

1 **FUNCTIONAL AND PHYLOGENETIC DIVERSITY OF SHARKS IN THE**
2 **NORTHEASTERN PACIFIC**

3 Zachary A. Siders^{1*}, Lauren B. Trotta², Fabio P. Caltabellotta^{1,3}, Katherine B. Loesser⁴,
4 Benjamin Baiser², Robert N. M. Ahrens⁵

5
6 ¹Fisheries and Aquatic Sciences Program, School of Forest, Fisheries, and Geomatics
7 Sciences, University of Florida, Gainesville, FL

8 ²Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL

9 ³Coastal Oregon Marine Experiment Station, Oregon State University, Newport, OR

10 ⁴Department of Oceanography and Coastal Sciences, Louisiana State University, Baton
11 Rouge, LA

12 ⁵Fisheries Research and Monitoring Division, Pacific Islands Fisheries Sciences Center,
13 National Oceanic and Atmospheric Administration, Honolulu, HI

14
15 *Corresponding Author:

16 Zachary A. Siders

17 zsiders@ufl.edu

18 Fisheries and Aquatic Sciences

19 University of Florida

20 7922 NW 71st Street

21 Gainesville, FL 32605

22
23 Acknowledgements:

24 This work would not be possible without support from University of Florida Biodiversity
25 Institute, College of Agricultural and Life Sciences, and College of Liberal Arts and
26 Sciences. Museum and private collections helped inform much of this data and we
27 would like to thank Dr. Gordon Hubbell and Dr. Andrea Kroetz for providing access to
28 their private collections. We would also like to thank the Florida Museum of Natural
29 History and Dr. Gavin Naylor, the Smithsonian Institution's National Museum of Natural
30 History and Dr. Jeff Clayton, and National Oceanic and Atmospheric Administration
31 Southeast Science Center Panama City Laboratory and Dr. Enric Cortés for providing
32 access to collections. No permits were necessary for this work and the authors have no
33 conflicts of interest to report.

34
35 Biosketch:

36 Zach Siders is a quantitative ecologist. He builds and applies integrative tools to discern
37 patterns and understand processes across the ecological hierarchy and inform resilient
38 management strategies.

39
40 Lauren Trotta is an ecologist applying phylogenetic approaches to better characterize
41 and understand drivers of diversity in communities.

42
43 Fabio P. Caltabellotta is a quantitative marine fisheries scientist. He uses advanced
44 data analysis tools and innovative approaches to improve marine fisheries resource
45 management and conservation.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jbi.14383

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Benjamin Baiser is a community ecologist and macroecologist. He takes empirical and theoretical approaches with a wide-range of organisms and systems to explore how species composition, traits, phylogenetic diversity, and interaction structure change over space and time.

Katherine Loesser is a graduate student studying estuary food web dynamics. She contributed to this work as part of her undergraduate thesis.

Robert Ahrens is a Fisheries Research Biologist at the NOAA Pacific Islands Fisheries Science Centers. He leads management strategy evaluations related to the management of fisheries and protected species.

Author contributions:

ZAS, LBT, and FPC conceived the ideas. ZAS designed the methodology. LBT built the phylogeny. KBL and FPC collated the trait values from the literature. KBL and ZAS did the photogrammetry. ZAS, KBL, and FPC collected pictographs. ZAS did the analysis. All authors contributed to synthesis and interpretation of results, the writing, and review.

Running Title: Shark biodiversity in the northeastern Pacific

68 **ABSTRACT**

69 *Aim:* The expansive spatial scale of pelagic communities and the difficulty in acquiring
70 pelagic species' functional traits has stymied an understanding of marine community
71 dynamics. We assembled and analyzed a shark trait database and community
72 phylogeny to identify the major axes of trait variation that define shark functional groups.
73 We tested whether membership to biophysical macroecological strata is related to these
74 functional or phylogenetic relationships.

75
76 *Location:* Northeastern Pacific, 180-255°E and 0-50°N

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78 *Major taxa studied:* Sharks (Class: Chondrichthyes, superorder: Selachimorpha)

79
80 *Methods:* We built a community phylogeny and collected habitat, reproductive, somatic
81 growth, trophic, and dentition traits. We used Principal Coordinates Analyses (PCoA) to
82 identify axes of trait variation and hierarchical clustering to classify functional groups.
83 We tested whether functional or phylogenetic relatedness determined species'
84 membership to strata from five macroecological gradients: latitude, habitat type,
85 thermal, carbon source, and bathymetry.

86
87 *Results:* We assembled 38 traits from 1,225 records from 130 sources, 260 pictographs
88 from seven sources, and 631 teeth from 79 jaw specimens. Life history, r versus K
89 selection, was responsible for the biggest division in the functional dendrogram. Vertical
90 habitat preference, growth rates, diet, and dental morphology generated further
91 divisions between r - or K -selected species. Vertical habitat preference, carbon source,

92 and biochemical habitat type were significantly dispersed or clustered on the functional
93 dendrogram or phylogram.

94

95 *Main conclusions:* Habitat and reproductive traits were the most important trait suites
96 driving shark functional diversity. Through ordination and clustering, we were able to
97 associate major axes of trait variation to the membership of shark functional groups.
98 The phylogram approximated well the functional dendrogram's backbone but was a
99 poor substitute for the trait diversity at the tips. Given the long evolutionary history of
100 sharks and coincident expansive trait diversity, merging functional and phylogenetic
101 approaches was necessary to capture the dimensions of shark biodiversity.

102

103 Keywords: dimensions of biodiversity, elasmobranchs, museum collections,
104 photogrammetry, pictographs, traits

105 **INTRODUCTION**

106 The pelagic ocean covers over 50% of the planet's surface, but little has been
107 explored of its community ecology (though see Grady et al., 2019; Pimiento et al.,
108 2020). Pelagic species, in particular marine megafauna, can range thousands of
109 kilometers and, as a result, pelagic "communities" span immense spatial scales, equal
110 to or greater than the scale of many terrestrial macroecological gradients. These
111 aspects impede the collection of specimens for measuring traits and reduce the
112 application of common community ecology quantitative approaches (Schlängel et al.,
113 2020). Thus, we do not have a baseline understanding of the functional and
114 phylogenetic diversity of many marine communities especially those in the pelagic
115 ocean. Neglecting this vast ecosystem stifles our understanding of the ecological
116 mechanisms determining community structure and function (Villéger et al., 2017).

117 In the pelagic ocean, sharks are the most abundant large-bodied species and
118 exert strong top-down control on ecosystems as apex predators, mesopredators, and
119 cannibals (Kitchell et al., 2002). Unlike other large-bodied pelagic fishes (e.g., tunas and
120 billfishes) that evolved in the Miocene (~17 mya), most extant shark lineages evolved
121 far earlier in the early Jurassic (Sorenson et al., 2014) and the first pelagic sharks
122 evolved far earlier in the Early Cretaceous (~140 mya). This long evolutionary history
123 coincides with an immense breadth of shark functional ecology. Sharks have evolved to
124 inhabit nearly every marine habitat (Compagno et al., 2005), exhibit a variety of
125 reproductive strategies from oviparity to various modes of viviparity (Parsons et al.,
126 2008), range in length from 20 cm to 18 m (Compagno et al., 2005), and are consumers
127 at almost every trophic level of the ocean food web (Motta & Huber, 2012). Further,
128 sharks are frequently caught in fisheries (Karp et al., 2011; WPRFMC, 2019) and, as a

129 result, many species have measured traits. Together, their ecological role, trait diversity,
130 and relatively thorough sampling makes shark assemblages a robust choice for
131 exploring pelagic community ecology.

132 Species' traits can provide insight into species functions, interactions,
133 distributions, and mechanisms that structure and maintain the diversity of communities
134 and the function of ecosystems (Cadotte et al., 2011; McGill et al., 2006). Further, traits
135 are the phenotypic expression of genetic diversity and combining trait-based
136 approaches with phylogenetic approaches provides multi-faceted information about the
137 evolutionary structure and resultant functioning of ecological assemblages (Mazel et al.,
138 2017; Tucker et al., 2018; Violle et al., 2007). In a macroecological context, traits can
139 provide insight into intra- and inter-specific distributions of niche breadth along
140 ecological gradients (Pigot et al., 2016; Read et al., 2018) as well as the structure of the
141 trait morphospace in an evolutionary lineage or community (Blonder et al., 2014; Price
142 et al., 2019). Typically, the influence of a macroecological gradient on a community is
143 assessed by comparing the taxonomic, functional, or phylogenetic diversity for a set of
144 locales spanning the gradient. However, the open ocean's sheer size, extreme depths,
145 strong seasonal changes, and the ability of pelagic species to move across these
146 dimensions reduce the applicability of a defined local community. Instead,
147 macroecological gradients (e.g., latitude, depth, temperature) can be divided into strata
148 and used to assign species' memberships from a regional pool using natural history
149 observations. The functional and phylogenetic relationships between species that co-
150 occur within a given strata can then be used to assess the influence of the
151 macroecological gradient on community structure (Li et al., 2019).

152 The ocean has classic latitudinal gradients as well as gradients coincident with
153 increasing depth, such as pressure, light, productivity, temperature, and oxygen, that
154 exert selective pressures on species traits (e.g., the evolution of bioluminescence,
155 Martini & Haddock, 2017), as well as influence community assembly processes (Martini
156 et al., 2019; Yasuhara et al., 2012). Previous studies have found that, at macro-scales,
157 lower latitudes and higher surface temperatures are generally correlated with increased
158 ectotherm diversity, while higher latitudes and lower surface temperatures are generally
159 correlated with lower ectotherm diversity (Worm et al., 2005) and higher endotherm
160 diversity (Grady et al., 2019). Macro-scale gradients result from changes in the carbon
161 source, assessed using stable isotopes, and can reflect a species preference for neritic,
162 transitional, or pelagic habitats (Davenport & Bax, 2002; Miller et al., 2008). At
163 mesoscales, habitat type – as defined by biochemistry (Raes et al., 2018), static
164 features (e.g., seamounts and hydrothermal vents) (Morato et al., 2010), or physical
165 forcing (e.g., eddies) (Carvalho et al., 2019) – can drive differences in oceanic
166 community composition.

167 The Northeastern Pacific (NEP) is an ideal location to explore pelagic biodiversity
168 at macroecological scales as it covers 60° of latitude, several oceanic biomes (Sayre et
169 al., 2021), a range of sea surface temperatures from tropical to Nearctic conditions,
170 neritic and pelagic habitats, and depths from the surface to over 8000 m. This region is
171 characterized by the Northeast Pacific Subtropical Gyre, an anticyclonic current
172 formation. Strong upwelling occurs in the east along the California coast while
173 numerous anticyclonic upwelling eddies occur far from the coast (Sun et al., 2019).
174 Slow zonal currents form a 40° latitudinal swath of warm surface temperatures

175 facilitating the expansion of tropical and sub-tropical species into higher latitudes while
176 the California Current and cold-core pelagic eddies provide suitable habitat for
177 temperate species at lower latitudes. Numerous oceanic seamounts, including the
178 Hawaiian Archipelago, provide opportunities for mixing between epi-, meso-, and
179 bathypelagic species in the same spatial area.

180 The goal of this study was to compare the community functional and
181 phylogenetic diversity of sharks occupying the NEP. Our objectives were to 1) collate a
182 trait database for sharks within the NEP using primary collection and literature search,
183 2) describe the major axes of functional diversity in trait suites, 3) characterize shark
184 functional groups and their associated phylogenetic diversity, 4) identify the principal
185 traits that drive the separation of shark functional groups, and 5) assess whether
186 membership to macroecological strata is related to the functional or phylogenetic
187 relationships between species.

188 **MATERIALS AND METHODS**

189 Our general methods were to 1) build a community phylogeny, 2) collect and
190 compile traits from a variety of sources, 3) conduct multivariate analyses (i.e.,
191 ordination, hierarchical clustering) to find major axes of trait variation among sharks and
192 identify shark functional groups, 4) test whether functional or phylogenetic relatedness
193 determined species' membership to macroecological strata.

194 **Regional Pool**

195 We compiled the regional species list for the NEP, 180-255°E and 0-50°N , from
196 published (Ebert et al. 2017) and online sources on Hawaiian and Californian ocean
197 biodiversity (e.g., <http://dlnr.hawaii.gov/sharks/hawaii-sharks/species-list/> and
198 <https://swfsc.noaa.gov/textblock.aspx?ParentMenuId=123&id=971>). For phylogenetic

199 analyses, we selected outgroup species from three lineages sister to Selachimorpha
200 (sharks) also found in this region of the NEP: Chimaeriformes, Myliobatiformes, and
201 Rajiformes.

202 *Phylogenetic Reconstruction*

203 As none of the recent Selachimorpha phylogenetic trees (Sorenson et al., 2014;
204 Stein et al., 2018) had complete coverage our regional pool, we built a community
205 phylogeny (or purpose-built phylogeny, sensu Li et al., 2019) to reconstruct the
206 evolutionary relationships between the co-occurring shark species. Briefly, we used four
207 mitochondrial loci *COI*, *CytB*, *NADH2*, and *16S*, and one nuclear locus, *Rag1*, to
208 reconstruct the phylogenetic relationships for this dataset (full details in Supplemental
209 Information 1). For each species, we downloaded sequences from GenBank
210 (Supplemental Table 1), aligned sequences using MAFFT v7.388 (Kato & Standley,
211 2013) plugin in Geneious Prime 2019.1.3 (<https://www.geneious.com>), and, using
212 PartitionFinder v. 2.1.1 (Lanfear et al., 2012), determined the optimal model of evolution
213 for each locus. We reconstructed phylogenetic relationships for individual gene trees
214 (Supplemental Figure 1) as well as all concatenated loci using Randomized Axelerated
215 Maximum Likelihood (RAxML) (Stamatakis, 2006, 2014). We applied an ordinal level
216 topological constraint to our concatenated RAxML analysis that reflects widely accepted
217 relationships between Selachimorpha lineages deep in the tree (Sorenson et al., 2014)
218 and is common practice in phylogenetic tree building in Selachimorpha (Sorenson et al.,
219 2014; Stein et al., 2018).

220 **Functional Traits**

221 We desired to capture a broad suite of traits reflecting the habitat use, life history
222 strategies, diet preferences, and morphological variation associated with the functional
223 ecology of the sharks in the regional pool (Violle et al., 2007). To do such, we compiled
224 traits (Supplemental Table 2)(Figure 1) for the species of interest using literature
225 search, pictographs (Supplemental Table 3), or enumeration and photogrammetry
226 (Supplemental Table 4). Pictographs of each shark species' lateral profile (or body
227 shape) were used to capture differences in relative external morphology (e.g.,
228 proportions, fin length, angle, and placement) as a supplement to the information on
229 maximum length. Enumeration of shark dentition was used to capture differences in the
230 number of teeth while photogrammetry was used to capture differences in the relative
231 morphology of a species' tooth crown. Each pictograph or photograph was converted to
232 a silhouette and its outline was reconstructed with Elliptical Fourier Analysis (EFA). The
233 resulting Fourier coefficients were used then decomposed using Principal Components
234 Analyses and the resulting principal component (PC) scores were used as traits in
235 downstream analyses. The remaining continuous trait values were from multiple
236 sources for each trait and were combined using a weighted average with the number of
237 citations as weights. All traits were standardized to approximate a standard normal
238 distribution for analyses. The complete trait set was then divided by biological theme
239 into trait suites: habitat, reproductive, trophic, somatic growth, and dental morphology
240 (Supplemental Table 2). Additional details on the trait collation and collection, weighting
241 scheme, and standardization are available in Supplemental Information 2.

242 **Principal Coordinates Analysis**

243 To identify and describe the major axes of shark functional diversity in each trait
244 suite and all suites combined, we conducted a Principal Coordinates Analysis (PCoAs)

245 on the Gower dissimilarity of the given trait suite. For each trait suite PCoA, all species
246 that had 50% or more coverage of the suite in question were included. The trait loading
247 ranks were calculated as a vector sum of the first and second PCo loadings weighted by
248 the percent variance explained by each PCo. All PCoAs were summarized in plots of
249 the first and second PCo scores for each species and the trait coverage within the suite
250 was calculated. Additional details on the PCoA are available in Supplemental
251 Information 3.

252 **Hierarchical Clustering**

253 We used hierarchical clustering with the complete linkage method on the overall
254 Gower trait dissimilarity matrix to construct a functional dendrogram. We identified the
255 optimal number of functional groups in the functional dendrogram using the gap statistic
256 and the first standard error maximum criterion (Maechler et al., 2019). Using the optimal
257 number of clusters, cluster membership was assigned to each species. The mean trait
258 value was calculated for each cluster removing any species with missing values. We
259 assessed the phylogenetic clustering of each trait and the phylogenetic diversity of each
260 functional group. For the former, the phylogenetic signal of each trait was evaluated by
261 calculating Pagel's lambda using the *phytools* package (Revell, 2012). For the latter,
262 three phylogenetic diversity metrics, phylogenetic distance (PD), the mean pairwise
263 distance (MPD), and the mean nearest taxon distance (MNTD), were calculated for
264 each functional group using the *picante* package (Kembel et al., 2010) using 999
265 iterations and an $\alpha = 0.05$ to assess significant standardized effect sizes (Z-scores)
266 (Webb et al., 2002) using a tip-swapping null model. Additional details on the
267 hierarchical clustering and optimal cluster search are available in Supplemental
268 Information 3.

269 **Macroecological relationships**

270 To test macroecological relationships of functional and phylogenetic diversity for
271 shark assemblages, we defined strata for five gradients: latitudinal gradient, habitat type
272 based on biochemistry (Sayre et al., 2021) (Supplemental Table 5), thermal gradient,
273 carbon gradient, and bathymetric gradient. These strata were defined using
274 independent sources on species' ranges, ecological marine units, sea surface
275 temperature, and stable isotopes as well as from the depth ranges defined during our
276 trait collection (strata definitions available in Supplemental Information 3). We then
277 tested the phylogenetic and functional dispersion for each stratum across each of the
278 macroecological gradients. The permutation-based standardized effect size was
279 calculated using *picante* package (Kembel et al., 2010) for three diversity metrics:
280 functional or phylogenetic distance (FD/PD), MPD, and MNTD using a tip-swapping null
281 model with 999 permutations and at an $\alpha = 0.05$.

282 **RESULTS**

283 **Regional Pool**

284 The regional shark list included 56 species, but four species had either zero
285 sequences (i.e., *Apristurus spongiceps*, *Centrophorus tessellatus*, *Etmopterus villosus*)
286 or a few low quality sequences (i.e., *Cephaloscyllium ventriosum*) available on Genbank
287 and thus were excluded from the regional pool, reducing the total to 52 species.

288 **Phylogeny**

289 In addition to the regional pool, six additional species were included in the
290 phylogeny as an outgroup (Supplemental Information 1). For all species (ingroup +
291 outgroup) our dataset had 81.4% coverage across all sequences for the regional pool
292 and the outgroup species (Supplemental Table 1). The final phylogram has 57 internal

293 nodes, 12 of which were constrained (Figure 1). For unconstrained nodes, bootstrap
294 values ranged from 27 to 100 with an average bootstrap value of 84.84%
295 (Supplemental Figure 2).

296 **Functional Traits**

297 Each trait included at least 58% of species in the regional pool (Figure 1).
298 Generally, age at maturity and von Bertalanffy k values were missing together and
299 missing most among the traits. Similarly, diet compositions and $\delta^{15}\text{N}$ were missing
300 together and missing the second most often among the traits. Minimum and maximum
301 depth of occurrence, maximum length, and reproductive mode all had 100% coverage.
302 Maximum depth, reproductive mode, size at birth, number of offspring, maximum length,
303 $\delta^{15}\text{N}$, and proportion of diet containing mollusks, crustaceans, zooplankton and plants
304 all had strong phylogenetic signal (Figure 1).

305 *Literature Traits*

306 Fourteen traits came solely from literature-derived sources (73% of all records),
307 while four were informed by additional data collection through the photogrammetry
308 process. A total of 1,225 trait value records were compiled from 130 unique sources.
309 The median number of records per species was 26 from a median of 8 sources, with a
310 minimum of 5 records (3 sources) and a maximum of 103 records (28 sources)
311 (Supplemental Figure 3 & 4). On average, the literature-derived trait coverage was 78%
312 per species with a minimum of 14% and a maximum of 100% (Supplemental Figure 5).
313 Four traits had 100% coverage (Figure 1) (Supplemental Figure 6).

314 *Pictograph Traits*

315 Body shape profiles (Figure 1) were compiled for 51 species (Supplemental
316 Table 3). In total, seven sources were used to compile body shape silhouettes
317 (Supplemental Figure 7) with a median of 5 sources per species, a minimum of 2
318 sources, a maximum of 7, and a total of 260 pictographs. Landmarks located at the
319 apical point of the rostrum, the first dorsal fin, and the upper caudal fin lobe
320 (Supplemental Figure 8) were needed to sufficiently align the silhouettes (Supplemental
321 Figure 9). After harmonic calibration, 15 harmonics were used in EFA of body shape
322 morphology (Supplemental Figure 10).

323 *Photogrammetric Traits*

324 Tooth crown morphology was compiled for 35 species from 80 specimens for a
325 total of 631 teeth (Figure 2, Supplemental Table 4). A minimum of one jaw specimen
326 per species was obtained, a maximum of 12, and a median of 2. Teeth were aligned
327 with centering and scaling (Supplemental Figure 11). After harmonic calibration, 16
328 harmonics were used in EFA of tooth crown morphology (Supplemental Figure 12).

329 **Trait Processing**

330 For the Principal Components Analysis on the EF pictograph coefficients, body
331 shapes varied principally in terms of fin erectness where species with the “classic” shark
332 profile such as Carcharhinids and Lamnids separated from species with more “torpedo”
333 profiles such as Squaliforms for PC1 (Supplemental Figure 13). Within the “classic”
334 shark profiles, further separation along PC2 occurred as a function of whether the
335 pectoral, dorsal, and caudal fins extended perpendicular to the anterior-posterior axis,
336 as in Longfin Mako Shark (*Isurus paucus*), or Oceanic Whitetip Shark (*Carcharhinus*

337 *longimanus*), or the caudal fin extended parallel to the anterior-posterior axis, as in the
338 Alopiids (Supplemental Figure 13).

339 For the PCA on EF photogrammetric coefficients, teeth shapes separated
340 whether the crown height was longer than the crown width or vice versa for PC1
341 (Supplemental Figure 14). Along PC2, convex teeth, as in Lamnids and Carcharhinus
342 species, separated from concave teeth, as in Gulper Shark (*Centrophorus granulosus*)
343 and in Gray Smoothhound Shark (*Mustelus californicus*). A large cluster of species was
344 identified that all roughly possessed the classic shark tooth, with roughly identical crown
345 heights and widths as well as slightly concave (Supplemental Figure 14).

346 **Principal Coordinates Analysis of Trait Variation**

347 The habitat PCoA scores split into two clusters (Figure 3A) defined by minimum
348 depths at and below the surface, while within those clusters, species separated by $\delta^{13}\text{C}$
349 and maximum depth (Supplemental Figure 15, Supplemental Table 6). Reproductive
350 PCoA scores separated by life history strategy (Figure 3B). Species with large size at
351 birth, late ages at maturity, low number of offspring, and high maternal investment
352 separated from species with small sizes at birth, early ages at maturity, high number of
353 offspring, and less maternal investment (Supplemental Figure 16). Similarly, the somatic
354 growth PCoA scores separated larger, slower growing species from smaller, faster
355 growing species (Figure 3C; Supplemental Figure 17). Nitrogen stable isotopic
356 signature ($\delta^{15}\text{N}$), a trait integrating across the diet categories, was the strongest loading
357 for the trophic trait suite PCoA (Supplemental Figure 18; Supplemental Table 5), with
358 clear separation between apex predators like Great White Shark (*Carcharodon*
359 *carcharias*), and zooplanktivores like Basking Shark (*Cetorhinus maximus*) (Figure 3D).

360 In the dental trait suite PCoA, species with higher dorsal and ventral symphyseal
361 and row counts separated from the rest of the species (Supplemental Figure 19). Teeth
362 PC scores grouped tightly by PC axis across all eight teeth positions (Figure 3E). In the
363 overall trait suite, the PCoA scores strongly separated by life history strategy, grouping
364 species by reproductive traits, and minimum depth of occurrence (Figure 3F)
365 (Supplemental Figure 20). Four of the five reproductive traits and two of the three
366 habitat traits were in the top ten ranked loadings of the overall suite (Supplemental
367 Table 5). Across PCoAs, species with trait coverage, that surpassed the exclusionary
368 threshold, but was still low tended to have extreme PCoA scores, but not all in the same
369 direction (Figure 3).

370 **Hierarchical clustering of functional groups**

371 We identified ten as the optimal number of functional groups from the shark
372 functional dendrogram (Figure 4). Group A was all Lamniforms with the exception of
373 Blue Shark (*Prionace glauca*; Carcharhiniformes) and was a cluster of viviparous,
374 mostly oophagous, pelagic species that on average exhibited a “classic” shark lateral
375 profile, grew slowly, matured late, were high on the food chain and more specialized on
376 cephalopods than teleosts with spear-shaped teeth (Figure 4B). Group B contained
377 large, pelagic Lamniforms with large sizes at birth, very slow growth rates, late ages at
378 maturity, and high tooth counts, at least for Megamouth (*Megachasma pelagios*) and
379 Basking sharks. Group C contained mostly Lamniforms except for the Sphyrnids and
380 had traits similar to group A but with higher nitrogen signatures from diets more
381 generalized on teleosts, cephalopods, and marine mammals, and with tooth crowns
382 equally wide and high. Group D was all Carcharhinid epipelagic, neritic, placentotrophic
383 species that exhibit a “classic” shark lateral profile and were mostly teleosts specialists

384 with tooth crowns equally wide and high. Group E was a small mesopelagic cluster of
385 viviparous oophagic species with mostly missing values.

386 Group F contained small-sized, pelagic, viviparous lecithotrophic mostly
387 Squaliform species but with entirely different tooth crown shapes, whose convex crowns
388 were angled laterally. Group G had only two species, Whale Shark (*Rhincodon typus*)
389 and Sixgill Shark (*Hexanchus griseus*), with extremely slow life history strategies
390 relative to the regional pool. Group H had the most taxonomic heterogeneity with species
391 from four shark orders that are viviparous lecithotrophic, diet generalists with tooth
392 crowns wider than high. Group I were crustacean feeding specialists with a fast life
393 history strategy relative to the regional pool and included only Carcharhiniforms with the
394 exception of Horn Shark (*Heterodontus francisci*; Heterodontiformes). Group J was
395 small-sized, viviparous lecithotrophic, mesopelagic Squaliform species. No shark
396 functional groups were significantly over-dispersed (Figure 4B). Overall, groups B, C, D,
397 and J were significantly under-dispersed across the phylogeny using the PD metric.
398 Further, groups C and D were significantly under-dispersed as measured by MNTD (i.e.,
399 near the tips of the tree), while groups C, D, J, and I were under-dispersed according to
400 MPD (i.e., deep in the phylogeny).

401 Overall, the functional diversity of the regional pool split broadly into two groups
402 along an axis of r (F-J groups) versus K (A-E groups) life history strategy: lecithotrophic
403 viviparous and oviparous species with many, small offspring or placentotrophic and
404 oophagous viviparous species with few, large offspring (Pianka, 1970) (Figure 4B).
405 Differences in bathymetric habitat selection, somatic growth rates (e.g., age at maturity
406 and Brody growth coefficient), and dietary specialization further split r -selected species.

407 In the *K*-selected group, carbon source (i.e., $\delta^{13}\text{C}$), zooplanktivory, tooth counts, and
408 tooth crown shape further split apart members. Species to species differences at the
409 tips or within a functional cluster tended to result from differences in continuous traits.
410 For example, in cluster D, differences in $\delta^{13}\text{C}$ gave rise to four subgroups likely
411 reflecting affinity for coastal zones. These comprised of an extremely coastal species,
412 Whitetip Reef Shark (*Triaenodon obesus*), coastal reef shark species, such as Gray
413 Reef (*Carcharhinus amblyrhynchos*) and Blacktip Reef Sharks (*C. melanopterus*),
414 continental slope species, such as Spinner Shark (*C. falciformis*), and, lastly pelagic
415 species, such as Oceanic Whitetip Shark.

416 **Macroecological signal**

417 In the macroecological analysis, only Leopard Shark (*Triakis semifasciata*) was
418 excluded from all analyses using AquaMaps distributions (latitude, thermal, and habitat
419 type), and species without $\delta^{13}\text{C}$ values were excluded from the carbon gradient test.
420 The composition (Supplemental Table 7) of the latitudinal strata, habitat types, thermal
421 strata, carbon source strata, and bathymetric strata had few significant instances of
422 over- or under-dispersion on the functional dendrogram or the phylogeny across all
423 diversity metrics (Figure 5). However, the epipelagic assemblage was over-dispersed
424 for FD, the bathypelagic assemblage was under-dispersed for MNTD, the neritic
425 assemblage was under-dispersed for both FD and MPD, and the Northern Subtropical
426 Epipelagic habitat assemblage (EMU 11) was under-dispersed for MNTD. For the
427 phylogeny, only neritic assemblages were significantly under-dispersed for MPD and
428 only North Pacific and Beaufort Sea Epipelagic habitat assemblages were significantly
429 over-dispersed for PD and MPD.

430 Of the five macroecological gradients we tested, bathymetric habitat selection
431 and carbon source had the most non-random dispersions relative to the functional
432 dendrogram and phylogeny (Figure 5F-G). Many species occur in the epipelagic
433 resulting in significant over-dispersion while bathypelagic species mostly come from
434 Squaliformes with similar functional ecology (group F) resulting in significant under-
435 dispersion (Figure 4). This can be clearly seen in the habitat trait suite PCoA where the
436 strongest clustering between species was along minimum depth preference (Figure 3A)
437 as well as by depth selection falling in the top three rankings of the habitat and overall
438 trait suite PCoAs (Table 1). Preference for neritic waters, identified by higher $\delta^{13}\text{C}$
439 values, also strongly matched the functional and phylogenetic structure. Differences in
440 carbon source tended to structure a few of the functional groups broadly, with group B
441 comprised of strongly pelagic species (low $\delta^{13}\text{C}$ values) and group D comprised of
442 neritic species (Figure 4A); however, most of the functional groups did not strongly align
443 to a particular end of the carbon gradient axis (Figure 5F). On the phylogeny, neritic
444 species were generally from Carcharhinidae and were clustered together deep in the
445 functional dendrogram and phylogeny (under-dispersed for MPD), but not at the tips
446 (random for MNTD) (Figure 5G).

447 **DISCUSSION**

448 By combining literature sources, pictographs, and primary photogrammetric
449 collection, we were able to produce a robust, novel trait database for sharks in the
450 Northeastern Pacific. Combining these trait data with a phylogeny, we described major
451 axes of functional diversity, tested shark traits for phylogenetic signal, defined shark
452 functional groups, and assessed the phylogenetic and functional relatedness of shark

453 species that co-occurred across a suite of macroecological gradients. Principally, we
454 found the diversity *within* a functional group was poorly explained by phylogenetic
455 distance and that the community phylogeny was a proxy for differences *between*
456 functional groups. This is empirical support of simulation studies that have suggested
457 that phylogenetic diversity may not encapsulate all the functional diversity in a
458 community (e.g., Mazel et al., 2017; Tucker et al., 2018). Across the macroecological
459 gradients we tested, we found bathymetry to be the strongest driver of community
460 structure, which parallels similar findings in teleosts both nearshore (Fujita et al., 1995;
461 Moranta et al., 1998) and offshore (reviewed by Sutton, 2013).

462 Likely as a result of the broad species' ranges of most species in our regional pool,
463 we did not find support for latitudinal or thermal gradients as other marine megafauna
464 studies have found (Grady et al., 2019; Worm et al., 2005)(Figure 5). We posit that the
465 scale of the contrast between the surface and vertical gradients drives this
466 phenomenon. For example, the surface thermal gradient in the NEP spans roughly
467 4000 km and varies from as low as 10°C in the California Current to as high as 30°C in
468 the Pacific North Equatorial Current. In contrast, the vertical thermal gradient is equally
469 as large within the first 500 m from the surface. Along with increasing pressures and
470 decreasing dissolved oxygen, depth is likely to be a stronger functional diversity driver
471 than latitude in the pelagic ocean (Rosa et al., 2008; Yasuhara et al., 2012). In addition,
472 our finding of weak support for functional and phylogenetic clustering based on carbon
473 source (Figure 5F-G) is similar to other studies that have documented changes as a
474 function of distance from shore for large taxa oceanic communities (Davenport & Bax,
475 2002; Morato et al., 2010).

476 Relative to other community ecology datasets, many NEP shark species are
477 large, mobile, marine organisms with close to circumglobal distributions (Supplemental
478 Table 7). Defining a community is difficult in these circumstances without fine-scale
479 occurrence data (Schlagel et al., 2020), which is often strongly biased against rare
480 species that can disproportionately contribute to functional diversity (Leitao et al., 2016).
481 Another consideration is that the habitat matrix is three-dimensional and strongly
482 dynamic. Increases in depth coincide with increases in pressure and decreases in light,
483 productivity, temperature, and oxygen generating sub-surface habitats that can result in
484 different assemblages (Farre et al., 2016; Martini et al., 2019). An inexact analog is
485 migratory birds whose community membership changes along their migratory pathways
486 (Chen et al., 2018; Zuckerberg et al., 2016). We use “inexact” purposefully as the
487 seasonal dynamics within a given locale in the NEP can be equivalent to the creation
488 and erosion of elevational gradients and 20° shifts in latitudinal gradients within a year
489 as eddies form and dissipate, current strength waxes and wanes, and sub-surface
490 features stabilize and abate. Subdividing these seasonal and vertical components more
491 explicitly may be necessary to draw better comparisons to between macroecological
492 gradients relevant to the pelagic ocean to those commonly studied in terrestrial,
493 freshwater, or neritic ecosystems.

494 An obvious caveat to our conclusions is the role of missing data within the trait
495 matrix. Not surprisingly, traits derived from more labor-intensive collection, such as
496 growth rates, standardized diets, and age at maturity, were missing for the greatest
497 number of species. Similarly, rare and deep-water species, such as Filled Shark
498 (*Chlamydoselachus anguineus*), were missing the greatest number of traits (Figure 1).

499 Compared to community studies of other taxa, many shark species in our regional pool
500 are exploited either directly or indirectly through fisheries bycatch (WPRFMC, 2019).
501 For example, Filetail Catshark (*Pseudotriakis microdon*) has been collected in fisheries-
502 independent surveys (Keller et al., 2014), but has not had a formal study on age and
503 growth. Thus, for some species, the hurdle to improving trait coverage is not the
504 collection of specimens but generating usable data from those collections.

505 Our use of pictographs for body morphology and photogrammetry for tooth crown
506 morphology represent one method to generate functional traits for these data-poor
507 species. These digitization efforts were designed to provide holistic traits with
508 reasonable species coverage (51/52 and 35/52 species, respectively). It appears this
509 holism was accomplished as the broad splitting of the functional dendrogram along the
510 *r-K* axis was reflected in the body shapes and tooth crown morphologies. The contrast
511 between species with elongated first dorsal and pectoral fins as well as a high aspect
512 ratio caudal fin (groups A-D) and species with more pronounced second dorsal and anal
513 fins as well as lower aspect ratio caudal fins (groups F-J)(Figure 4) is consistent with the
514 groups from the seminal pictograph analyses on shark body shapes by Thomson and
515 Simanek (1977). Similarly, groups A-E had tooth crowns with centered apexes, often
516 long crowns, and flat root margins while F-J groups had off-centered apexes, short
517 crowns, and, for three of the five groups, bulbous root margins. We were impressed with
518 this parallelism across trait axes as the pictographs and photographs were analyzed in
519 a scale-free way. We recommend other functional ecology studies attempt similar
520 efforts for difficult to acquire traits based on their ease of implementation (at least for the
521 pictographs) and success herein.

522 In terms of impact of trait coverage on our analyses, species with lower coverage
523 tended to be on the fringes of the PCoAs; especially those in trait suites with a mixture
524 high and low coverage (e.g., habitat, reproductive, somatic growth, and overall) (Figure
525 3 and Supplemental Figures 15-20). Low trait coverage played a role in determining the
526 functional groups with groups E and H seemingly defined by it (Figure 4). A reasonable
527 assumption would be that species with many missing trait values would likely be
528 reassigned to other clusters or grouped into a larger cluster with improved data
529 coverage. This is important for considering downstream applications, such as
530 calculating functional diversity at finer spatiotemporal scales, because the dendrogram
531 structure is partially influenced by coverage, and is likely to change as new data are
532 included (Kim et al., 2018).

533 For our phylogenetic analyses, we chose to use a phylogram over a chronogram.
534 This allowed us to focus on comparing trait diversity to feature diversity rather than
535 divergence time between species (Jantzen et al., 2019). Phylogenies are often used as
536 proxies for functional diversity based on the assumption that, when using a robust
537 phylogeny and including numerous functional traits, the two should be highly correlated;
538 though this is not always the case (Mazel et al., 2017; Tucker et al., 2018). In this study,
539 we sought to explicitly relate the multiple facets of functional diversity to the
540 phylogenetic information derived from our highly sampled, well-resolved community
541 phylogeny (Gerhold et al., 2015). We found that individual traits tend to either have very
542 high or very low phylogenetic signal (Figure 1). Across functional groups, half of them
543 were clustered deep within the phylogeny and 40% were clustered overall. Despite this
544 strong similarity in the functional dendrogram and phylogram's backbone structure, only

545 20% of functional groups had species clustered near the branch tips. Thus, for our
546 shark species, the phylogram is a proxy for extreme differences in functional traits
547 derived from evolutionary divergence deep in the tree but, not for the diversity within a
548 functional group occurring near the functional dendrogram tips.

549 Lastly, conducting PCoAs alongside the functional dendrogram analyses
550 facilitated a better understanding of how the structure of the functional dendrogram was
551 generated. Distinct clustering and strongly loading traits in the habitat and reproductive
552 trait suite PCoAs reflected deep splits and influential traits in the functional dendrogram
553 while equivocal clusters in somatic, trophic, and dentition trait suite PCoAs reflected
554 shallower splits. Additionally, by conducting PCoAs on the suites independently, we
555 could identify major axes of variation for each suite and compare to how those axes
556 integrated in the functional dendrogram, in the functional groups, and in the overall
557 PCoA. This is entirely expected as the functional dendrogram and PCoAs used the
558 same data but, by facilitating different visualization, yielded complementary and
559 confirmative approaches.

560 Trait datasets have a multitude of applications within functional ecology and
561 community phylogenetics (Cadotte et al., 2011). Applying trait filling approaches to our
562 trait matrix is a likely necessary step for pursuing some of these applications. The
563 strong signal of bathymetry and carbon source gradients apparent in the PCoAs and
564 functional groups are an opportunity to explore the correlates of macroecological
565 turnover in taxonomic, functional, and phylogenetic diversity in the pelagic ocean.
566 Lastly, there are opportunities to apply these diversity enumerations to the management
567 of sharks for the numerous fisheries operating in the NEP. The listing of Oceanic

568 Whitetip Shark and Scalloped Hammerhead Shark (*Sphryna lewini*) under the
569 Endangered Species Act places considerable pressure on United States fisheries to find
570 solutions to reduce shark-fishing interactions (Karp et al., 2011; WPRFMC, 2019). This
571 trait database and community phylogenetics analysis can be a complementary way to
572 categorize bycatch risk across shark species, define appropriate surrogates for risk
573 analyses of data-deficient species, and provide holistic metrics of shark biodiversity
574 impacts.

575

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772 identified through dynamic species distribution modelling. *Diversity and*
773 *Distributions*, 22(6), 717–730. <https://doi.org/10.1111/ddi.12428>

774

775 **DATA AVAILABILITY STATEMENT**

776 All scripts and data to reproduce the data and supplementary information can be found
777 at <https://osf.io/eszvb/>.
778

779 **TABLE 1**

780 Percent of total variance explained by each principal coordinate (PCo) for each trait

781 suite and the top three loadings from the Principal Coordinates Analysis of NE Pacific

782 shark functional traits.

Trait Suite	PCo1	PCo2	PCo3	Top 3 loadings
Habitat	58	21	7	min. depth, max. depth, $\delta^{13}\text{C}$
Reproductive	41	17	15	Size at birth, reproductive mode, # of offspring
Somatic Growth	46	17	14	k_{male} , k_{female} , L_{MAX}
Trophic	19	13	11	$\delta^{15}\text{N}$, % mollusks, % teleosts
Dental	39	31	9	D symph, V symph, D row count
Overall	31	12	11	Size at birth, reproductive mode, min. depth

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786

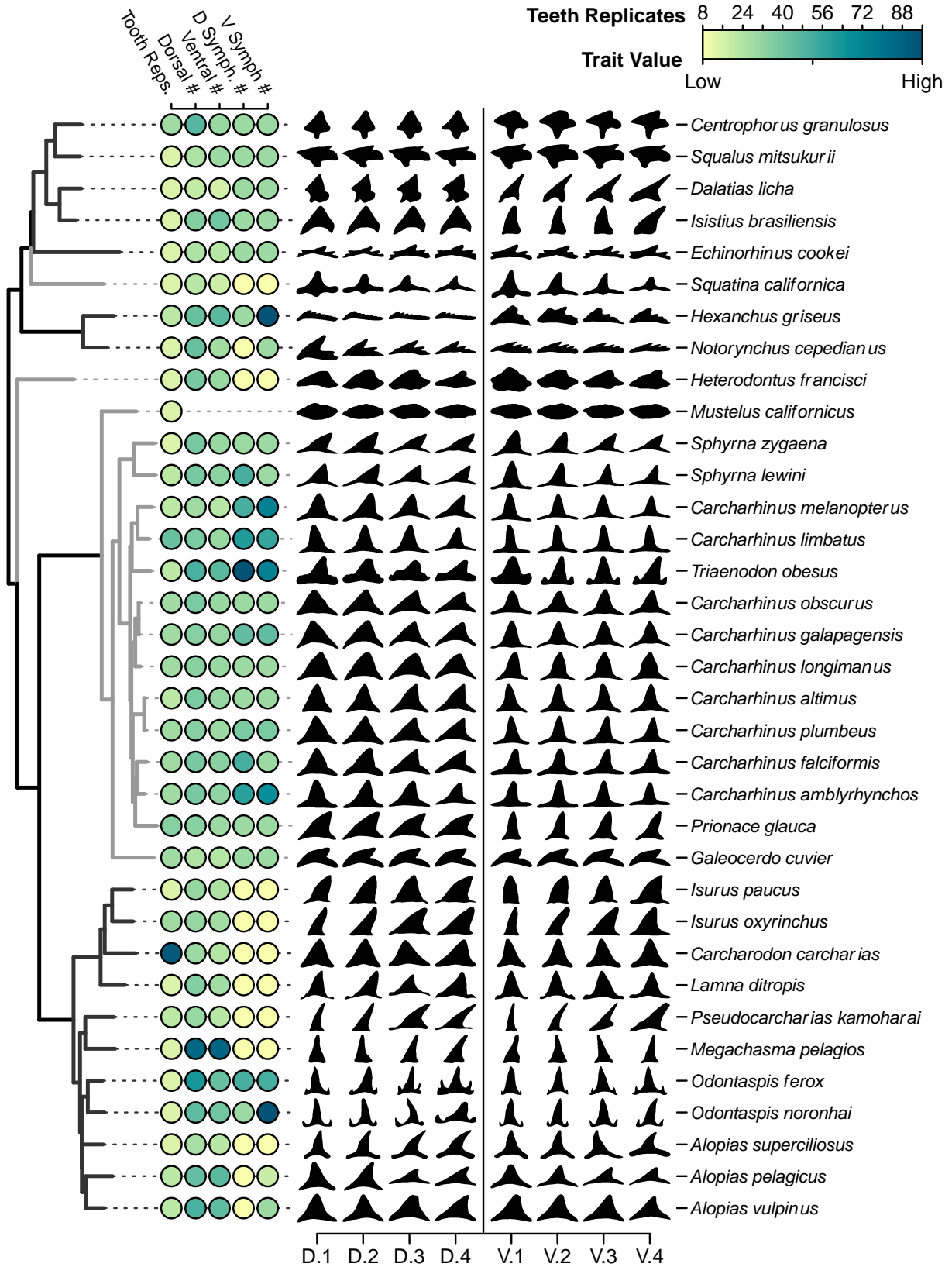
787

788 Summary of the phylogram (left-side) and trait table (right-side) for the 52 shark species

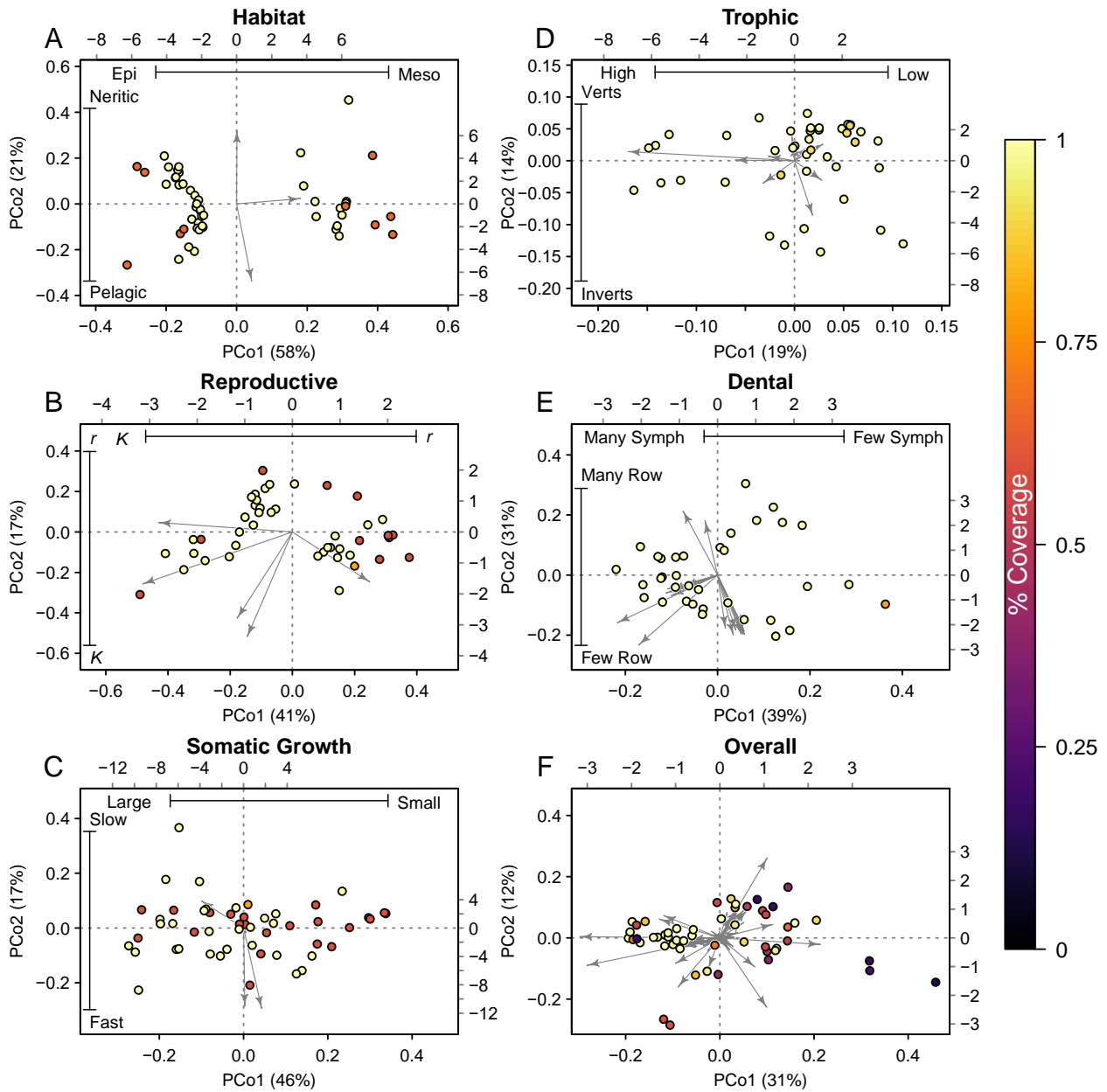
789 in the NE Pacific regional pool. Different colors in the phylogram identify different shark

790 orders. All traits are blocked by suite (habitat, reproduction, somatic growth, and trophic)

791 with darker colors indicating higher scaled values for continuous traits. The four
792 reproductive modes are colored individually. The proportion of the trait filled and the
793 phylogenetic signal of the trait, measured by Pagel's λ , are along the bottom with darker
794 colors indicating values closer to 1 (i.e., complete coverage or strong phylogenetic
795 signal for a particular trait). The mean body shape from pictographs for each species is
796 shown on the right.



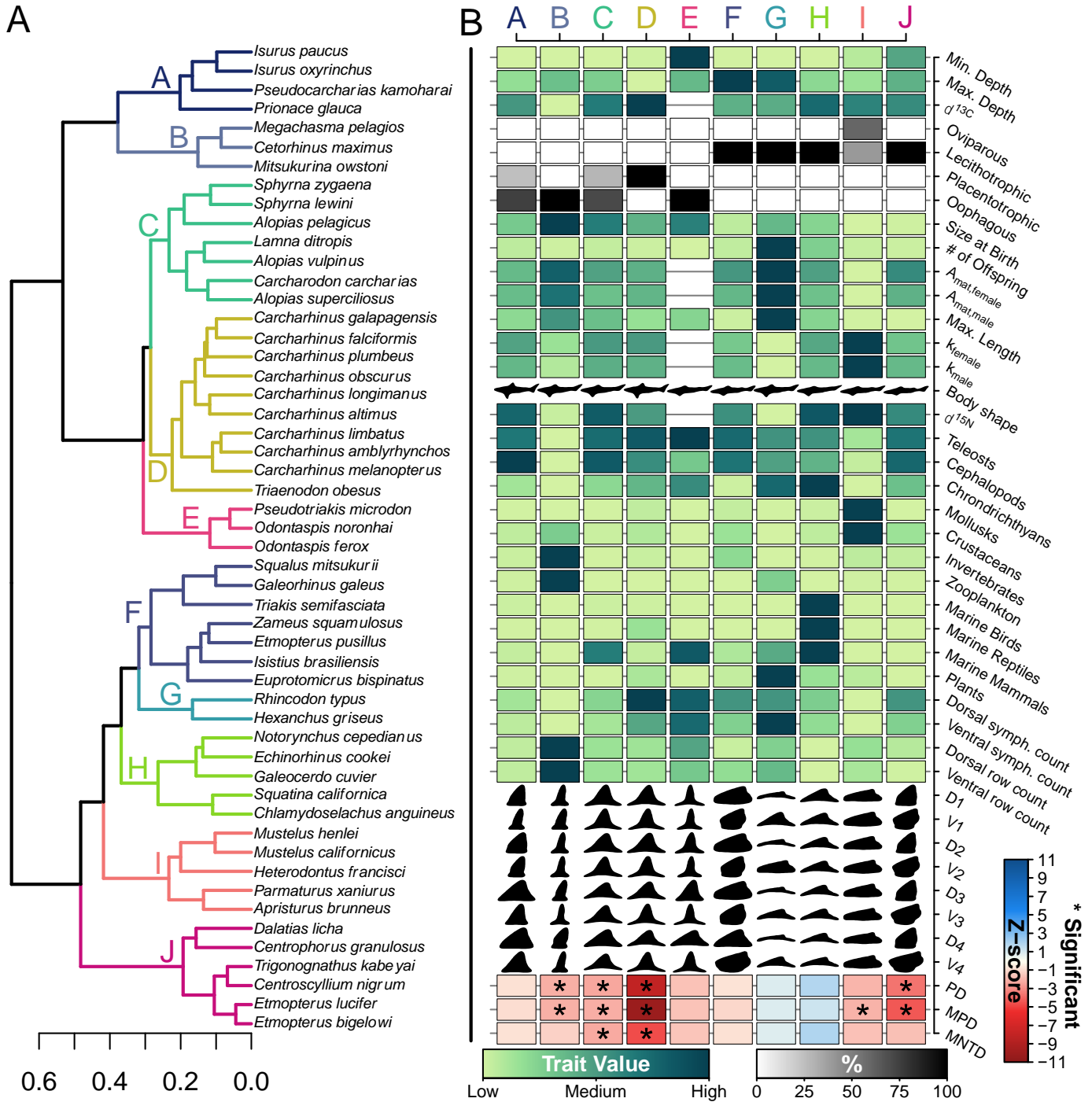
799 Summary of the dental traits and subset of the phylogram (left-side) for NE
800 Pacific shark species with jaw specimens. The number of teeth replicates (ranging from
801 8 to 96), the dorsal row count, ventral row count, dorsal symphyseal count, and ventral
802 symphyseal count are shown in colored circles on the left, warmer colors indicate higher
803 trait values. The mean tooth shape is drawn in black for each dorsal (D) and ventral (V)
804 position one through four adjacent to the symphysis.



806
807

808 The first and second principal coordinate from a Principal Coordinates Analysis (PCoA)
809 of each trait suite, habitat (A), reproductive (B), somatic growth (C), trophic (D), dental
810 (E), and the overall trait matrix (F) for the NE Pacific shark regional pool. For each
811 PCoA, the percent variance explained by the principal coordinate is shown in the axis
812 labels, the coordinates of each shark species included in the analysis is shown in the

813 circles colored by the percent trait coverage for each suite, and the loadings are shown
814 in the gray arrows. Loadings are provided to show the relative variation in trait loading
815 across suites, see Supplemental Figures 15-20 for loading labels. The scales of the
816 coordinates are shown along the lower and left axes while the scales of the loadings are
817 shown along the right and top axes. Ecological interpretations of the PCoAs are
818 provided above the bottom axis for PCo1, to the right of the left axis for PCo2, and
819 denoted by T arrows.



821

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The functional dendrogram for the NE Pacific shark regional pool from the full trait

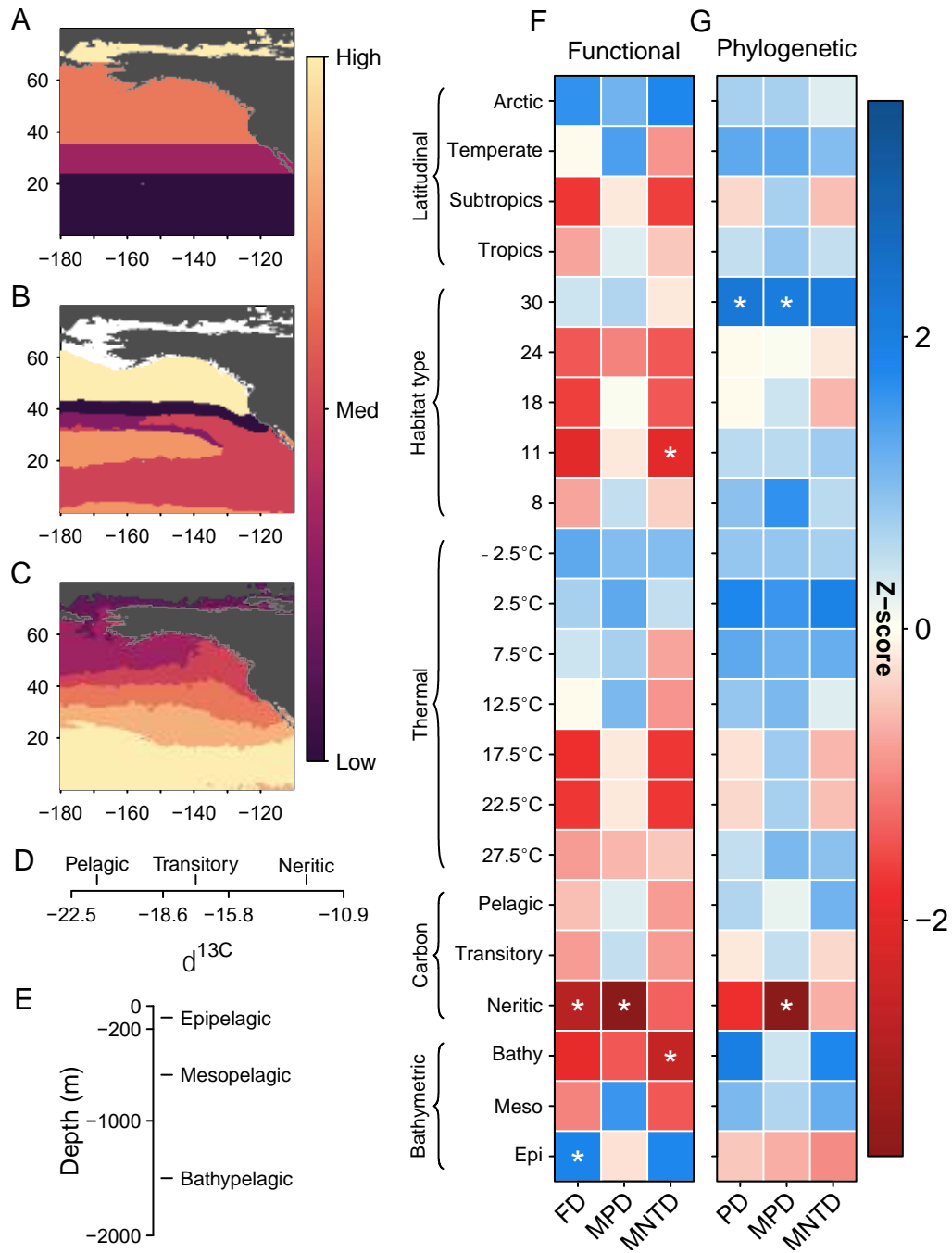
824

matrix (A) with the ten functional groups identified by the gap statistic and first standard

825

error max criterion denoted by each color block. The cluster means for each functional

826 group are shown for each trait (B) with darker colors indicating high trait values. For the
827 pictograph and photogrammetric silhouettes, the mean silhouette is shown. The Z-score
828 for phylogenetic distance (PD), mean pairwise distance (MPD), and mean nearest taxon
829 distance (MNTD) is also shown for each cluster, warmer colors indicate under-
830 dispersion while cooler colors indicate overdispersion and asterisks indicate significant
831 values at $\alpha = 0.05$.



833

834

835 Macroecological strata (A-E) and their clustering on the functional dendrogram (F) and

836 the phylogram (G) for the NE Pacific shark regional pool. A species membership to

837 specific (A) latitudinal strata (tropics, subtropics, temperate, and arctic), (B) habitat type

838 based on ecological marine unit (EMU) classification, or (C) thermal strata based on
839 average sea surface temperature were determined by their distribution defined by a
840 species' 50% probability of presence. Membership to (D) carbon source gradient strata
841 was based on a species' carbon stable isotope signature and to (E) bathymetric strata
842 were based on a species minimum and maximum depth. The standardized effect size
843 (Z-score) of the functional distance (FD), phylogenetic distance (PD), mean pairwise
844 distance (MPD), and mean nearest taxon distance (MNTD) was determined from
845 permutation using a tip-swapping null model using the functional dendrogram (F) or the
846 phylogeny (G). Significant Z-scores were denoted by asterisks ($\alpha = 0.05$). All maps are
847 projected in WGS 84.