

1 Distribution and relative abundance of scalloped (*Sphyrna lewini*) and Carolina (*S. gilberti*)
2 hammerheads in the western North Atlantic Ocean

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39

40 **Abstract**

41 The scalloped hammerhead (*Sphyrna lewini*) and its cryptic congener, Carolina
42 hammerhead (*S. gilberti*), are sympatrically distributed in the western North Atlantic Ocean.
43 Because the species are indistinguishable based on external morphology, little research focused
44 on Carolina hammerheads exists. In this study, the distribution of Carolina hammerheads in
45 waters of the United States off the east coast (U.S. Atlantic) and Gulf of Mexico (Gulf) was
46 examined and their abundance relative to scalloped hammerheads assessed by genetically
47 identifying 1,232 individuals using diagnostic single nucleotide polymorphisms. Both species
48 were found in the U.S. Atlantic, where 27% of individuals were Carolina hammerheads, but only
49 scalloped hammerheads were identified in the Gulf. In Bulls Bay, SC, a well-known
50 hammerhead nursery, assessment of relative abundance from May to September showed
51 scalloped hammerheads were more abundant May-June and Carolina hammerheads more
52 abundant July-September. Results of this study suggest Carolina hammerheads have a spatially
53 limited distribution in the western North Atlantic and highlight the importance of Bulls Bay as a
54 nursery for the species. In addition, the results suggest Carolina hammerheads may comprise a
55 non-trivial proportion of what is considered the U.S. Atlantic scalloped hammerhead stock and
56 should be considered in future decisions regarding management of the hammerhead complex.

57 **1. Introduction**

58 Advancements in molecular techniques have led to the discovery of hidden genetic
59 diversity (cryptic species) within morphologically conserved taxa across metazoans and
60 biogeographic regions (Pfenninger and Schwenk, 2007). Cryptic species are groups of
61 evolutionary independent lineages that appear morphologically indistinguishable from one
62 another (Bickford et al., 2007; Sáez and Lozano, 2005). Genetic differentiation with a lack of
63 morphological change is thought to occur when mating cues are nonvisual (e.g. chemical or
64 auditory) or when there is strong selective pressure that promotes preservation of morphological
65 characters (Bickford et al., 2007). Strong selection also could promote convergence in
66 morphology, resulting in genetically distinct species that are similar in appearance (Fišer et al.,
67 2018). Alternatively, cryptic species may have diverged too recently for morphological
68 differentiation to take place (Fišer et al., 2018).

69 Cryptic species may have different habitat requirements, life history characteristics, and
70 responses to disturbance and therefore pose a challenge to conservation and management. The
71 inability to distinguish species based on external morphology makes it difficult to monitor
72 populations (Lintott et al., 2016; Morningstar et al., 2014; Schönrogge et al., 2002) and
73 appropriately manage stocks (Bickford et al., 2007; Rocha et al., 2007). Molecular methods have
74 revealed several cryptic species complexes in commercially important marine fishes (e.g.
75 grouper, Craig et al., 2009; rockfish, Hyde et al., 2008; amberjack, Martinez-Takeshita et al.,
76 2015), and in some cases, these cryptic lineages co-occur (e.g. bonefish, Colborn et al., 2001;
77 opah, Hyde et al., 2014). Additional challenges arise when cryptic species coexist in all or part of
78 their range and, in these cases, research is needed to understand how potential differences in life

79 history, reproductive ecology, behavior and habitat use may need to be accounted for in
80 approaches to co-management.

81 Many groups of elasmobranchs (sharks, skates and rays) are morphologically conserved,
82 and challenges associated with species-level identification have historically been an impediment
83 to effective management. Recent estimates indicate 18.8% of elasmobranchs assessed under
84 International Union for Conservation of Nature (IUCN) Red List criteria are considered to be
85 threatened with extinction (IUCN, 2019), and declines have been largely driven by targeted
86 fisheries and mortality as bycatch (Dulvy et al., 2017). Catch records often lump sharks into
87 broad categories based in part on morphological and or biological similarity, making it difficult
88 to accurately assess what species were caught (Barker and Schluessel, 2005; Clarke et al., 2006).
89 Complicating the issue is the growing number of cryptic lineages that have been revealed by
90 molecular techniques, highlighting the importance of genetic methods in monitoring exploited
91 elasmobranchs (Ovenden et al., 2015; Portnoy and Heist, 2012; White and Last, 2012).
92 Molecular techniques have not only been used to identify cryptic elasmobranch species (e.g.
93 wobbegong, Corrigan et al., 2008; skates, Griffiths et al., 2010; guitarfishes, Sandoval-Castillo et
94 al., 2004; dogfishes, Ward et al., 2007), but also to understand distributions of morphologically
95 conserved species and evaluate their relative abundance in regions in which they are sympatric
96 (e.g. houndsharks, Giresi et al., 2015; blacktip sharks, Ovenden et al., 2010).

97 Sphyrnids, collectively known as hammerhead sharks, are a morphologically conserved
98 group of international conservation concern. Great hammerheads (*Sphyrna mokarran*), scalloped
99 hammerheads (*S. lewini*), and smooth hammerheads (*S. zygaena*) are often confused for one
100 another despite having distinct morphological characteristics, and thus have been reported under
101 a general category of “hammerheads” (Miller et al., 2013). Sphyrnids have experienced declines

102 in abundance throughout their range due to slow growth rates and relatively low reproductive
103 outputs compared to bony fish (Branstetter, 1987), high directed catch due to their desirability in
104 the global fin trade market (Abercrombie et al., 2005), and high rates of at-vessel as well as post-
105 release mortality associated with non-target commercial catch (Gallagher et al., 2014; Gulak et
106 al., 2015; Morgan and Burgess, 2007). As a result, both scalloped and great hammerheads are
107 considered Critically Endangered on a global scale by the IUCN and smooth hammerheads are
108 considered Vulnerable (Rigby et al., 2019a, 2019b, 2019c).

109 Management and conservation of scalloped hammerheads in the Atlantic Ocean is further
110 complicated by the presence of the sympatrically distributed cryptic congener, the Carolina
111 hammerhead (*S. gilberti*). The existence of a cryptic hammerhead lineage in the Atlantic was
112 first detected in the mid-2000s (Abercrombie et al., 2005; Duncan et al., 2006; Quattro et al.,
113 2006), and the species was formally described in 2013 (Quattro et al., 2013). Scalloped and
114 Carolina hammerheads are indistinguishable based on external morphology and can only be
115 identified using precaudal vertebrae counts (83-91 Carolina hammerhead, 92-99 scalloped
116 hammerhead) or genetics (Quattro et al., 2013). Limited data suggest that Carolina hammerheads
117 are found primarily off the southeastern United States (hereafter U.S.; Abercrombie et al., 2005;
118 Duncan et al., 2006; Quattro et al., 2006), with the exception of three individuals reported near
119 southern Brazil (Pinhal et al., 2012). Data collected from Carolina hammerheads have likely
120 been included in previous stock assessments of scalloped hammerheads in the U.S. Atlantic
121 (Hayes et al., 2009) and this could create a variety of problems. For example, Carolina
122 hammerheads are thought to reach a smaller maximum size than scalloped hammerheads,
123 (Quattro et al., 2013) and this could bias age and growth estimates that are important components
124 of fisheries stock assessments (Cailliet et al., 2006; Pardo et al., 2013). Further, when a status

125 review was conducted in 2013 to determine if protection under the U.S. Endangered Species Act
126 (ESA) was warranted for scalloped hammerheads (Miller et al., 2013), the presence of a
127 sympatrically distributed cryptic species was known, but a lack of data on distribution,
128 abundance and life history for Carolina hammerheads prevented species-specific assessments
129 and could not be factored into listing decisions. Under the ESA, listing decisions are applied to
130 specific portions of a species range (distinct population segments), rather than listing the species
131 as a whole. In the final determination, four out of six distinct population segments were listed as
132 Threatened or Endangered, however protection was not warranted for scalloped hammerheads in
133 the U.S. Atlantic and Gulf of Mexico (hereafter Gulf; NMFS, 2014), where the species are
134 thought to overlap.

135 Both scalloped and Carolina hammerheads employ a reproductive strategy in which
136 females utilize discrete coastal nursery habitats (Branstetter, 1987; Quattro et al., 2006). Shark
137 nurseries are defined as areas where young sharks are encountered more commonly than other
138 areas, remain resident for extended periods of time, and use the habitat repeatedly across years
139 (Heupel et al., 2007). In the U.S. Atlantic, estuarine waters of South Carolina, most notably,
140 Bulls Bay, SC (hereafter Bulls Bay), and nearshore waters of Cape Canaveral, Florida (hereafter
141 Cape Canaveral) have been identified as primary nursery habitat for scalloped hammerheads
142 (Adams and Paperno, 2007; Castro, 1993; Ulrich et al., 2007). Bulls Bay is a shallow estuarine
143 system composed of *Sporobolus sp.* saltmarsh flats with anastomosing small creeks, large
144 shallow mudflats, and barrier islands. The seafloor is primarily composed of fine sediments with
145 occasional shell rakes, and gently slopes from exposed mudflats to 4 m deep (at low tide) 6 km
146 offshore. The bay has minimal freshwater discharge, and waters are turbid with high (32-36 ppt)
147 salinities. The nearshore nursery habitats off Cape Canaveral have no direct estuarine influence

148 and extend approximately 5000 m offshore from the shoreline. The Southeast Shoal area is
149 characterized by shallow, low-relief shoal habitat (1-5 m depths) with sand-shell substrate.
150 Canaveral Bight, a deeper basin habitat (6-10 m depth) south of the shoals is characterized by
151 more turbid water with fine sediments, and the shelf transition zone directly south of Canaveral
152 Bight are also frequently used by scalloped hammerhead young-of-the-year (YOY; Adams and
153 Paperno, 2007). Scalloped hammerhead YOY are also frequently observed in the Tolomato
154 River, Florida (hereafter Tolomato River), a portion of the Atlantic Intracoastal Waterway that
155 appears to serve as a unique, inshore primary nursery for this species based on comparisons of
156 catch data from other northeast Florida estuaries (B. Wargat and J. Gelsleichter, unpublished
157 data). Additional nursery habitat may exist in Georgia and North Carolina. In the Gulf, scalloped
158 hammerhead YOY have been found in estuaries, bays, and beaches in Florida and Texas (Hueter
159 and Tyminski, 2007). Coastal waters of South Carolina are also thought to provide important
160 nursery habitat for Carolina hammerheads (Quattro et al., 2006), but their occurrence elsewhere
161 has not been thoroughly evaluated.

162 In this study, a panel of diagnostic single nucleotide polymorphisms (SNPs) was
163 generated using double-digest restriction associated DNA sequencing (ddRAD) to identify
164 scalloped and Carolina hammerheads sampled in the U.S. Atlantic and Gulf, with a focus on
165 known and potential nursery areas (hereafter nurseries). Data were used to describe the
166 distribution of Carolina hammerheads and determine their abundance relative to scalloped
167 hammerheads. An understanding of the relative abundance of scalloped and Carolina
168 hammerheads in U.S. waters will be needed in future assessments, and results of this study will
169 help managers identify nursery areas for both species and are an important first step toward
170 developing appropriate, species-specific management strategies.

171

172 **2. Methods**

173 A total of 1,241 individuals were sampled in the U.S. Atlantic and Gulf (Fig. 1, Table 1)
174 between 2010-2019. Tissues were stored in 20% salt-saturated DMSO buffer (Seutin et al., 1991)
175 or molecular grade EtOH initially and subsequently transferred to DMSO buffer for long-term
176 storage. Sharks were captured using longlines, gillnet, otter trawl, or hook and line from a
177 combination of targeted collection and fishery independent surveys. Fin clips were also obtained
178 from mortalities in commercial shrimp trawls. Collections were made following animal care and
179 use protocols of academic partners and standard operating procedures of state and federal
180 agencies (see animal care statement). Genomic DNA was extracted using a Mag-Bind® Blood &
181 Tissue DNA Kit (Omega Bio-Tek), and preparation of ddRAD libraries followed methods
182 described in Barker et al. (2019). Following sequencing, individuals were demultiplexed using
183 the script *process_radtags* (Catchen et al., 2013), and the DDOCENT pipeline was used for *de*
184 *nov*o reference construction, read mapping and SNP calling (Puritz et al., 2014). A *de novo*
185 reference assembly was constructed from twenty individuals (15 scalloped hammerheads, 3
186 Carolina hammerheads, and 2 great hammerheads) sequenced as a paired-end run on an Illumina
187 MiSeq sequencer, with initial species identifications based on mitochondrial control region
188 (mtCR) haplotypes (Barker et al., 2017). Great hammerheads were included as the morphology
189 of YOY great hammerheads is similar to that of the other two species and YOY great
190 hammerheads are sometimes misidentified as scalloped hammerheads (Barker et al., 2017). The
191 twenty individuals used to construct the reference assembly were subsequently screened for
192 SNPs that could be used to distinguish scalloped, Carolina, and great hammerheads. Raw
193 variants were filtered using VCFTOOLS (Danecek et al., 2011) with a minimum quality score of

194 20 and mean minimum depth of 10. Indels and sites with any missing data were removed, and
195 the dataset was thinned to retain only one SNP per contig. Two panels of diagnostic SNPs were
196 identified, the first to distinguish great hammerheads from scalloped and Carolina hammerheads
197 (Panel 1) and the second to distinguish scalloped hammerheads from Carolina hammerheads
198 (Panel 2). Panel 1 was designed by calculating allele frequencies in GENODIVE (Meirmans and
199 Van Tienderen, 2004) and selecting SNPs that were completely fixed between great
200 hammerheads and (scalloped + Carolina hammerheads). To design Panel 2, great hammerheads
201 were removed from the dataset and allele frequencies recalculated to identify SNPs that were
202 completely fixed between scalloped and Carolina hammerheads. A total of 2,695 diagnostic
203 SNPs were identified for Panel 1 and 1,491 for Panel 2.

204 The remaining individuals were sequenced across 11 lanes on an Illumina HiSeq 4000
205 DNA. Each sequencing run contained a mix of individuals from different sampling locations to
206 minimize library effects. DDOCENT was used to map reads and call SNPs and raw variants were
207 filtered to retain only diagnostic SNPs using VCFTOOLS. Individuals were first identified as
208 either great hammerhead or scalloped/Carolina hammerhead using composite genotypes of Panel
209 1 SNPs and a custom Python script (see Data Availability). Species identity was considered
210 unknown if an individual had less than a 95% match to a single category. Individuals identified
211 as a great hammerhead or unknown were removed from the dataset, and the remaining
212 individuals identified as either a scalloped hammerhead, Carolina hammerhead or undetermined
213 by using composite genotypes of Panel 2 SNPs and a custom Python script. As above, a match of
214 95% to one species was required for positive species identification, and if an individual did not
215 meet this threshold for any one species it was classified as undetermined. Individuals that were
216 not genotyped at a minimum of 300 diagnostic SNPs were removed from the dataset (see below).

217 The program NEWHYBRIDS (Anderson and Thompson, 2002) was used to assess if undetermined
218 individuals could be assigned into a hybrid (F1 hybrid, scalloped hammerhead backcross,
219 Carolina hammerhead backcross) or non-hybrid category (scalloped hammerhead, Carolina
220 hammerhead) following the methods of Barker et al. (2019).

221 Due to sequencing variation within and across runs, individuals varied in the number of
222 diagnostic SNPs that were successfully genotyped. Additionally, due to the small number of
223 Carolina and great hammerheads used to initially identify diagnostic SNPs and individual
224 variation, as well as potential admixture between species (Barker et al., 2019), it was expected
225 that at least some of the diagnostic SNPs would not be completely fixed in all individuals of a
226 given species. To determine the minimum number of diagnostic SNPs required for accurate
227 species identification, a resampling technique (custom script) was employed using the
228 individuals from the first HiSeq library (n = 128; great hammerhead = 1, scalloped hammerhead
229 = 89, Carolina hammerhead = 27, mixed ancestry = 11). Random subsets of loci ranging in
230 number from 5-2,000 loci in Panel 1 and 5-1,200 loci in Panel 2 were selected and individuals
231 reidentified. This procedure was repeated for 1,000 iterations, and the average number of correct
232 identifications (i.e., matched original identification from the full panel of SNPs) for each
233 individual with each subset of loci was determined.

234 Relative abundance (as a percentage) was determined by dividing the number of
235 individuals of each species (scalloped hammerhead and Carolina hammerhead) by the total
236 number of individuals across both species. Relative abundance was calculated for each region, as
237 well as for known and potential nurseries, defined in this study as areas in which at least 20 YOY
238 or small juveniles (stretch total length $\leq 1,000$ mm) were sampled. Regions were generally
239 defined by state boundaries (North Carolina, South Carolina, and Georgia) with the exception of

240 Florida, which was split into five regions (Atlantic northern Florida, Atlantic central Florida, the
241 Florida Keys, Gulf central Florida, and Gulf northern Florida). Temporal trends in relative
242 abundance of YOY over the sampling season for both species were assessed in Bulls Bay by
243 pooling catch data across years (2013-2018) and standardizing to catch per unit effort (CPUE,
244 sharks caught/gillnet set). Permutation tests implemented in the R package COIN (Hothorn et al.,
245 2008) were used to test for associations between species identity and environmental variables
246 (salinity, dissolved oxygen, and water temperature) measured at the time of sampling using a
247 YSI Pro 2030 (YSI Inc./Xylem Inc.). Generalized linear models were used to test for
248 associations of environmental variables and month with the relative probability that a sampled
249 individual was a scalloped or Carolina hammerhead. All models were compared against a null
250 model and tested for goodness of fit and the optimal model was selected to minimize AIC values.
251 Abundance trends and associations with environmental variables were evaluated only in Bulls
252 Bay because YOY Carolina hammerheads were not identified in large enough numbers in other
253 nurseries.

254

255 **3. Results**

256 Identification accuracy for Panel 1 was high even when very few SNPs were used, with
257 an overall average of 99.1% correct identification with five loci. The overall average correct
258 identification for Panel 2 was similarly high for five loci (96.2%), however, individual variation
259 in correct identification was substantial (50.7-100.0%; Fig. S1). Reliable and accurate
260 identification (>99% individuals identified correctly in >95% of the iterations) with Panel 2 was
261 not achieved until 300 loci were used, and 500 loci were required for 100% of individuals to be
262 identified correctly in >95% iterations.

263 A total of 1,120 individuals were identified with the panels of diagnostic SNPs (scalloped
264 hammerhead = 878, Carolina hammerhead = 236, great hammerhead = 6), and 83 individuals
265 were assigned into a hybrid category by NEWHYBRIDS (F1 = 37, scalloped hammerhead
266 backcross = 38, Carolina hammerhead backcross = 8; Table 2). NEWHYBRIDS also identified an
267 additional 13 scalloped hammerheads and 15 Carolina hammerheads that could not be identified
268 with the diagnostic panel, and these individuals were added to species totals for subsequent
269 analysis. One individual could not be distinguished by Panel 1 and had a mix of
270 scalloped/Carolina hammerhead alleles and great hammerhead alleles. The anomalous
271 individual, which was sampled in the U.S. Atlantic near central Florida, was sequenced at the
272 mitochondrial cytochrome oxidase subunit 1 (COI, see supplementary methods) gene and
273 identified as a smooth hammerhead (*S. zygaena*; accession no MT863713). Nine individuals
274 were genotyped at too few loci and were removed from the dataset. Scalloped hammerheads
275 were identified in all areas sampled in both the U.S. Atlantic and Gulf. Carolina hammerheads
276 were identified across the sampled area in the U.S. Atlantic, though not in every location, and
277 were absent in the Gulf (Fig. 2). Carolina hammerhead abundance was heavily concentrated in
278 South Carolina.

279 The relative abundance of Carolina to scalloped hammerheads was highest in South
280 Carolina (56.4%, total hammerheads = 351) and North Carolina (33.3%, total hammerheads =
281 12; Table 3). Relative abundance of Carolina hammerheads roughly decreased along a latitudinal
282 gradient, with the lowest relative abundance observed in the Florida sampling locations.
283 However, Carolina hammerhead abundance was higher in central Florida (12.9%, total
284 hammerheads = 194) than northern Florida, where Carolina hammerheads were particularly rare
285 (3.6%, total hammerheads = 195). Relative abundance of Carolina hammerhead YOY was

286 calculated for six nurseries in the U.S. Atlantic (Fig. 3) and was highest in Bulls Bay (61.0%,
287 total hammerheads = 287) and lowest in Tolomato River (0%, total hammerheads = 148; Table
288 4).

289 In Bulls Bay, Carolina hammerheads were more abundant than scalloped hammerheads
290 in all years but two, however, the relative proportion of Carolina to scalloped hammerheads was
291 variable, ranging from 31.2% in 2019 to 87.0% in 2012 (Table 5). Analysis of CPUE data from
292 May to September showed that YOY of both species were present in Bulls Bay in May.
293 Scalloped hammerheads were relatively more abundant from May through June, but both species
294 increased in abundance during this time and abundances peaked at the end of July (Fig. 4).
295 Scalloped hammerhead CPUE decreased rapidly after July, and the species was absent by the
296 end of August. Carolina hammerhead CPUE increased sharply in July and declined through
297 August and September. Permutation tests showed that salinity ($Z = 4.636$, $P < 0.001$) and water
298 temperature ($Z = 5.059$, $P < 0.001$) were significant predictors of species identity. The optimal
299 generalized linear model also indicated salinity ($Z = 3.771$, $P < 0.001$) was significant, as well as
300 month ($Z = 2.360$, $P = 0.018$) and these variables had a significant positive association with
301 Carolina hammerhead abundance, meaning that the relative probability that a sampled individual
302 was a Carolina hammerhead increased with higher salinity and later months in the sampling
303 period (Fig. S2).

304

305 **4. Discussion**

306 Hammerhead sharks sampled along the U.S. Atlantic and Gulf of Mexico were
307 genetically identified to describe the relative abundance and distribution of scalloped and
308 Carolina hammerheads. In the U.S. Atlantic, 63.6 % of identified hammerhead sharks were

309 scalloped hammerheads, 27.0% were Carolina hammerheads, 8.9% had mixed ancestry, and
310 0.4% were smooth or great hammerheads. Scalloped and Carolina hammerheads were identified
311 in the U.S. Atlantic from North Carolina to Florida. In the Gulf, 99% of identified hammerhead
312 sharks were scalloped hammerheads and no Carolina hammerheads were identified; the
313 remaining 1% were great hammerheads. Carolina hammerheads were more abundant than
314 scalloped hammerheads in South Carolina, but the relative abundance of Carolina hammerheads
315 decreased with latitude.

316 Though the focus of the study was scalloped and Carolina hammerheads, genetic
317 identifications revealed that four different species were sampled, with three great hammerheads
318 sampled in the Gulf, and three great hammerheads and one smooth hammerhead sampled in the
319 Atlantic. Most misidentified hammerheads were small juveniles (5 of 7 <1,000 mm STL),
320 demonstrating that even experienced researchers and fishers may have difficulty differentiating
321 among known sphyrnids, especially at small sizes. The shape of the anterior margin of the
322 cephalofoil is one of the morphological characters used to distinguish among scalloped, great and
323 smooth hammerheads, but cephalofoil shape changes with age and distinguishing features are not
324 always apparent in small individuals (Castro, 2011; Gilbert, 1967). Data regarding the early life
325 history of smooth and great hammerheads is limited, and minor diagnostic morphological
326 differences present in YOY of different species may be easily missed when certain species are
327 not reported to occur in a given area.

328 Relative abundance of Carolina hammerheads was highest in Bulls Bay (61%, n = 287),
329 and more than 70% of all Carolina hammerheads identified in this study were sampled there.
330 Reasons for such high abundance (relative and absolute) in a limited geographic area are not
331 clear. One possible explanation is that Carolina hammerheads exhibit a high degree of natal

332 philopatry, with a large proportion of breeding females in the western North Atlantic having
333 been born in Bulls Bay and then returning to the same site to give birth. Philopatric behavior at a
334 regional scale has been documented in a number of shark species (reviewed in Chapman et al.,
335 2015), but evidence of natal philopatry is less common. A combination of tag-recapture and
336 genetic data has shown that some lemon sharks (*Negaprion brevirostris*) in Bimini, Bahamas
337 exhibit strong long-term site fidelity to their natal nursery, despite the availability of other
338 appropriate nursery habitat nearby (Feldheim et al., 2014). Natal philopatry has also been
339 suggested in blacktip reef sharks (*Carcharhinus melanopterus*) in Moorea, where some females
340 made repeated migrations to the same nursery outside their usual home range (Mourier and
341 Planes, 2013). Long term genetic profiling of Carolina hammerhead YOY and genetic
342 reconstruction of parental genotypes would be needed to determine if the progeny of individual
343 female sharks use Bulls Bay year after year.

344 In Bulls Bay the abundance of scalloped and Carolina hammerhead YOY varied across
345 the sampling season. Both species were first documented in the nursery in early May and both
346 increased in abundance until peaking in July. Scalloped hammerheads were more abundant until
347 mid-July, when a large spike in Carolina hammerhead abundance was observed (Fig. 4).
348 Carolina hammerheads were more abundant for the remainder of the season and appeared to stay
349 in the nursery at least a month longer than scalloped hammerheads. The increase in abundance
350 for both species from May to July suggests parturition may occur over a prolonged period, but
351 the surge of Carolina hammerhead abundance in July may indicate that time of peak parturition
352 in Carolina hammerheads is offset from that of scalloped hammerheads. In addition, parturition
353 in one or both species may occur at locations outside the nursery area, a reproductive strategy
354 seen in Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*; Ulrich et al., 2007) and

355 bonnetheads (*S. tiburo*; Frazier et al., 2014). If Carolina hammerhead parturition occurs at a more
356 remote location, the observed increase in July could reflect an offset in time of peak arrival. The
357 observation of a temporal offset in abundance is consistent with temporal habitat partitioning, a
358 mechanism that minimizes competition among species because shared limited resources are used
359 at different times (Ross, 1986; Schoener, 1974). Temporal partitioning can occur on a diel scale,
360 where competitors are active during different times of the day (Kronfeld-Schor and Dayan, 2003)
361 or on a seasonal scale, such that peak abundance occurs during different times of the year (Paine,
362 1963; Sandercock, 1967). If Carolina hammerheads give birth later or delay movement into the
363 nursery until scalloped hammerhead neonates have grown, it could minimize overlap of resource
364 usage.

365 By contrast to the results seen in South Carolina, relatively few Carolina hammerheads
366 were captured in northern Florida, with none found in the Tolomato River, even though the
367 Tolomato River was well-sampled (n = 148), and Carolina hammerheads were found in areas
368 north and south of the nursery, including adjacent coastal waters near Jacksonville. The
369 Tolomato River differs from other sampled nurseries along the U.S. Atlantic in that it is behind a
370 series of barrier islands and therefore not directly connected to the western North Atlantic.
371 Instead, it only receives saltwater influx from the St. Johns River to the north and St. Augustine
372 inlet to the south, both of which are approximately 20 miles in distance from the sampling site.
373 Higher salinity was a significant predictor of Carolina hammerheads in Bulls Bay, and average
374 monthly salinity was consistently lower in the Tolomato River than in Bulls Bay (Table 6). The
375 other nurseries sampled in Florida occur in nearshore waters rather than estuaries, with stable
376 salinities more closely matching oceanic conditions (Cape Canaveral ~36 ppt, Jacksonville ~32
377 ppt, Table 6; Iafrate et al., 2019). In Georgia nurseries, scalloped hammerheads were sampled in

378 both estuaries as well as nearshore waters, while Carolina hammerheads were sampled almost
379 solely in nearshore waters (Fig. S3). Salinity is one of the most important predictors of shark
380 species abundance in estuaries and bays in the Gulf and U.S. Atlantic (Bethea et al., 2015; Ulrich
381 et al., 2007), and a preference for higher salinity waters may explain the absence of Carolina
382 hammerheads in the Tolomato River.

383 Carolina hammerheads also were absent in the Gulf, a result that is somewhat surprising
384 given the high dispersive capability of hammerheads. One possibility is that Carolina
385 hammerheads prefer temperate waters, which restricts their movement around the southern
386 Florida Peninsula and into the Gulf. A preference for temperate water is consistent with the
387 identification of Carolina hammerheads in southern Brazil, the only location that Carolina
388 hammerheads have been identified outside the southeast U.S. (Pinhal et al., 2012), and the
389 observation that the relative abundance of Carolina hammerheads decreased from north to south
390 in the western North Atlantic. South of Cape Canaveral is a well-known biogeographic break
391 that marks the transition from temperate to tropical fauna of south Florida and coincides with
392 genetic divergence between Atlantic and Gulf populations of many coastal marine fishes,
393 including sharks (Awise, 1992; Portnoy et al., 2014, 2015, 2016). Similarly, the range of the
394 closely related smooth hammerhead was also thought to include mostly temperate water of the
395 Atlantic (Castro, 2011), though the collection of one individual in the Gulf was recently reported
396 (Deacy et al., 2020). Few samples of mature adult Carolina hammerhead were obtained, and it is
397 possible that adult Carolina hammerheads move into the Gulf, but despite robust sampling (n =
398 303) no YOY or juvenile Carolina hammerhead were caught, consistent with the species being
399 absent. This is further supported by the fact that admixture between Carolina and scalloped
400 hammerheads was detected in the Atlantic but not in the Gulf. An aversion to lower salinity

401 waters could also partially explain the absence of Carolina hammerheads in the Gulf as there are
402 several significant freshwater inflows in the northern temperate Gulf, including the Mississippi
403 River, Mobile Bay and Atchafalaya River (Morey et al., 2003), but this does not explain the
404 absence of Carolina hammerheads from more saline habitat along the West Florida Shelf and the
405 coast of Texas. This potential lack of appropriate nursery habitat types or conditions coupled
406 with philopatric behavior may have contributed to the present-day absence of Carolina
407 hammerheads in the Gulf.

408 Research on Carolina hammerheads has thus far focused on immature individuals,
409 making it difficult to relate relative abundances in nurseries to relative abundances within
410 managed populations of mature hammerheads. Samples for this study were collected primarily
411 from fishery-independent surveys in which large juveniles and adults are not commonly
412 encountered (n = 87; Atlantic = 47, Gulf = 40; Fig. S4). Three adult male Carolina hammerheads
413 were captured offshore of South Carolina on longlines along with large juvenile and adult
414 scalloped hammerheads. It is unclear if the species are spatially segregated as adults or if they
415 use similar habitat at all life stages, but contemporary hybridization between species indicates
416 some overlap of reproductive habitat (Barker et al., 2019). Recent methods using morphometrics
417 and machine learning have been developed to aid in field identification of cryptic blacktip
418 (*Carcharhinus limbatus*) and Australian blacktip sharks (*C. tilstoni*), and while large individuals
419 were accurately identified 96% of the time in field trials, identification was less successful for
420 smaller sharks (<1,200 mm total length; Johnson et al., 2017). Continued research on Carolina
421 hammerheads of all sizes may reveal subtle differences that may be useful in differentiating the
422 species based on morphology and thus enable a further understanding of species-specific habitat
423 utilization based on field identifications.

424 Differences in life history characteristics have been observed in cryptic shark species, and
425 similar differences could exist between scalloped and Carolina hammerheads. For example, the
426 blacktip shark and Australian blacktip shark are difficult to distinguish morphologically, but
427 differ in length at maturity, maximum body size, habitat requirements, and time of parturition
428 (Harry et al., 2012, 2019). These differences in life history and reproductive ecology have
429 significant management implications because the species differ in their susceptibility to
430 exploitation and respond differently to management measures (Harry et al., 2012, 2019). In
431 addition to physiological differences suggested by the observed preference for higher salinity,
432 Carolina hammerheads are reported to have a smaller size at birth than scalloped hammerheads
433 (Quattro et al., 2013) and this may be indicative of life history differences between mature
434 scalloped and Carolina hammerheads (e.g. differences in maternal length or brood size).
435 Currently insufficient data exist to determine if size differences persist throughout their life span.
436 Differences in body size can act as a mechanism that maintains species boundaries through
437 assortative mating in sympatrically distributed species (Nagel and Schluter, 1998), but
438 hybridization between scalloped and Carolina hammerheads (Barker et al., 2019) indicates that if
439 there are differences in adult size they do not act as a complete reproductive barrier.

440 The large panel of diagnostic SNPs used for species identification was reliable and
441 accurate, but the molecular methods employed in this study would not be cost-effective for
442 future studies focused only on species identification. MtDNA and nuclear ribosomal ITS2 are
443 cheaper and more accessible methods that can be used to discriminate sphyrnids (Abercrombie et
444 al., 2005; Quattro et al., 2006), however, neither of these methods can be used to identify hybrids
445 and characterize backcrossing (Barker et al., 2019). Future work could use a subset of the
446 diagnostic SNPs in a Genotyping-in-Thousands by sequencing (GT-seq) approach (Campbell et

447 al., 2015) to genetically identify thousands of individuals in an economically efficient manner
448 while discriminating hybrids. Recently developed CRISPR-based SHERLOCK methodologies
449 may also be an accessible and cost-effective approach for rapid species identification in the
450 future (Baerwald et al., 2020). Although the approach used in this study is more costly, data can
451 be used simultaneously in a population genetics framework (Dimens et al., 2019; Portnoy et al.,
452 2015), and to provide relevant information for conservation and management such as estimates
453 of effective size (Waples et al., 2016) or abundance using a close-kin-mark-recapture framework
454 (Bravington et al., 2016; Hillary et al., 2018).

455 Over 25% of hammerheads sampled in the U.S. Atlantic were identified as Carolina
456 hammerheads, and if mature individuals are found in a similar proportion, they would comprise a
457 significant part of what is currently considered to be the U.S. Atlantic scalloped hammerhead
458 stock. Scalloped hammerheads in the U.S. Atlantic are currently considered overfished with
459 overfishing occurring and managed as part of the hammerhead shark complex, which also
460 includes great and smooth hammerheads. Quotas for the hammerhead complex are set according
461 to the total allowable catch of scalloped hammerhead (Hayes et al., 2009; NMFS, 2013). If past
462 assessments include data from a second species that differs biologically, it would have
463 significant implications for management of the hammerhead complex. There is also a critical
464 need for Carolina hammerhead life history data. The results of this study suggest that Carolina
465 hammerheads have a limited range in the western North Atlantic, and only three Carolina
466 hammerheads have been identified in the South Atlantic (Pinhal et al., 2012). Although the
467 effects are difficult to predict, ongoing hybridization and backcrossing with scalloped
468 hammerheads could contribute to the loss of Carolina hammerheads over time (Barker et al.,
469 2019). Further, given the observed limited range, unknown life history characteristics, and

470 continued directed and incidental fishing pressure, there is potential for Carolina hammerheads
471 to be overfished in the U.S. Atlantic. Scalloped hammerheads are listed as Critically Endangered
472 on the IUCN Red List of Threatened Species (Rigby et al., 2019c), and international trade is
473 regulated by the Convention on International Trade in Endangered Species of Wild Fauna and
474 Flora (CITES, Appendix II). However, the status of Carolina hammerheads has not been
475 assessed. Consideration of Carolina hammerheads separate from scalloped hammerheads in
476 future national and international management is warranted but will likely require the
477 development of methods to differentiate them in the field.

478

479 **Animal Ethics and Welfare**

480 Animals collected by Texas A&M University-Corpus Christi personnel were collected
481 under Scientific Research Permit No. SPR-0614-111 and IACUC AUP #03-15 and samples
482 provided by Texas Parks and Wildlife were sampled under Scientific Collection Authorizations.
483 Samples from the Florida State University Coastal and Marine Lab were collected under FSU
484 IACUC Protocol 1718 and Florida Fish and Wildlife Conservation Commission Special
485 Activities Licenses SAL-1345 and SAL-1092. Animals from the GULFSPAN Survey were
486 collected under Florida Fish and Wildlife Conservation Commission Special Activities License
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488 Resources were conducted under SCDNR Scientific Permit #2212. Samples collected by
489 University of North Florida personnel were collected under FWC Special Activity Permit SAL-
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492 were collected under Georgia DNR Scientific Collecting Permit #1000520150 and Georgia

493 Southern IACUC I17001. Samples from NMFS Southeast Fisheries Science Center Mississippi
494 Laboratories were collected under permit NMFSPD 04-112-01.

495

496 **Data Availability**

497 The panels of diagnostic SNPs, individual genotypes, scripts, and sample metadata are available
498 at https://github.com/marinegenomicslab/HH_abundance [doi #####]. The COI haplotype is
499 available on the GenBank Nucleotide Database at <https://blast.ncbi.nlm.nih.gov> and can be
500 accessed with accession no MT863713.

501

502 **Supplementary Material**

503 Supplementary methods for amplification of mitochondrial cytochrome oxidase subunit 1 (COI)
504 gene and supplementary figures are available with the online version of this article.

505

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816 Table 1. Total number of young-of-the-year and small juveniles (Sjuv, 365-1000 mm stretch
817 total length), large juveniles (Ljuv, 1021-1751 mm stretch total length), and mature (Mat, 1829-
818 2750 stretch total length) individuals sampled in each region: North Carolina (NC), South
819 Carolina (SC) , Georgia (GA), Atlantic northern Florida (Atl FL-N), Atlantic central Florida (Atl
820 FL-C), Florida Keys (FL-KY), Gulf central Florida (G FL-C), Gulf northern Florida (G FL-N),
821 Central Gulf (CG), Texas (TX). One sample was from an unspecified location in the Atlantic
822 (Atl-U).

Location	Sjuv	Ljuv	Mat	Total
NC	8	1	5	14
SC	389	1	30	410
GA	93	1	10	104
Atl FL-N	198	0	1	199
Atl FL-C	199	10	1	210
FL-KY	0	23	13	36
G FL-C	3	0	0	3
G FL-N	116	2	0	118
CG	0	33	20	53
TX	84	2	7	93
Atl-U	0	1	0	1
Total	1080	74	87	1241

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825 Table 2. Species identifications in each region: North Carolina (NC), South Carolina (SC) ,
826 Georgia (GA), Atlantic northern Florida (Atl FL-N), Atlantic central Florida (Atl FL-C), Florida
827 Keys (FL-KY), Gulf central Florida (G FL-C), Gulf northern Florida (G FL-N), Central Gulf
828 (CG), Texas (TX). One sample was from an unspecified location in the Atlantic (Atl-U). Scal
829 indicates scalloped hammerhead, Car indicates Carolina hammerhead, Great indicates great
830 hammerhead, F1 indicates a first-generation hybrid, ScBX indicates scalloped hammerhead
831 backcross, CarBX indicates Carolina hammerhead backcross and UND indicates the sample
832 could not be identified using diagnostic panel or NewHybrids.

Location	Scal	Car	Great	F1	ScBX	CarBX	Und
NC	8	4	0	2	0	0	0
SC	153	198	1	27	23	7	0
GA	72	17	2	4	5	0	0
Atl FL-N	188	7	0	0	1	0	0
Atl FL-C	169	25	0	4	9	1	1
FL-KY	36	0	0	0	0	0	0
G FL-C	3	0	0	0	0	0	0
G FL-N	117	0	1	0	0	0	0
CG	53	0	0	0	0	0	0
TX	91	0	2	0	0	0	0
Atl-U	1	0	0	0	0	0	0
Total	891	251	6	37	38	8	1

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838 Table 3. Relative abundance (as a percentage) of scalped (Scal) and Carolina (Car)
839 hammerheads in sampled regions of the U.S. Atlantic: North Carolina (NC), South Carolina
840 (SC), Georgia (GA), Atlantic northern Florida (Atl FL-N), Atlantic central Florida (Atl FL-C). N
841 indicates the total number of individuals used to calculate relative abundance. Locations are
842 listed from highest to lowest latitude.

Location	N	Scal	Car
NC	12	66.7	33.3
SC	351	43.6	56.4
GA	89	80.9	19.1
Atl FL-N	195	96.4	3.6
Atl FL-C	194	87.1	12.9

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844

845 Table 4. Relative abundance (as a percentage) of scalped (Scal) and Carolina (Car)
846 hammerhead young-of-the-year and small juveniles (≤ 1000 mm stretch total length) in nurseries
847 in the U.S. Atlantic: Bulls Bay, SC (BB), Sapelo Island, GA (SI), Cumberland Island, GA (CI),
848 Jacksonville, FL (JV), Tolomato River, FL (TR), Cape Canaveral, FL (CC). N indicates the total
849 number of individuals used to calculate relative abundance. Locations are listed from highest to
850 lowest latitude.

Location	N	Scal	Car
BB	287	39.0	61.0
SI	24	95.8	4.2
CI	25	68.0	32.0
JV	21	76.2	2.8
TR	148	100.0	0.0
CC	177	87.0	13.0

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852

853 Table 5. Relative abundance (as a percentage) of scalloped and Carolina hammerhead young-of-
 854 the-year in Bulls Bay, SC from 2012-2014 and 2016-2019 during the months May-August. N
 855 indicates the total number of individuals used to calculate relative abundance.

856

	2012	2013	2014	2016	2017	2018	2019
Scal	13.00	59.60	42.90	48.00	41.40	21.60	68.80
Car	87.00	40.40	57.10	52.00	58.60	78.40	31.20
N	23	47	28	25	70	74	16

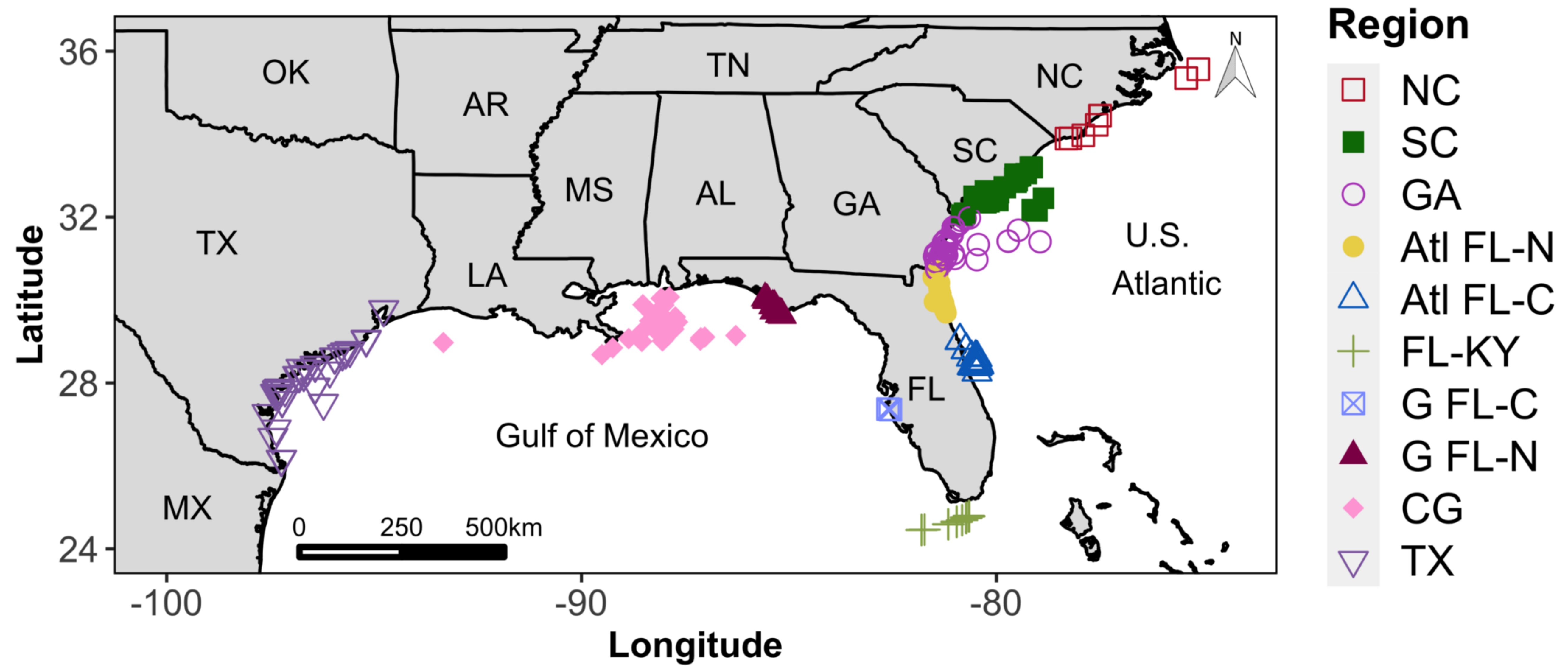
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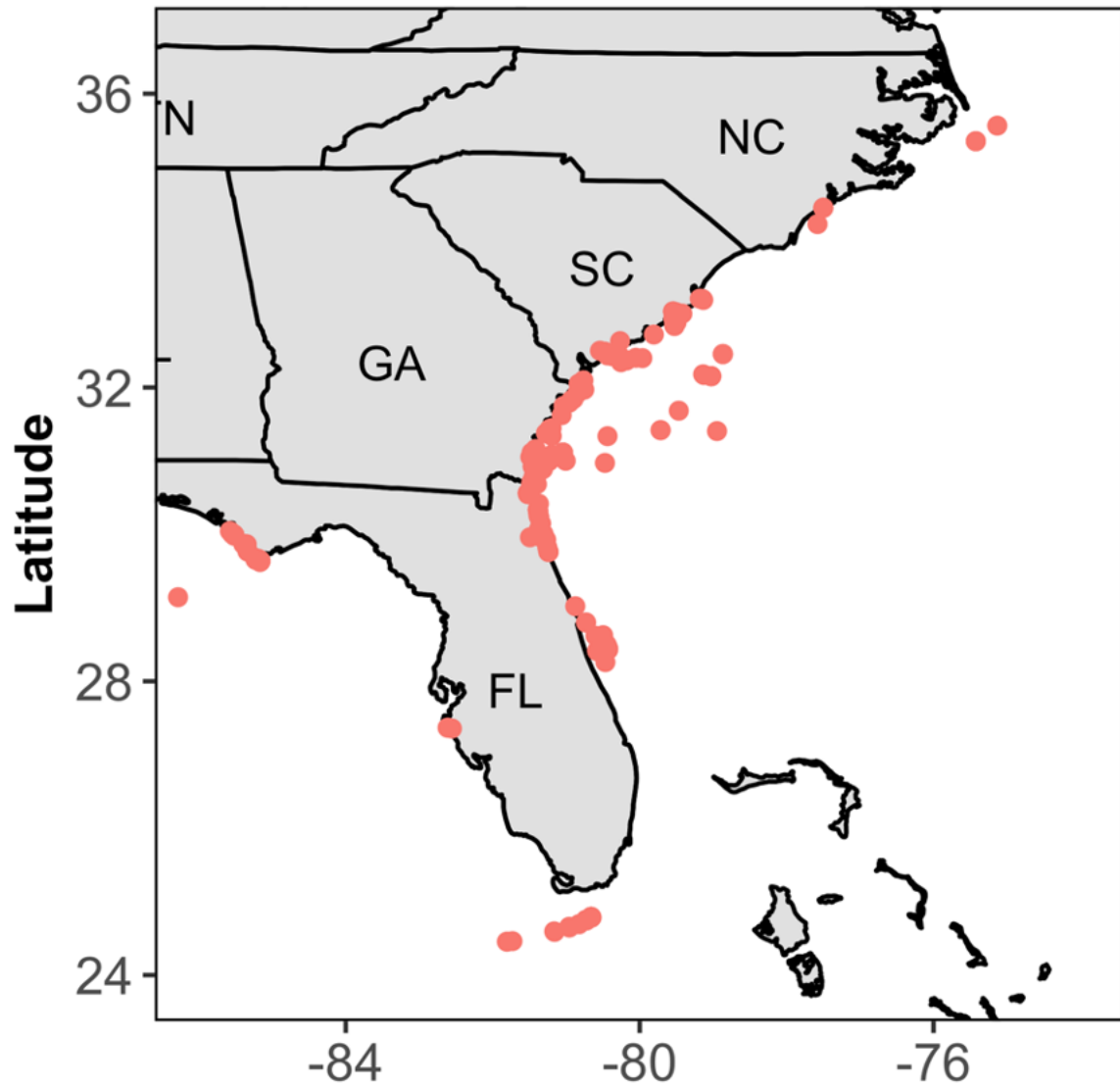
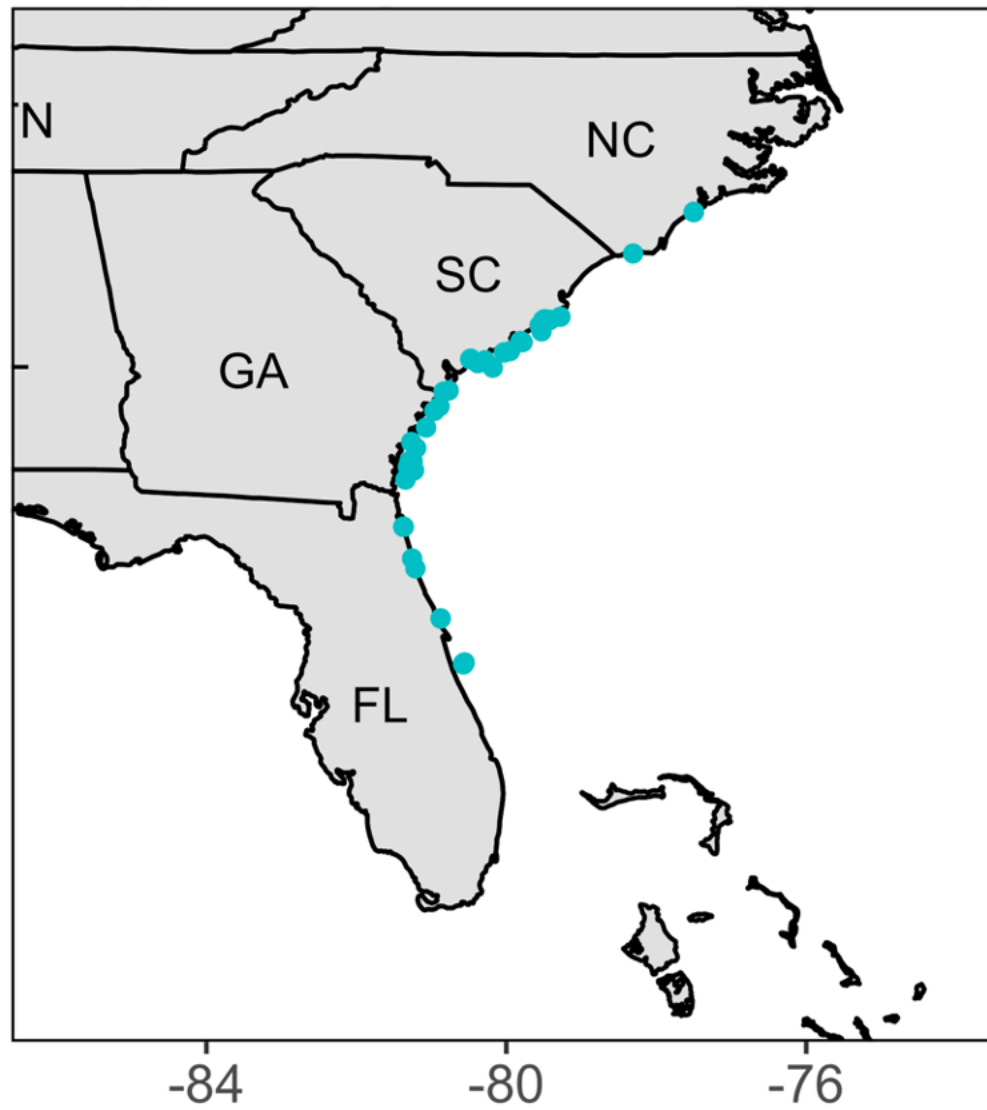
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859 Table 6. Average salinity in U.S. Atlantic nurseries during sampling seasons from August 2012-
 860 June 2019: Bulls Bay, SC (BB), Jacksonville, FL (JV), and Tolomato River, FL (TR).

Nursery	May	June	July	Aug	Sept
BB	32.06	31.45	31.33	32.52	30.70
JV	31.60	NA	32.04	32.83	32.39
TR	30.53	28.62	24.61	24.3	22.19

861



A**B****Longitude**

