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

Zachary Gold[1 ¶*], McKenzie Q. Koch[1¶], Nicholas K. Schooler[2], Kyle A. Emery[2], Jenifer E. Dugan[2], Robert J. Miller[2], Henry M. Page[2], Donna M. Schroeder[3], David M. Hubbard[2], Jessica R. Madden[2], Stephen G. Whitaker[2,4], and Paul H. Barber[1]

[1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, CA, USA

[2]Marine Science Institute, University of California Santa Barbara, CA, USA

[3]Bureau of Ocean Energy Management, Camarillo, CA, USA

[4]Channel Islands National Park, Ventura, CA, USA

* Corresponding Author

Email: zjgold@ucla.edu

Phone: +1(310)-795-0020

¶ These authors contributed equally to this work.

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

53 ## 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].

Traditional methods for monitoring surf zone ecosystems are based on surveys using nets, such as seines or bottom trawls, or hook and line fishing to capture surf zone fish [1,3,20]. Net, and hook and line surveys are advantageous as they can provide detailed information on size, sex, and age structure of fish populations, and are not influenced by poor underwater visibility. However, these capture surveys have known biases that limit their reliability and repeatability. Hook and line fishing surveys are often species-specific due to the choice of tackle and bait, and observer skill affects capture rates [21]. Wave and weather conditions can affect seine surveys by reducing the capture efficiency of nets and creating hazards to researchers in heavy surf (Table 1). Seines are also sensitive to slight variation in mesh size, width of opening, and speed of implementation, impacting repeatability and comparability of results [10,22]. Seines are also less effective for sampling large, fast-moving species [23,24] as well as small benthic fishes, such as flatfish (Families Pleuronectidae and Paralichthyidae), that pass through or under the nets. In addition, both these techniques are highly labor-intensive, and can be destructive, often injuring or killing captured specimens [25] (Table 1).

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

Alternative surf zone biomonitoring approaches rely on visual surveys, either via SCUBA or snorkel transects or baited remote underwater video (BRUV) units [1,26,27]. BRUVs are increasingly used to overcome diver avoidance behavior [20,28–30], instead employing baited video cameras that record fish passing through the field of view, allowing for non-invasive measurements of fish diversity, abundance, and behavior. However, BRUV surveys also have biases that limit their reliability and repeatability (Table 1). Large waves, inclement weather, light conditions, and drifting macrophytes, can all reduce visibility and impair species identification and detection [31,32]. BRUV methods are also sensitive to bait choice, length and location of deployment [10,22], may not attract planktotrophic and herbivorous fish that are not attracted to the bait, and are poor at detecting cryptic species [22]. Moreover, they are challenging to deploy by kayak or swimming in the surf zone, and can require processing of hundreds of hours of underwater video [27]. Together, these limitations affect the reliably and effectiveness of visual monitoring approaches of surf zone fish communities, highlighting the need for new approaches.

A promising new approach for surveying the diversity of coastal marine ecosystems is environmental DNA (eDNA) metabarcoding [33,34]. eDNA refers to the collection, capture, sequencing, and identification of DNA from recently dissociated cells of organisms inhabiting a particular ecosystem [35,36]. Studies indicate that eDNA metabarcoding is highly sensitive and provides an accurate, practical, and cost-effective method of monitoring marine biodiversity [37–41].

Studies of eDNA highlight some key advantages relative to seining and BRUVs (Table 1). In particular, eDNA identifies a broad diversity of marine life, frequently detecting more species than other methods [42–45], including cryptic, rare, invasive, and endangered species [46–50], and is effective across a variety of marine ecosystems, including coral reefs [51,52], kelp forests [53], estuaries [31,54], and coastal oceans [37,55,56]. eDNA is largely independent of developmental stage, allowing for the detection of larval and juvenile life stages, identifying potential nursery grounds [34]. In addition, eDNA samples are simple to collect, encouraging citizen and community science, and are also cost effective, permitting increased sampling efforts across both time and space [34,57–59].

Yet eDNA also has limitations. For example, the need for molecular expertise and laboratory space to process samples may limit some research groups and monitoring agencies where such resources are not already available [41]. Additionally, eDNA does not provide key information needed for fishery and stock assessments (e.g., size, age, sex), and it is unclear whether eDNA results accurately reflect the relative abundance of marine species [31,40,60,61].

There are also unresolved questions about the fate and transport of eDNA, particularly in highly dynamic coastal marine ecosystems. For example, previous students report spatial resolution of eDNA in nearshore marine environments is on the scale of 50-1000 m [53,62–65]

and temporal resolution is on the scale of hours to days [66–68], complicating the ecological interpretation of detected community assemblages [62,68–73]. However, these studies were not conducted in surf zone ecosystems which are strongly affected by wave driven longshore transport and nearshore currents with higher velocities (e.g., rip currents) and tides compared to the subtidal ecosystems previously studied, potentially integrating ecological signatures over greater space and time, and mixing species detections across ecosystems [1].

Although eDNA and BRUV surveys hold promise for monitoring surf zone habitats, evaluating how well these methods perform compared to traditional seine surveys and each other is a crucial information gap [27,74,75]; to date, only two studies [73,76] employed eDNA to assess fish biodiversity in surf zones habitats. To address this gap, we compared the ability of seine, BRUV, and eDNA methods to describe surf zone fish communities using a series of surveys where we simultaneously employed all three methodologies at 18 open coast surf zones associated with beaches in southern California. We compared these results to assess how the different survey methods performed in surf zone habitats, information critical to resource managers charged with monitoring these important coastal ecosystems.

Methods

Study Sites

To compare the effectiveness of seine, BRUV, and eDNA survey techniques for monitoring surf zone bony (teleost) and cartilaginous (elasmobranch) fish communities, we deployed the three survey techniques contemporaneously at 18 sandy beach sites across southern California, USA (Figure 1;Table S1); 14 on the California Channel Islands and 4 on the mainland. These 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-

222), a non-inhaled agents approved in the "AVMA Guidelines for the Euthanasia of Animals: 2013 Edition" for finfish [77].

Baited remote underwater video (BRUV) surveys

We conducted BRUV surveys following methods modified from Vargas-Fonseca et al. [78] and Borland et al. [26]. Each BRUV consisted of a GoPro Hero2 camera (GoPro Inc., San Mateo, California, USA, 2020) mounted on a five kg weight with a line and float attached for ease of retrieval. We then attached a bait bag containing ~152 g of frozen squid (*Loligo* sp.) to the weight with a PVC pipe, positioning it one meter in front of the camera. Snorkelers deployed three haphazardly spaced BRUV units along the outer edge of the surf zone at a depth of greater than two meters within two hours of low tide after conducting sein hauls, except for at sites where sufficient personnel allowed for concurrent sampling. We deployed each BRUV for one hour, producing three hours of video per beach. We reviewed videos to determine fish abundance, species richness, and community composition, using the *MaxN* statistic, the maximum number of individuals of one species in one frame during the hour-long footage [79].

Environmental DNA (eDNA) surveys

We collected three replicate 0.5 L samples of seawater (herein referred to as sample replicates) using sterile collapsible enteral feeding bags. We then gravity filtered samples through 0.2 µm Sterivex filters following the methods of Gold et al. [80] (See Supplement for detailed description), storing filters at -20˚C prior to extraction via a modified Qiagen DNAeasy Blood and Tissue kit (Qiagen Inc., Gernmantown, MD, USA) [81]. We amplified eDNA samples in triplicate using both *12S* MiFish Universal teleost (MiFish-U) and elasmobranch (MiFish-E)

primer sets [82], and then prepared sequencing libraries preparation followed Gold et al. [80] using Nextera Unique Dual Indices (Illumina, San Diego, CA, USA). We pooled all samples in equimolar concentrations by primer set, resulting in a MiFish-U and a MiFish-E library which were separately sequenced on NextSeq PE 2 x 150 bp mid-output at the Technology Center for Genomics & Bioinformatics at the University of California – Los Angeles (UCLA) with 20% PhiX added to both sequencing runs.

eDNA bioinformatics

We processed the resulting eDNA metabarcoding sequences using the *Anacapa Toolkit* (version 1) [83], conducting quality control, amplicon sequence variant (ASV) parsing, and taxonomic assignment. Taxonomy was assigned using a curated reference database composed of fishes from the California Current Large Marine Ecosystem following Gold et al. [80] (See detailed description in Supplement). The resulting taxonomic tables were transferred into *R* for further processing [84]. We employed a multifaceted decontamination approach developed by Kelly et al. (2018) to remove field contamination, lab contamination, and index hopping [71,85–87]. We then summed the total reads of ASVs by assigned taxonomy including multiple ASVs from the two MiFish markers employed. From these processes, we obtained decontaminated eDNA species-by-sample community tables with counts of total sequence reads.

We transformed the eDNA read counts into eDNA index scores according to Kelly et al. [71], which normalizes the read count per technical PCR replicate per species. This index was computed by first calculating the relative abundance of each species in each technical PCR replicate. The relative abundance was then divided by the maximum relative abundance for a

given species across all samples, yielding the eDNA index score, which ranges from 0 to 1 and allows for comparisons of relative abundance for specific taxa across samples.

Data analysis

To explore the relative efficacy of seines, BRUV, and eDNA surveys for characterizing surf zone fish communities, we compared the total number of teleost and elasmobranch species identified by each method using the *phyloseq* (version 1.28.0) and *vegan* packages (version 2.5-7) [88,89] in *R* (version 3.6.1, R Core Team 2020). Comparisons were made in two ways: 1) all detected fish taxa and 2) only surf zone fish taxa. Surf zone taxa were determined using habitat descriptions from FishBase.org and the literature [3,90,91] (Table S2). We determined and visualized the overlapping and unique fish species detected by each survey method across all 18 sites using the *VennDiagram* package (version 1.6.20) [92], comparing species richness of each method using Analysis of Variance (ANOVA) and post-hoc Tukey tests using the *vegan* package [89].

To examine survey method performance on a site-by-site basis, we calculated and compared the overlap of presence/absence site-species detections [84,93,94]. Here, we define a site-species detection as the detection of a species at a given site (e.g., Top smelt detected at Bechers Bay). Comparisons of site-species detections were conducted for both the surf zone fishes and all fishes, observed by seine, BRUV, and eDNA, respectively. We estimated sample coverage, the fraction of the total incidence probabilities of the discovered species for a set of sampling units, from rarefaction and extrapolation models for species richness (Hill number q=0) for each method using the *iNext* package (version 2.0.20) [95].

To determine whether the presence or absence of a species is a true reflection of biological reality or due to issues in the sampling process [96,97], we also conducted a site-occupancy analysis of species detections at each site following the methods of Chambert et al. [87] as implemented by Kelly et al. [98]_ The binomial model yields the likelihood that a taxon detected is truly present in the sample. The model, implemented in Stan for *R* (version 2.2.12; [100]), depends upon three parameters: 1) the commonness of a taxon in the dataset (denoted P_{si}), 2) the probability of a detection given that the taxon is truly present (true positive detection; denoted P_{11}), and 3) the probability of a detection given that the taxon was not truly present (false positive; denoted P_{10}). The probability of occurrence function used was the following:

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

Where K is the number of samples taken within a site and N is the number of species detections within a site (See Supplemental methods for detailed description). For each species we calculated the number of detections out of the number of replicate surveys taken at each site. The occurrence of either a single sequence or single individual for one species in a given replicate was treated as a detection at that site.

In addition to probability of occurrence we also calculated the mean sensitivity, the proportion of true positive detections correctly identified as positive using the following equation for each species:

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

We also calculated the mean specificity, the proportion of true negative detections correctly identified as negative, using the following equation for each species:

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

We then compared the probability of occupancy, mean sensitivity, and mean specificity of each method across all species detected [101]. We further compared differences in the eDNA-derived probability of occurrence of surf zone and non-surf zone associated species to test if occupancy rates are a potential function of transport dynamics.

To analyze differences in the composition of surf zone fish detected among methods and across sites, we conducted a PERMANOVA and companion multivariate homogeneity of group dispersions on Jaccard-Binary dissimilarity indices based on presence/absence data using the *adonis* and *betadisper* functions in the *vegan* package [89]. The PERMANOVA was conducted using the following model:

$$Detection \sim Survey\ Method + Site.$$

We excluded the Soledad site on Santa Rosa Island given the lack of a BRUV survey. We further visualized community beta diversity among sampling methods using a constrained canonical analysis of principal components (CAP) through the *vegan* package [84,88].

Lastly, to assess the ability of eDNA to capture relative abundance, we compared mean eDNA index scores to both the average catch counts per seine as well as average *MaxN* counts per BRUV station using species-specific linear regressions. Similarly, we compared BRUV-derived average *MaxN* counts against average seine counts. We focused our analyses on species detected jointly by each method at three or more sites.

Results

Our beach seine surveys captured a total of 1,359 individuals in 72 hauls across all sites (4 hauls per site). Seven of the 72 hauls produced 0 individuals. In total, seining detected 24 species of

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

fish species not observed in seines, including 3 species of elasmobranchs, 6 species of rocky reef associated species, and 2 coastal-pelagic predator species.

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

In contrast, eDNA detected the majority (83.3%, 30 out of 36) of species found in seine and BRUV surveys (Figure 2). Similarly, when only focusing on surf zone fish (Table S2), eDNA detected 83.3% (25 out of 30) of species detected in seine and BRUV surveys (Figure S2). eDNA methods failed to detect six species found in the seine and BRUV surveys including three species of surfperch, the most abundant and widespread family (*Embiotocidae*) detected in the seine surveys. Undetected species include the walleye surfperch *(Hyperprosopon argenteum),* silver surfperch *(Hyperprosopon ellipticum),* barred surfperch (*Amphistichus argenteus*), white seabass *(Atractoscion nobilis)*, kelp pipefish *(Syngnathus californiensis),* and the soupfin shark (*Galeorhinus galeus)*. However, eDNA surveys detected 59 fish species not detected in seine or BRUV surveys (Table S5 & S6), including 13 surf-zone associated species and 46 species more typically associated with reef and pelagic habitats (Table S2). Thus, eDNA had high overlap with both BRUV and seine surveys in addition to capturing additional surf zone and nearshore marine fishes.

Composition of detected taxa varied significantly among survey methods (Figures 3 and S3; CAP ANOVA $p < 0.001$) driven by biases in detection of specific taxa. Seines and BRUVs

commonly detected barred surfperch (*Amphistichus argenteus*), whereas eDNA only could not resolve surfperches below family level. Similarly, eDNA and BRUV surveys more frequently detected leopard shark (*T. semifasciata*), California bat ray (*M. californica*), and kelp bass (*Paralabrax clathratus*) compared to seine surveys. In contrast, eDNA detected many more species than BRUVs or seines, including opaleye (*Girella nigricans*), Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), giant kelpfish (*Heterostichus rostratus*), California grunion (*Leuresthes tenuis*), dwarf perch (*Micrometrus minimus*), and black surfperch (*Embiotica jacksoni*) (Figure 3).

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

In total, survey method explained 41.5% of the total variation observed in the composition of detected taxa, while site explained an additional 28.8% (PERMANOVA p <0.0001). We found no significant difference in homogeneity of dispersions across methods or sites (betadisper > 0.05) (Table S7). We also found similar differences in fish communities between survey methods when we limited our comparisons to only taxa observed by both visual and eDNA methods. Survey method explained 33.1% of the total variation observed in the 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

The three methods yielded different levels of detection both overall and of individual species of surf zone fish. Our eDNA samples more consistently detected 96.7% (29/30) of all species jointly observed by either BRUV or seines. However, seine surveys more frequently detected barred surfperch (*Amphistichus argenteus*) and walleye surfperch (*Hyperprosopon* argenteum) than eDNA and BRUV surveys. Seine surveys also more frequently detected California corbina (*Menticirrhus undulatus*), northern anchovy (*Engraulis mordax*), giant kelpfish (*Heterostichus rostratus*), and kelp pipefish (*Syngnathus californiensis*) than BRUV surveys, but not for eDNA surveys. Our BRUV surveys detected elasmobranchs and flatfishes (Families Pleuronectidae and Paralichthyidae) more frequently than seine surveys. Leopard shark (*Triakis semifasciata*) was the only species more frequently detected with BRUV (15/18) than eDNA methods (14/18). In total, eDNA only failed to detect five species observed in seine surveys at a single site: round stingray (*Urobatis helleri*), California grunion (*Leuresthes tenuis*), black surfperch (*Embiotoca jacksoni*), dwarf perch (*Micrometrus minimus*), and giant kelpfish (*Heterostichus rostratus*). Likewise, eDNA only failed to detect three species observed with BRUV: leopard shark (*Triakis semifasciata)* and speckled sanddab (*Citharichthys stigmaeus*) at two sites and California bat ray (*Myliobatis californica*) at one site.

Across all sites, eDNA had higher sample coverage estimates (98.9%) than both BRUV (89.6%) and seine (85.2%) surveys (Figure 6). From species rarefaction curves of all species surveyed at the site level, we estimate that both BRUV and seine surveys would have to be conducted at more than 100 sites to achieve similar sample coverage estimates as eDNA at the 18 sites surveyed here. However, within each site surveyed, we found no significant differences in sample coverage estimates between methods (seine mean = 92%, BRUV mean = 91.6%, eDNA mean = 90.3%; ANOVA, $p > 0.05$, Table S9).

Fig 6. Sample Coverage Estimates of eDNA, Seine, and BRUV surveys
Across all sites, environmental DNA surveys had an estimate sample coverage of 98.9%, higher than the sample coverage of BRUV (89.6%) and seine (85.2%) surveys. Shaded area represents 95% confidence intervals. Sample rarefaction curves across sites suggest BRUV and seine surveys would have to be conducted at more than 100 sites to achieve similar sample coverage estimates to eDNA surveys conducted at the 18 sites surveyed here.

Comparisons of relative abundance among survey methods

Estimates of relative abundance varied significantly among the three survey methods and were generally not correlated. We found a significant positive relationship between BRUV *MaxN* values and seine counts ($R^2 = 0.31$, $p = 0.032$, Table S10, Figure S9) for only one species, topsmelt (*Atherniops affinis*). Likewise, there was a significant positive relationship between seine counts and eDNA index scores for only two species, topsmelt, $R^2 = 0.32$, $p = 0.014$, Table S11, Figure S10), and California corbina, *Menticirrhus undulatus* ($R^2 = 0.82$, $p < 0.001$, Table S11). Similarly, there was a significant positive relationship between BRUV *MaxN* and eDNA index for only three species (kelp bass, *Paralbrax clathratus*, shovelnose guitarfish, *Psuedobatos productus*, and round stingray *Urobatis halleri*) (respective R^2: 0.45, 0.41, and 0.94, $p < 0.005$, Table S12, Figure S11).

Discussion

Despite extreme methodological differences, seine, BRUV, and eDNA surveys captured largely overlapping, but distinct fish assemblages in surf zone habitats with notable taxonomic biases. Seines more consistently detected surfperches, including the most abundant fished species, barred surfperch (*Amphistichus argenteus*) while BRUV surveys efficiently revealed larger predatory species, particularly elasmobranchs as previously documented [102]. eDNA captured the highest species richness of all three methods, including the majority of species detected by

seine and BRUV surveys (30/36). The mismatch in fish assemblages sampled by each method made comparisons of relative abundance difficult, highlighting a key challenge of comparing survey methods [44].

Importantly, similar to other studies (see Bakker et al. 2017a, Boussarie et al. 2018, Stat et al. 2019, Cole et al. 2021, Fediajevaite et al. 2021, Mirimin et al. 2021), we found that eDNA analysis had higher sensitivity than the two traditional methods, and more frequently detected nearly all jointly observed species at a given site. Our results suggest that seine, BRUV, and eDNA approaches are complementary and their use in tandem provides the most accurate characterization of surf zone fish communities. Recent studies using two of these three methods reached similar conclusions [102,106].

Species assemblages characterized by each method

Only half of fish species detected by seine and/or BRUV surveys overlapped (18/36) indicating that these methods target different species assemblages. Compared to BRUV surveys, seine surveys captured additional surfperches and croakers associated with surf zone habitats as well as planktivorous coastal pelagic species. In contrast, BRUV surveys detected a greater number of elasmobranch and rocky reef species, particularly carnivores and scavengers, suggesting that fish are attracted from adjacent habitats to the bait, or our current understanding of species' surf zone habitat utilization is limited. Combined, our results align well with previous findings from tropical shorelines indicating that BRUV and seines capture distinct, but overlapping fish assemblages in surf zone habitats [102].

Our finding that eDNA approaches detected 83% (30 out of 36) of fish species observed using seine and BRUV methods, with higher overlap in detected fish assemblages. Importantly,

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

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],

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

not readily available for data from seine and BRUV surveys, where taxonomic identification depends on the presence of easily observed morphological characteristics and the resolution of video still captures. For example, topsmelt (*Atherinops affinis*) and California grunion (*Leurethes tenuis*) are morphologically very similar, with the potential for misidentification, particularly under low visibility conditions for BRUV surveys.

The variation in temporal and spatial scales sampled by each of the three survey methods may also drive differences in site-species detections [27,62,66–68,102,111]. Beach seines survey 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 snapshot of sampling [3,31]. In contrast, BRUV units were deployed for an hour at 2-3 m depth and likely attracted species across tens to hundreds of square meters [27,102,105,111]. Although the spatial and temporal scales of eDNA methods in marine systems are still an active area of research, previous studies have found that eDNA integrates across spatial scales from 50 – 1,000 meters and degrades *in situ* between 2 and 12 hours, although laboratory experiments suggest degradation rates on the order of days [53,62,67,68,73,115]. Thus the ecological integration time of each of these surveys is substantially different and likely contributes to the differences we observed in species detections [44,73].

Differences in species detection among methods are also likely driven by the dynamics of eDNA. eDNA shedding rates can vary among [116] and within species [117], driven by differences in physiology and behavior. Increased shedding rates result in higher eDNA detection probabilities, thus biasing which species are successfully detected within surf zone ecosystems. For example, eDNA methods have the potential to be biased during spawning events when high DNA concentrations are released [118]. Likewise, the interaction between high water

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

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

621 ## 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

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653

Data reporting

All data, accession numbers, and code used to conduct analyses will be made publicly available on Dryad, NCBI, and GitHub upon acceptance of the manuscript.

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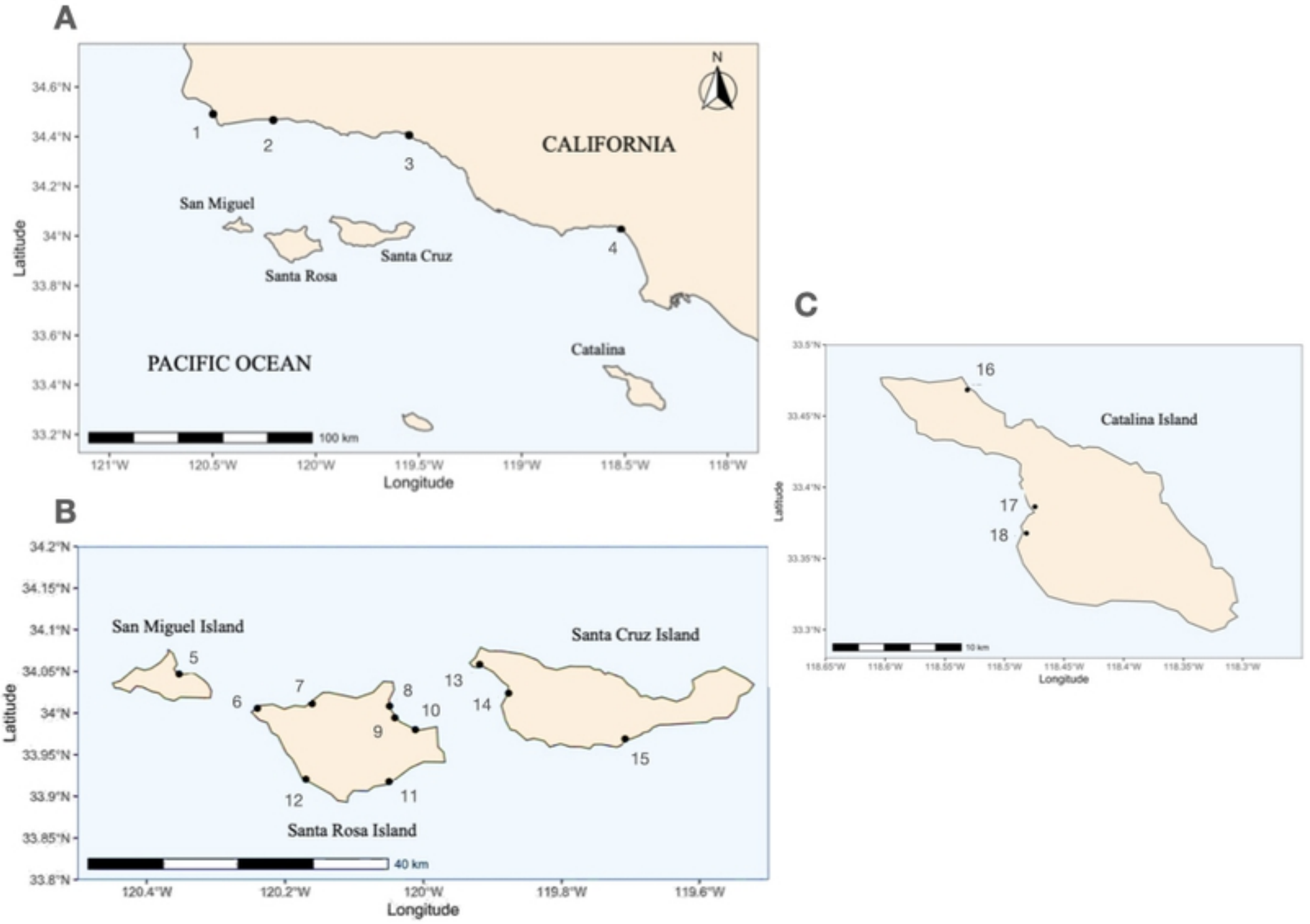
A
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PACIFIC OCEAN
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Figure 1

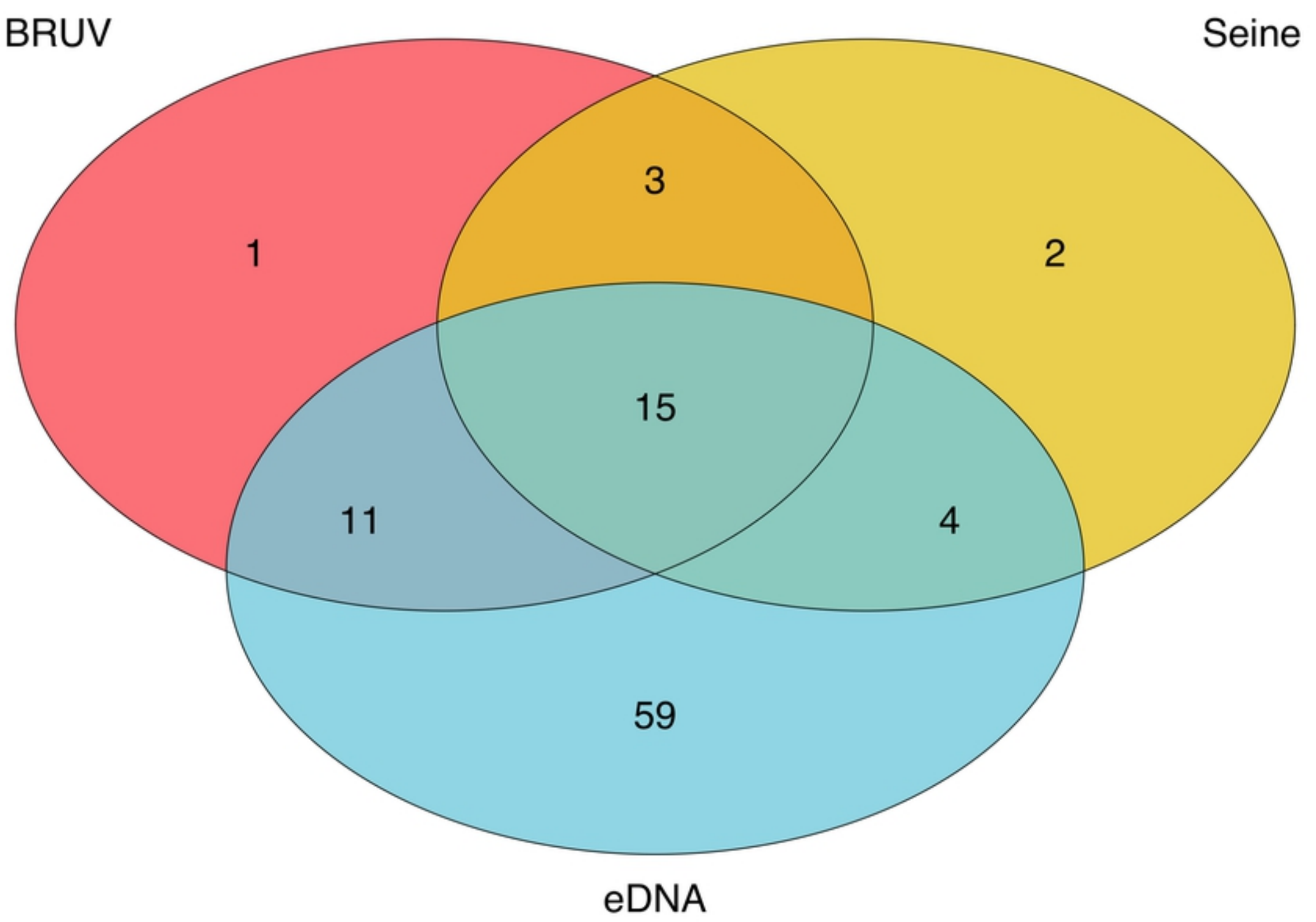

Figure 2

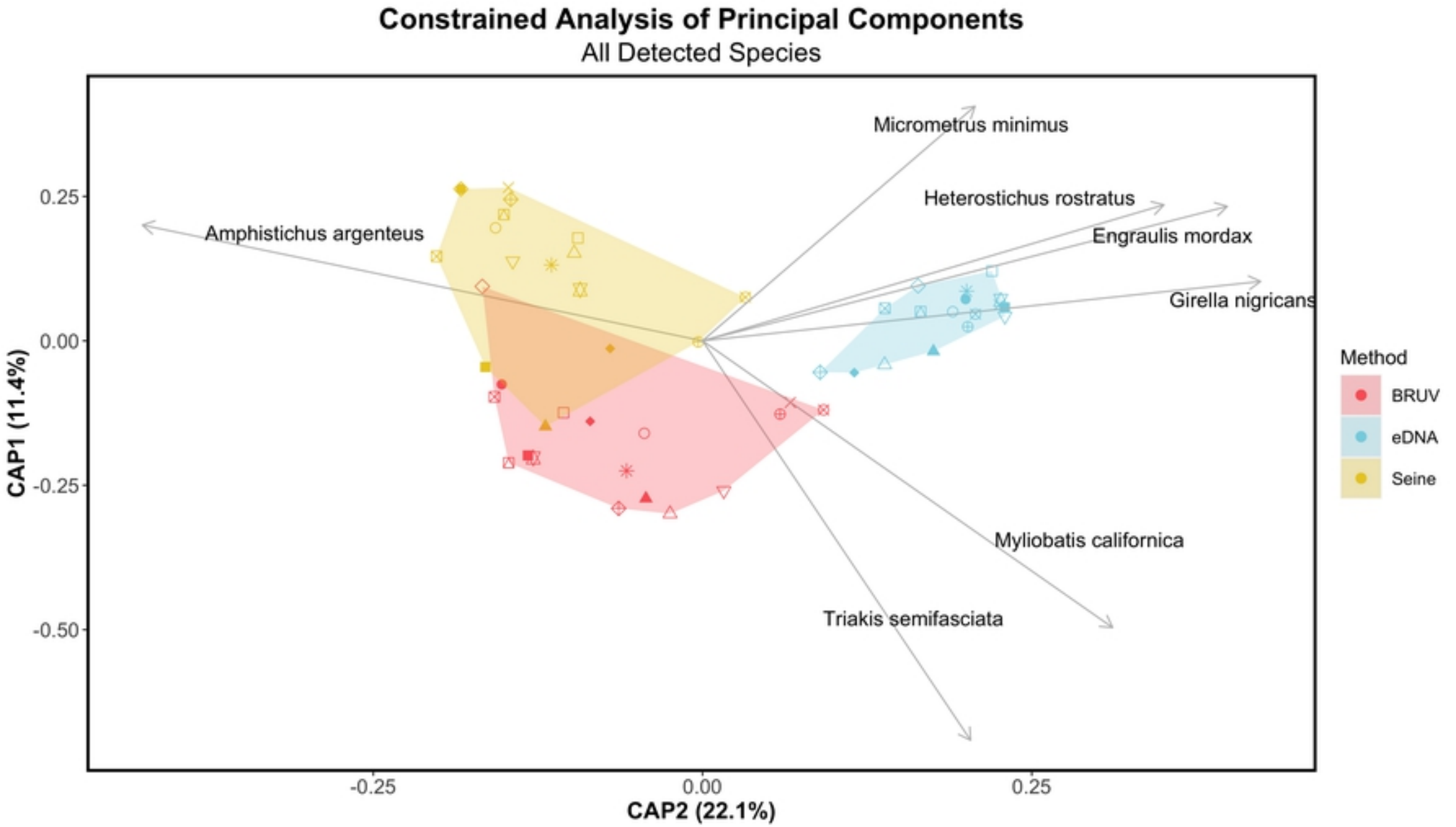
Constrained Analysis of Principal Components
All Detected Species
Micrometrus minimus
Heterostichus rostratus
Engraulis mordax
Girella nigricans
Amphistichus argenteus
Myliobatis californica
Triakis semifasciata
Method
BRUV
eDNA
Seine
0.25
0.00
-0.25
-0.50
CAP1 (11.4%)
-0.25
0.00
0.25
CAP2 (22.1%)

Figure 3

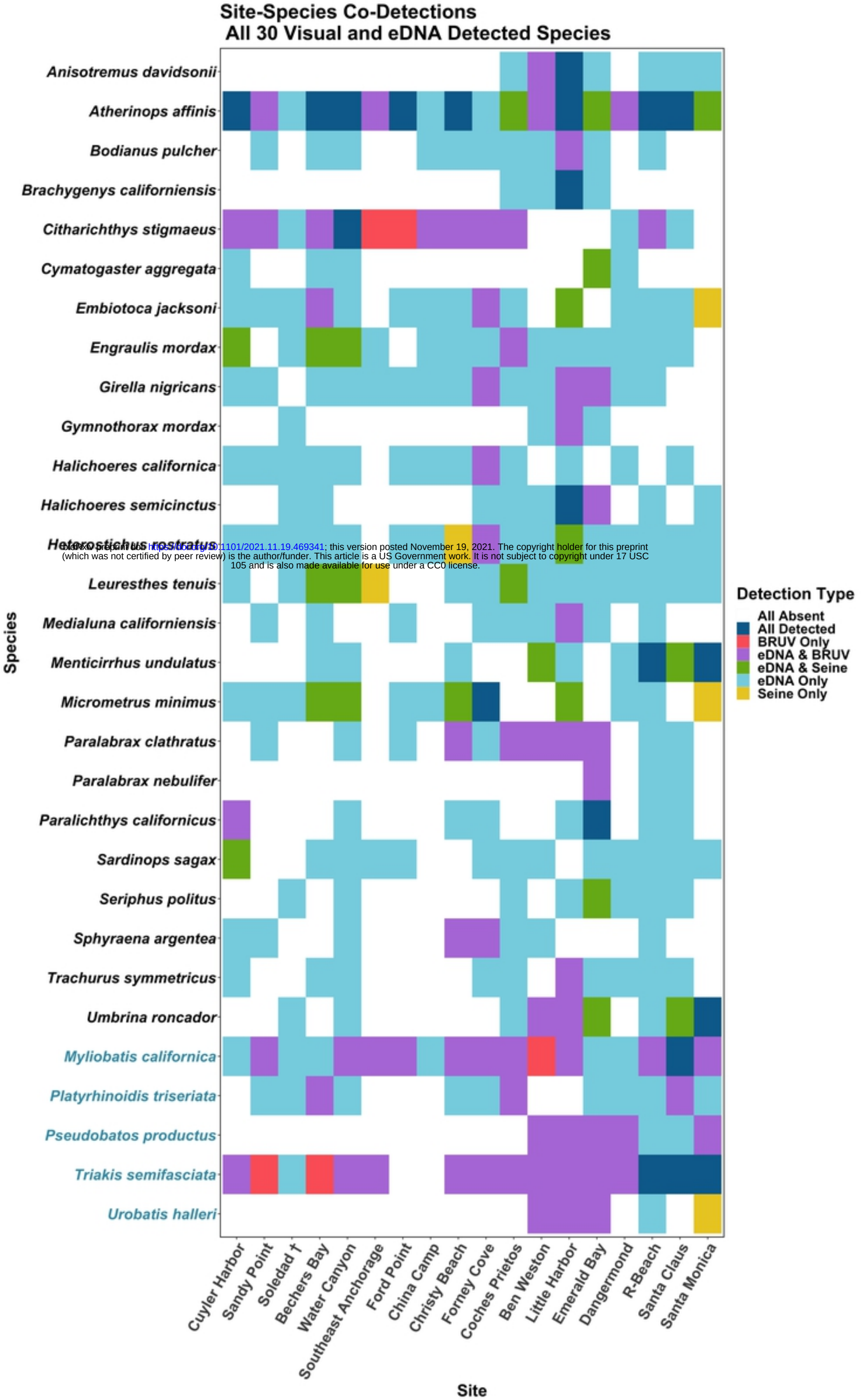

Figure 4

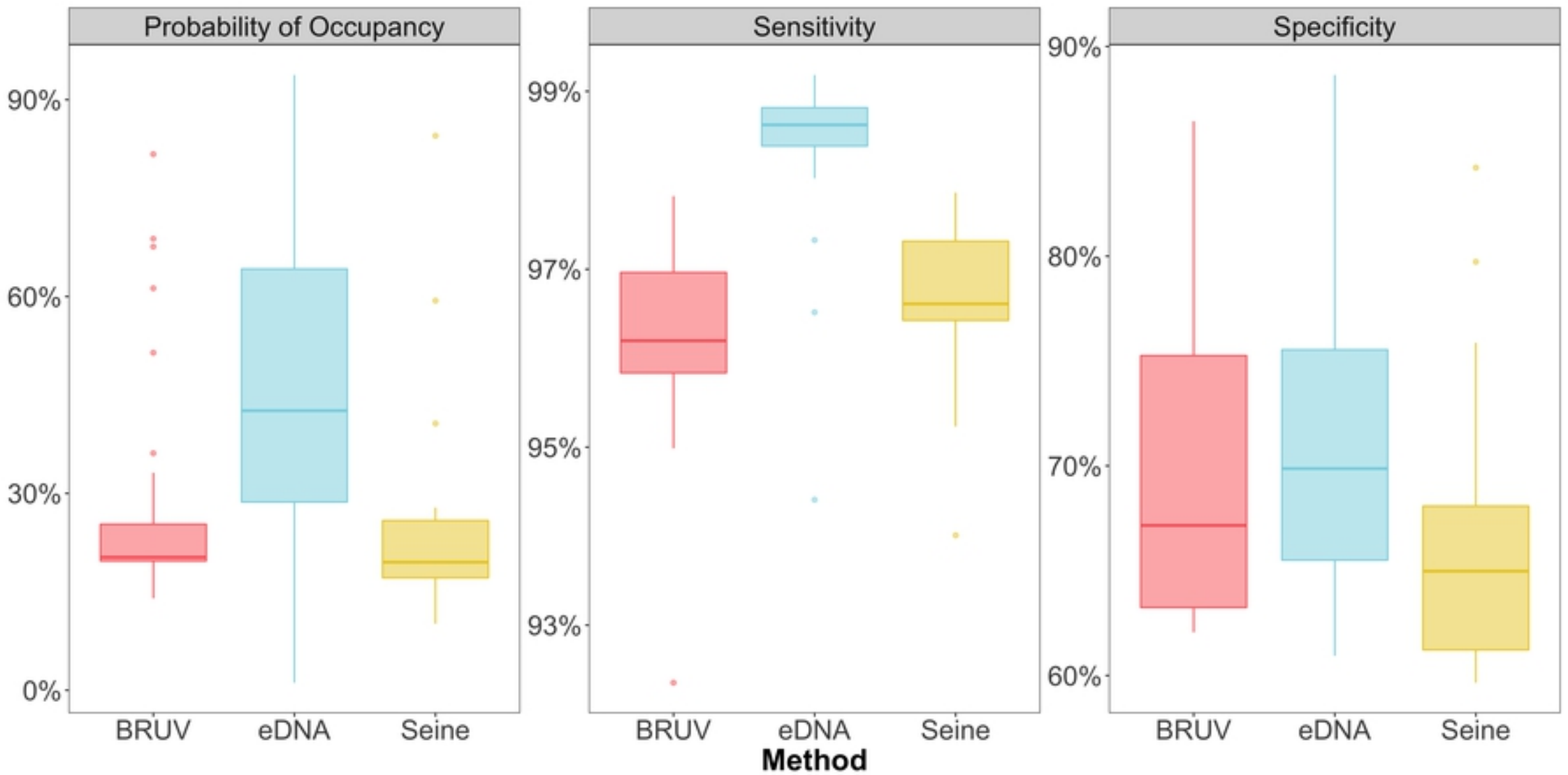
Probability of Occupancy
Sensitivity
Specificity
90%
60%
30%
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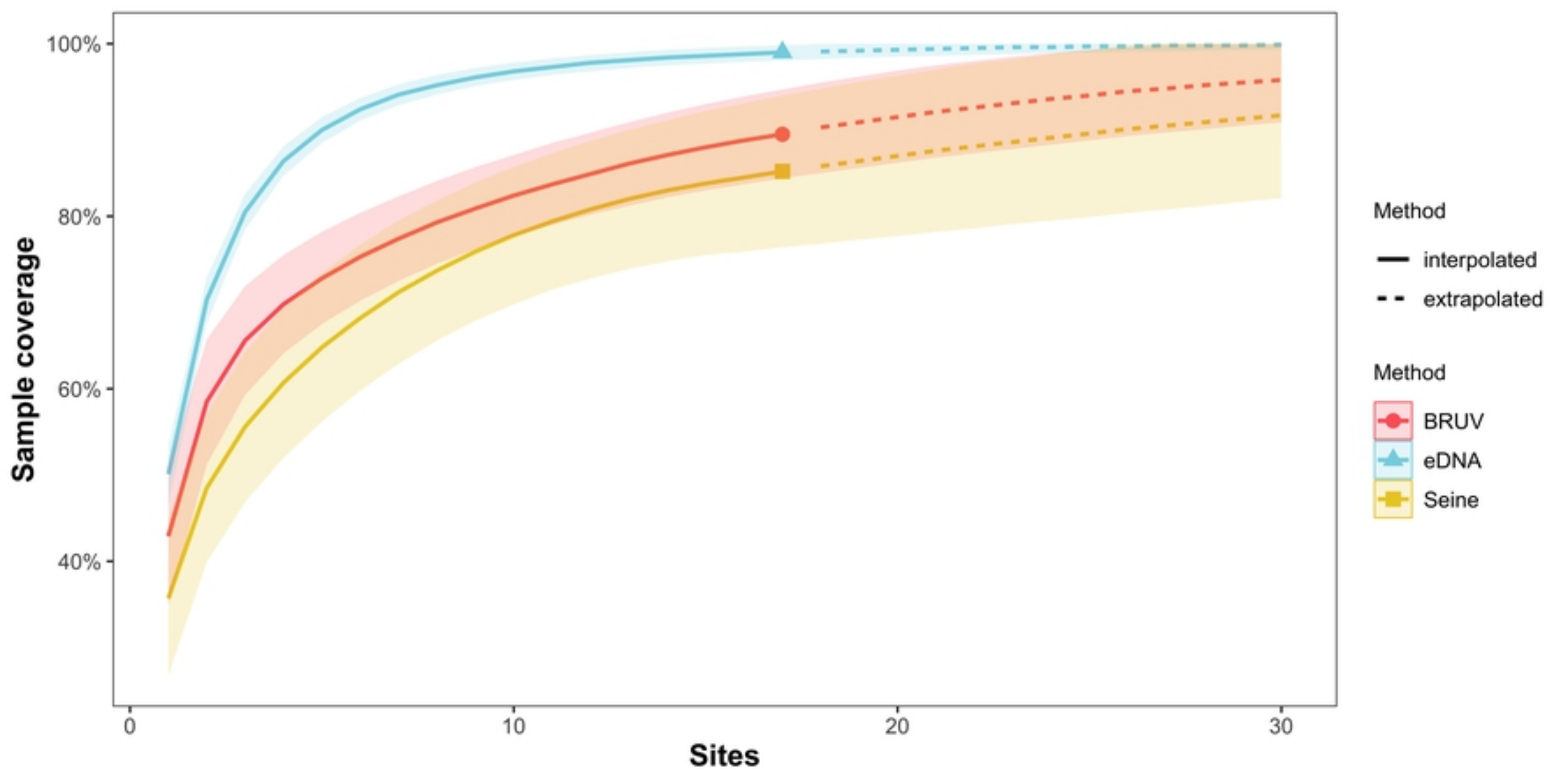
Figure 5


100%
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Sample coverage
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Sites
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interpolated
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Figure 6