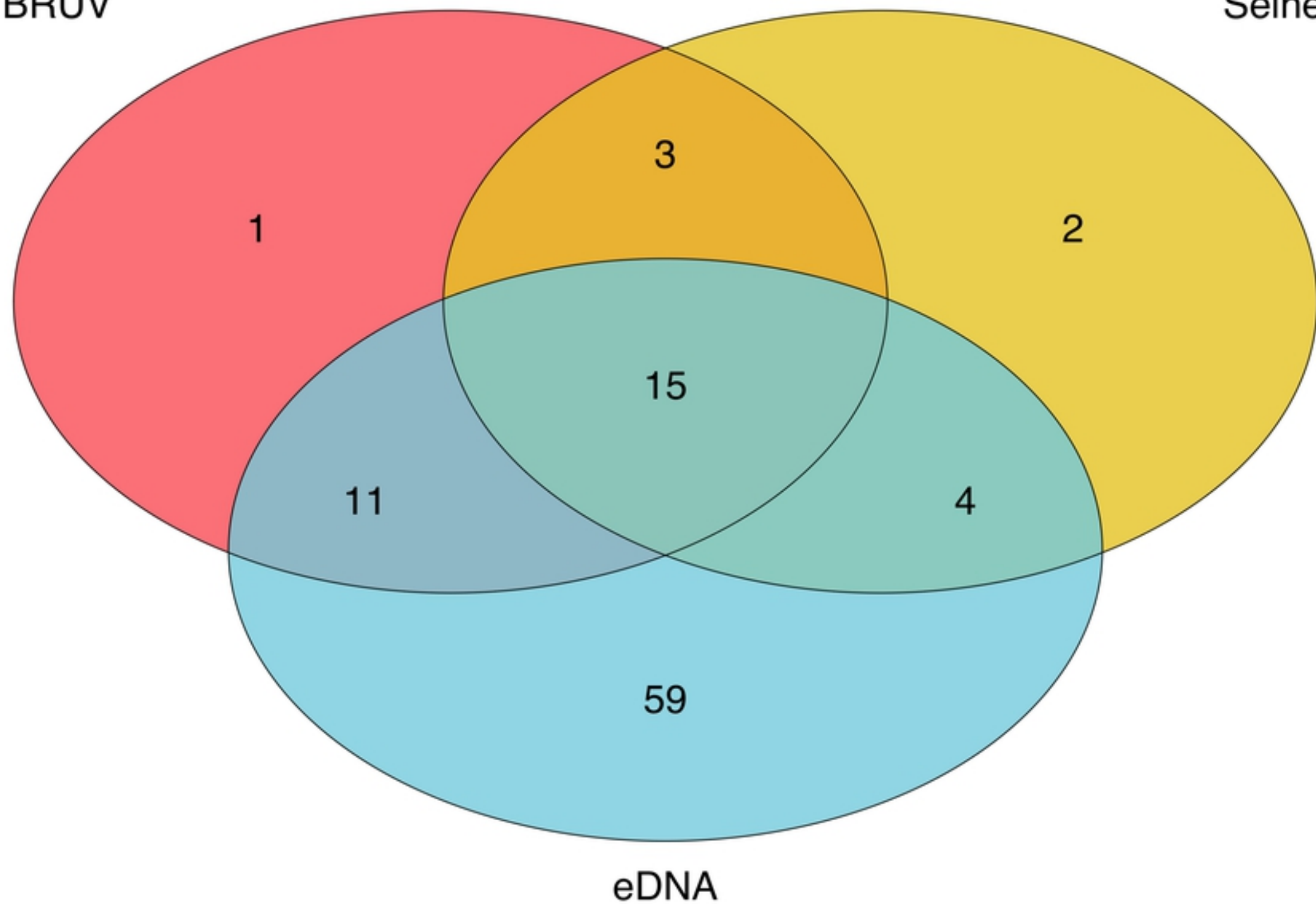
Figure 2

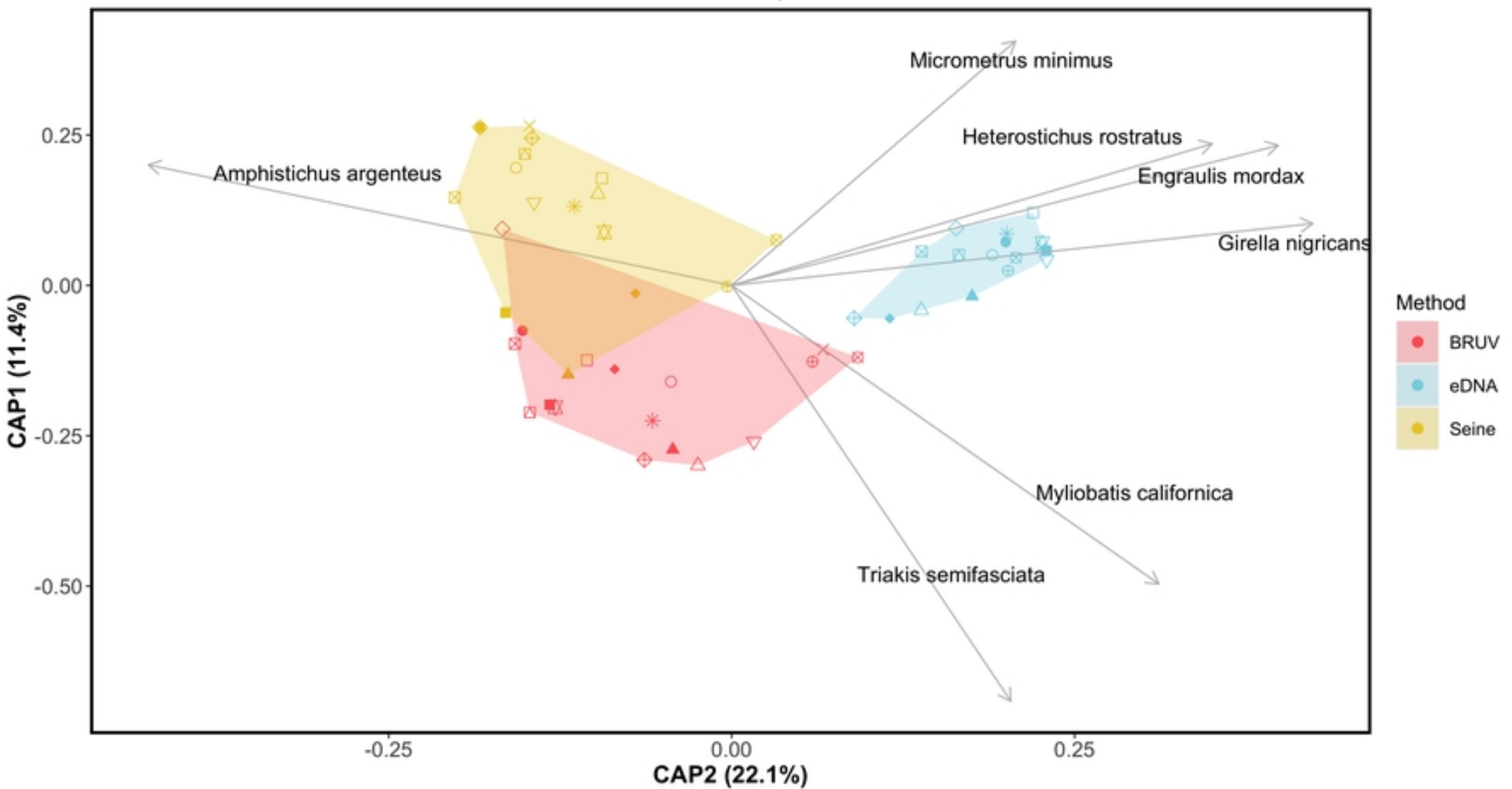**Constrained Analysis of Principal Components**

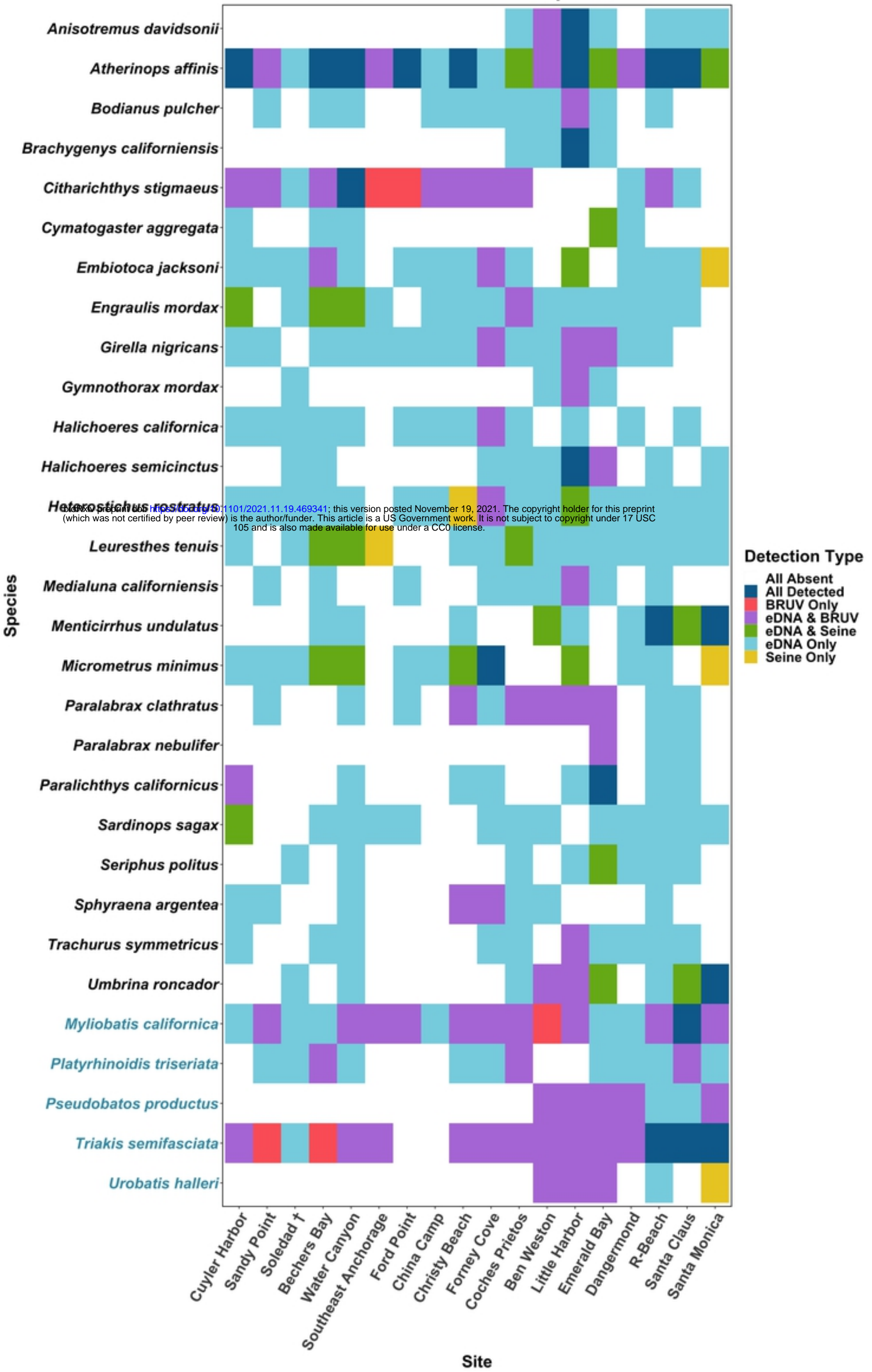All Detected Species

Figure 3

Site-Species Co-Detections
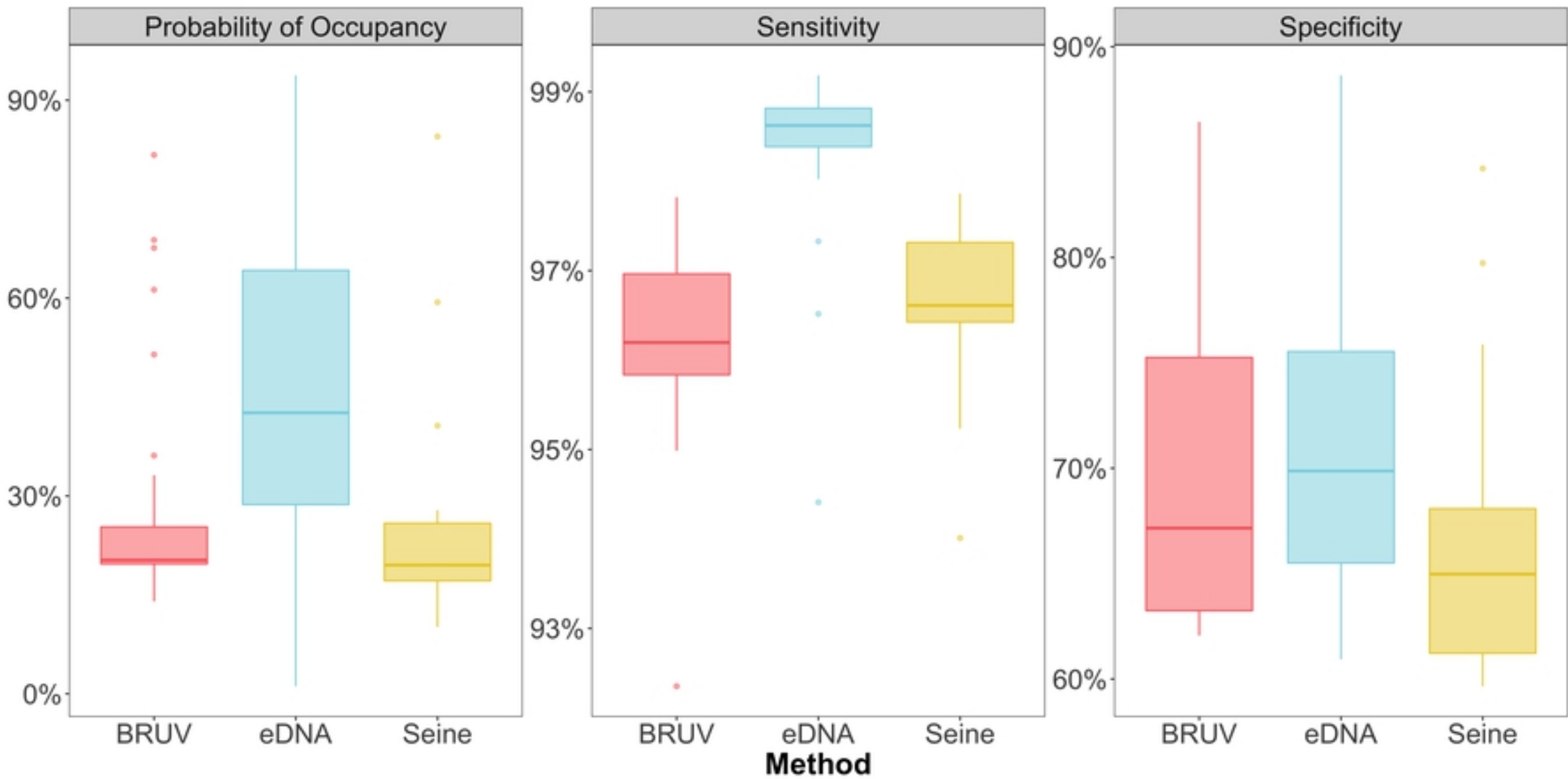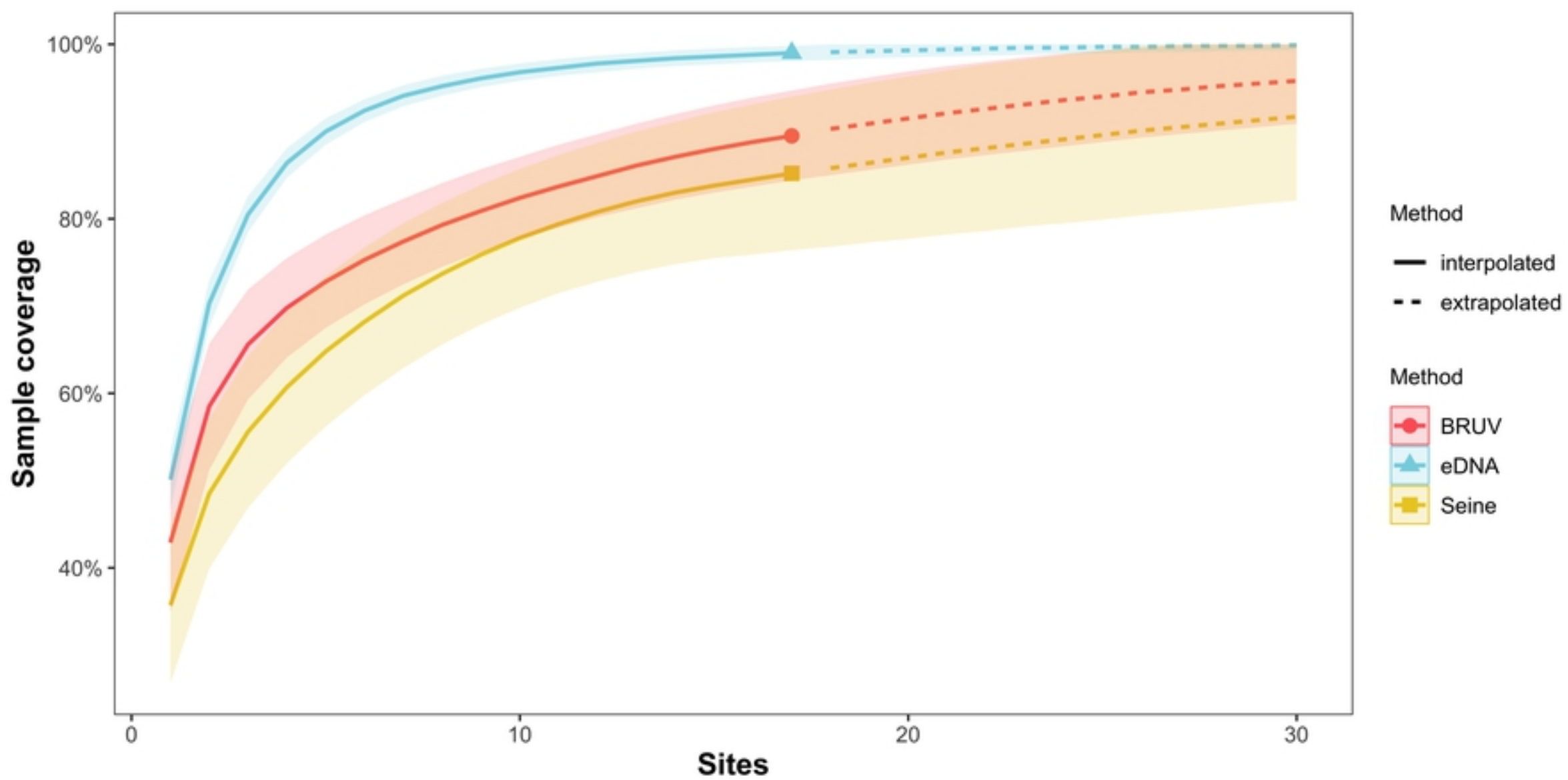## All 30 Visual and eDNA Detected Species

Figure 4

Figure 5

Figure 6