1 **Sharks associated with a large sand shoal complex: Community**

2 **insights from longline and acoustic telemetry surveys**

3

4 Eric Reyier[1*], Bonnie Ahr[1], Joseph Iafrate[2], Douglas Scheidt[1], Russell Lowers[1], Stephanie Watwood[2], and

5 Brenton Back[1]

6

7 [1] Herndon Solutions Group, LLC, NASA Environmental and Medical Contract, Kennedy Space Center,

8 Florida, United States of America

9 [2] Naval Undersea Warfare Center Division Newport, Newport, Rhode Island, United States of America

10

11 *Corresponding author

12 E-mail: eric.a.reyier@nasa.gov

13

14

15

16

17

18

Abstract

Offshore sand shoals are a coveted sand source for coastal restoration projects and as sites for wind energy development. Shoals often support unique fish assemblages but their habitat value to sharks is largely unknown due to the high mobility of most species in the open ocean. This study pairs multi-year longline and acoustic telemetry surveys to reveal depth-related and seasonal patterns in a shark community associated with the largest sand shoal complex in east Florida, USA. Monthly longline sampling from 2012-2017 yielded 2,595 sharks from 16 species with Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacknose (*Carcharhinus acronotus*), and blacktip (*C. limbatus*) sharks being the most abundant species. A contemporaneous acoustic telemetry array detected 567 sharks from 16 species (14 in common with longlines) tagged locally and by researchers elsewhere along the US East Coast and Bahamas. PERMANOVA modeling of both datasets indicate that the shark species assemblage differed more across seasons than water depth although both factors were important. Moreover, the shark assemblage detected at an active sand dredge site was similar to that at nearby undisturbed sites. Water temperature, water clarity, and distance from shore were habitat factors that most strongly correlated to community composition. Both sampling approaches documented similar single-species and community trends but longlines underestimated the shark nursery value of the region while telemetry-based community assessments are inherently biased by the number of species under active study. Overall, this study confirms that sharks can be an important component of sand shoal fish communities but suggests that deeper water immediately adjacent to shoals (as opposed to shallow shoal ridges) is more valuable to some species. Potential impacts to these nearby habitats should be considered when planning for sand extraction and offshore wind infrastructure.

Introduction

As a group, sharks have proven highly prone to population declines from fishing harvest and habitat loss, and increased management intervention is urgently required in many regions of the world [1–3]. Understanding the habitat needs of sharks is a central component of effective management policy, especially for coastal species that are most directly exposed to human disturbances [4]. Habitat considerations are already incorporated into management policy in some countries. In US waters for example, where there is evidence of recent recovery in shark abundance and diversity [5,6], most species now have recognized Essential Fish Habitat (EFH) whose boundaries are established to minimize habitat impacts from commercial fishing, dredging, military operations, and other human activity [7]. Yet even here, shark habitat requirements and seasonal distributions are often only broadly described, as is the function and relative value of different marine habitat types in supporting shark populations and communities.

Several fishery-independent shark surveys are underway in continental shelf waters of the US Atlantic and Gulf of Mexico (see Peterson et al. [6] for a review). These efforts [5,8–11], based on traditional sampling gears including longlines and gill nets, are designed, in part, to better describe shark habitat needs and assemblage structure. Because these surveys often span wide stretches of coastline, replication at any given location is low with shark abundance and diversity insights largely focusing on the role of oceanographic factors (e.g., temperature, chlorophyll, depth, salinity) [12]. Year-round sampling of sharks associated with specific geomorphological features of the continental shelf are uncommon but can provide details on seasonal abundance trends and habitat associations that are often lacking in coarse-scale regional surveys. Such surveys are also easier to complement with acoustic tagging that reveals patterns in space use, improves the detectability of rare and rapidly migrating species, and overcomes certain known biases associated with traditional sampling gears.

65   Offshore sand shoals are submerged ridges, bars, or banks formed from sand or gravel that are

66   shallower in depth than surrounding areas [13]. In addition to their complex bathymetry, shoals are

67   generally characterized by higher wave energy, elevated turbidity, and heterogeneous sediments and

68   ocean currents when compared to adjacent deeper water [14]. There is growing interest in understanding

69   the habitat value and species composition of shoal communities because these features are important

70   sand sources for coastal restoration projects. Sand is removed from offshore shoals with large dredges

71   and deposited along the shoreline to counteract erosion resulting from storms, human development, and

72   rising sea levels. Demand for sand from these offshore deposits is expected to grow rapidly in the US and

73   around the world [15]. Shoals are also preferred sites for offshore wind farms since their shallow depth

74   and soft sediments reduce turbine construction and maintenance costs [16].

75   Shoal fish communities have received less attention than those associated with other shelf

76   habitats but they appear to be unique, albeit sometimes depauperate, species assemblages [17–21].

77   Dredging can negatively impact fish communities through direct mortality of immobile species in the

78   dredge, removal of benthic invertebrate prey, as well as temporary increases in noise and turbidity which

79   may result in avoidance responses [22,23]. Previous shoal fish surveys have relied heavily on camera sleds

80   and trawls, with catches dominated by small species. Although shoals are common shelf features in many

81   regions (and cover five percent of the shelf by area in the US South Atlantic [12]), sharks have never been

82   a focus of shoal fish surveys, presumably due to their high mobility and naturally lower density on the

83   open shelf. Nonetheless, most coastal shark species depend on the benthos to some degree for foraging,

84   predator refuge, and navigation and therefore may also be impacted by shoal dredging activity and other

85   human disturbances.

86   The overarching purpose of this study is to document the shark community associated with a large

87   sand shoal complex in east Florida, USA, a region of high shark diversity—and intensive research—that

88   serves as an overwintering area for many species. Our specific goals are to explicitly test whether the

89   shark assemblage differs between shallow shoals and adjacent deeper water, as well as across seasons,

90   and to test whether the community observed at an active dredge site differs from that of a nearby

91   undisturbed site. Moreover, we then explore how potentially influential habitat factors such as water

92   depth, temperature, turbidity, and sediments, help explain patterns in the shark community. Notably, this

93   study is strengthened by complementing traditional longline sampling with passive acoustic telemetry

94   over periods of five and six years, respectively. Longlines target a broad assortment of coastal sharks,

95   providing estimates of abundance, size, and sex, while acoustic telemetry allows for detailed monitoring

96   of shark habitat associations for species implanted with acoustic transmitters. Results are intended to

97   improve our understanding of shark community patterns in the US southeast while helping refine best

98   practices for sand extraction activities that minimize habitat impacts to this important group of fish.

99

Materials and methods

Study area

102   Cape Canaveral was selected as the study area due to the presence of the most expansive sand

103   shoals on the Florida east coast and because it typifies other cape-associated shoals in the US southeast.

104   Prominent features include the Southeast Shoal and Chester Shoal, shore-connected shoals with

105   minimum depths of 2 and 4 meters (m), respectively, as well as several smaller detached shoals located

106   farther offshore (Fig. 1). The shallow wave-swept shoal ridges are generally comprised of medium to

107   coarse quartzose-mollusk sand and shell. The deeper troughs between or in the lee of the shoals retain

108   finer sand and muds with the most significant deposits found in the Canaveral Bight [24,25]. The study

109   area includes one active 5 km^2 dredge site that has served as a sand source for eight beach nourishment

110   projects since 2000. Hard-bottom substrates are sparse in the core project area but natural limestone reef

111 outcroppings are common a few kilometers to the east and north of the shoals. The region exhibits a

112 strong north-south gradient in winter water temperature due to the divergence of the warm Florida

113 Current from the coastline [26]. No major coastal inlets occur locally so salinity remains roughly 36 psu

114 year-round. Human development is limited to widely spaced NASA and US Space Force rocket launch

115 infrastructure although commercial and recreational shark fisheries occur within the project footprint.

116

117 **Fig. 1. Canaveral Shoals study area**. (A) Locations of all longline sets 2012-2017. (B) Map of acoustic

118 receiver stations 2013-2020 as well as the active sand dredge site and nearby control site. Map B inset

119 includes locations of five reef receiver stations established farther offshore. (**SEE END OF MANUSCRIPT**

120 **FOR ALL FIGURES)**

121 # Longline sampling

122 A 427 km^2 longline sampling universe was established to encompass the major shoal features off

123 Cape Canaveral (Fig. 1). Sixteen bottom longline sets were conducted monthly for five years from October

124 2012–September 2017 with samples divided equally among a shallow and deep depth zone. The shallow

125 zone included shoal ridges less than 6.1 m (20 ft) depth, while the deep zone included deeper shoal flanks

126 and the troughs between shoals out a maximum depth of 20 m (66 ft). Within each zone, new sample

127 points were selected each month using a random point generator in ArcGIS 10.3 (ESRI, Redlands, CA).

128 Additional targeted (i.e., non-random) longline sets were performed periodically, primarily in winter in

129 the Canaveral Bight, to obtain additional sharks for acoustic tagging. Catch from these sets is presented

130 separately and excluded from statistical analyses.

131 Each longline set spanned 617 m with a mainline of 318 kg monofilament anchored to the sea

132 floor and marked at each end with large floats. Forty gangions were attached to each set, spaced at 15.2

133   m intervals. Gangions consisted of a stainless steel clip, 0.7 m of 181 kg test monofilament, with 12/0 and

134   15/0 circle hooks alternating along the mainline. Bait consisted exclusively of mullet (*Mugil* spp.), a

135   regionally abundant forage fish. Longline soak time averaged 48 (± 24) minutes from the midpoint of

136   deployment to midpoint of retrieval, with the mainline deployed and retrieved using a small electric

137   winch. The short gangions, short soak times, and two hook sizes were designed to target a broad

138   assortment of managed fishes (e.g., sharks, red drum [*Sciaenops ocellatus*], reef fish), increase sample

139   replication, and reduce the likelihood of attracting fish from alternate habitats. Sampling occurred during

140   daylight from an 8-m skiff embarking out of Port Canaveral. Habitat data collected at each set location

141   included water temperature (°C), dissolved oxygen (mg/l), salinity (psu), all measured in the middle of the

142   water column (mean 2.9 m and 6.2 m for readings at shallow and deep sites, respectively) with a YSI

143   600XLM water quality sonde calibrated daily. Secchi depth (i.e., water clarity), mean water depth

144   (averaged from boat depth sounder readings at the origin and end of each set), seafloor slope (the depth

145   difference between origin and end of each set), distance from shore (km), and GPS coordinates were also

146   recorded. A summary of longline habitat conditions under which each species was captured is presented

147   in Table S1.

148   All captured sharks were identified, sexed, and measured to the nearest 0.5 cm precaudal length

149   (PCL), fork length (FL), and natural total length (TL). Individuals were classified as either neonate/young-

150   of-the-year (YOY), juvenile, or adult through examination of claspers in males, the degree of umbilical scar

151   healing in young animals (a sign of recent birth), and published lengths of 50% maturity. All animal

152   capture, handling, and tagging was conducted in accordance with a State of Florida Special Activity License

153   SAL-12-512-SR and renewals, National Marine Fisheries Service Biological Opinion F/SER/2011/05647, and

154   under the auspices of Kennedy Space Center Institutional Animal Care & Use Committee protocol GRD-

155   06-049. Further details on longline and acoustic telemetry survey methods are found in Iafrate et al. [27].

Acoustic telemetry

157   An existing acoustic telemetry array at Cape Canaveral (hereafter the 'Canaveral Array') was

158   utilized from December 2013 to February 2020 (6.25 years) to independently assess the distribution of

159   acoustically tagged fishes in the project area (Fig. 1). The Canaveral Array is located near the center of the

160   FACT Network, a multi-agency collaboration tracking fish and sea turtle movements in the US south

161   Atlantic and Bahamas [28]. Fifty-seven acoustic receiver stations (Vemco VR2W and VR2AR, Innovasea,

162   Nova Scotia) were permanently deployed on and immediately adjacent to the shoals from the surf zone

163   out to 14 km offshore (2-16 m depth). Analogous to longline sampling, each station was deployed in the

164   shallow (<6.1 m, n = 27) or deep (>6.1 m, n = 30) depth zone. Most stations were arranged in a non-

165   overlapping grid layout although the design also included a 12-station receiver ring surrounding the sand

166   dredge area on the Southeast Shoal and an identical 'control' ring at a reference site 15 km to the north

167   on Chester Shoal. This control site was similar to the dredge site in many respects including water depth,

168   distance from shore, and sediment qualities. These rings were used to explore for any large-scale

169   differences in fish use of the dredge site vs. nearby undisturbed sites. To avoid dredge strikes, dredge site

170   stations were deployed on the site boundary or within setbacks around identified rocket debris, and thus

171   monitored disturbed and undisturbed benthic habitat in equal proportions, while control site stations

172   monitored only undisturbed habitat. In September 2015, five additional stations were established along

173   the offshore reef tract (10-22 km offshore, 15-25 m depth) to document any animal movements between

174   shoals and reefs. All 62 stations were anchored to the seafloor with large sand augers or 40 kg metal disk

175   weights, and with receivers retrieved twice annually for downloads using SCUBA. Multi-week range testing

176   trials at three Canaveral Array stations confirmed that receivers could detect high power acoustic tags

177   with a 50% efficiency at roughly 400 m on average [27].

178   Five shark species were acoustically tagged including adult and large juvenile finetooth

179   (*Carcharhinus isodon*; n = 61), blacknose (*C. acronotus*; n = 60), and Atlantic sharpnose sharks (n = 44), as

180   well as juvenile scalloped hammerhead (*Sphyrna lewini*; n = 39) and lemon sharks (*Negaprion brevirostris*;

181   n = 30; Table 1). Sharks were primarily captured by longlines but also by hook-line (sharpnose shark), cast

182   net (lemon sharks), and gill net (scalloped hammerhead) at multiple locations on the shoals, and across

183   years. All sharks were measured and transferred to a seawater tank where they were oriented ventral

184   side up to induce tonic immobility, and a small pump was used to circulate tank water across their gills.

185   After injection of 2-5 cc of lidocaine, a ~2 cm incision was made along the ventral midline, a coded acoustic

186   transmitter was inserted, and the incision and was closed with absorbable sutures and Vetbond™ tissue

187   adhesive. Sharks were allowed to recover in the tank briefly before release at their capture site.

188

Table 1. Details of sharks acoustically tagged in the Canaveral Shoals study area.

Target Species	No.	Mean FL (Range)	Sex Ratio (F:M)	Tagging Dates	Tag Model, Ping Interval (sec), Batt Life (yrs)
Finetooth Shark	61	104 (64–130)	39:22	Dec 2013–Sep 2016	V16–4H or –6H, 90, 5.2–9.7
Blacknose Shark	60	96 (89–115)	33:27	May 2014–Sep 2016	V16–4H or –6H, 90, 5.2–9.7
Sharpnose Shark[b]	44	74 (67–83)	24:19	Jul 2016–Aug 2017	V16–4H, 90, 5.2
Lemon Shark[a]	30	87 (65–143)	15:15	Dec 2009–Dec 2020	V16–4H or –6H, 90, 5.2–9.7
Scalloped Hammerhead[ac]	40	45 (37–115)	17:23	May 2013–Sep 2014	V13–1L, V16–4H, 90, 2.2–5.2

[a] Most lemon and hammerhead sharks were tagged prior to dedicated monitoring of Canaveral Shoals but were included in analyses if detected after December 2013.

[b] Considered *Rhizoprionodon terraenovae* (not *R. porosus)* based on local genetic findings [29]

[c] Considered *Sphyrna lewini* (not *S. gilberti*) based on local genetic findings [30]

189

190   Numerous other sharks tagged elsewhere along the US Atlantic coast and the Bahamas were also

191   seasonally present in the Canaveral Array and were identified to species by consulting tag lists maintained

192   by the FACT and Atlantic Cooperative Telemetry Networks. By convention, these animal detections belong

193   to the tagging organization [28]. References to sharks released by other groups are included here with

194   written permission in all instances and in a manner that does not reveal size, sex, or migration details that

195   are the focus of other ongoing studies. All shark detections were then combined into a single database

196   and screened with a custom R script to remove any non-moving tags (presumed mortality events) or false

197   detections that occasionally arise from tag signal collisions.

198   As with longlines, various habitat variables were also paired to the acoustic telemetry dataset

199   including water temperature, water clarity, depth, seafloor slope, distance from shore, and latitude.

200   Temperature and water clarity are not continuously monitored so satellite-derived monthly values were

201   obtained for each station using the jplMURSST41 sea surface temperature dataset (0.01° resolution, daily

202   composite) and erdMH1kd4908day K490 irradiance dataset (i.e., the mean diffuse attenuation coefficient

203   at wavelength 490 mm, a proxy for turbidity; 4 km resolution, 8-day composite). These data are archived

204   on the NOAA CoastWatch ERDDAP [31] and were queried using the rerddapXtracto package in R [32].

205   Seafloor slope at each receiver was calculated as the maximum vertical relief within 500 m of a station

206   based on published NOAA charts. Sediment percent fines (i.e., muds) and organic content estimates were

207   also available for all stations from a concurrent study of benthic communities on the Canaveral Shoals

208   [25]. Samples were drawn from surficial cores collected once at each station via SCUBA. Fines consisted

209   of sediment grains <63 um diameter as determined by wet sieving through a series of US standard sieves.

210   Organics were the materials lost after ashing dried sediment samples in a muffle furnace at 500°C for four

211   hours. A summary of habitat conditions under which all species were detected is found in Table S2.

212

Data analysis

213

214   Longline catch was used to test for differences in overall shark abundance across water depths

215   and seasons. Catch was first converted to catch-per-unit-effort (CPUE) in the form of sharks caught per

216   100 hook-hours of soak time. Monthly-averaged shark CPUE was then compared across *Depth Zone*

217   (shallow ridge vs. deeper troughs) and *Season* (winter = Dec–Feb, spring = Mar–May, summer = Jun–Aug,

218   fall = Sep–Nov) using a two-way ANOVA with an interaction term ($\alpha = 0.05$), and with least-square means

219   to identify any pairwise differences across seasons. ANOVAs were run both with and without the

220   numerically dominant Atlantic sharpnose shark included in CPUE values.

221   Patterns in the shark community were analyzed separately but similarly for longline and telemetry

222   datasets. For longlines, species CPUE values from single sets were averaged for each combination of *Depth*

223   *Zone* (2), *Season* (4), and *Year* (5.25). These 42 composite samples were necessary since individual sets

224   often yielded only 1-2 species. For acoustic telemetry data, the total count of uniquely tagged sharks

225   within each species detected at each station (coded *a priori* as deep or shallow) were tallied for each

226   season (247 samples). This approach allowed us to explore *Season* and *Depth* trends while retaining

227   *Station* as a factor nested within *Depth*. Raw shark counts for each species were then converted to

228   proportions. While variation in acoustic receiver performance due to water depth and other site-specific

229   factors may bias the raw number of sharks detected at a given station, it should not affect species ratios.

230   Notably, *Study Year* was not considered as a factor in telemetry analyses because acoustic tagging of

231   additional shark species occurred as the study progressed.

232   Community differences across *Depth Zone* and *Season* were visualized with non-metric multi-

233   dimensional scaling (MDS) plots in the PRIMER v7 software package [33]. Data were square root-

234   transformed to allow less common species help explain differences between samples, and a sample

235   similarity matrix based on the Bray-Curtis similarity coefficient served as the basis for MDS plots.

11

236   Permutational multivariate ANOVA (PERMANOVA) models were then run to formally test for differences

237   in the shark assemblage. PERMANONA is well suited for multi-species datasets containing a large fraction

238   of zeros, and it allows for hierarchical designs, random effects, and tests for interactions [34]. For both

239   longline and acoustic telemetry data, the PERMANOVA was a two-way crossed design (Type III sum of

240   squares) with *Depth Zone* and *Season* as fixed factors plus an interaction term. The telemetry

241   PERMANOVA also included a random effect of *Station* nested within *Depth Zone*. Data from all five reef

242   stations and seven of 12 stations in both the dredge and control rings were excluded from the telemetry

243   model to ensure that all included stations had identical deployment timelines and non-overlapping

244   detection ranges. *Post hoc* homogeneity of multivariate dispersion (PERMDISP) tests were used to

245   determine if observed community differences across depths and seasons were due solely to differing

246   species complements or were also influenced by uneven sample variance within treatment groups. Two-

247   way similarity percentages analyses (SIMPER [35]) were also run on the same longline and telemetry

248   samples to identify which shark species were most responsible for community difference across depths

249   and seasons.

250   Separately, a simple one-way PERMANOVA on telemetry data was used to test for assemblage

251   differences between five more specific receiver station groups. These included the dredge site and control

252   site, as well as all other nearshore shoal stations (<1.5 km from shore), offshore shoal stations (>1.5 from

253   shore), and reef stations. The rationale for these latter three groups is that some sharks may closely follow

254   the shoreline for navigation while others are known reef associates, behaviors which may also influence

255   community patterns within the study area. Rarefaction curves were also generated to better assess overall

256   species richness across these same station groups, a comparison otherwise complicated by the uneven

257   receiver coverage. Longlines were not used to directly compare dredge and control sites because the small

258   size of each site did not allow for sufficient sample replication.

259   Finally, the degree to which habitat conditions explained patterns in the shark community was

260   explored with a BEST procedure, a routine that identifies combinations of measured environmental

261   variables most strongly correlated to the species assemblage [36]. Certain oceanographic variables (e.g.,

262   temperature, water clarity) change rapidly across space and time so this routine was run using individual

263   (not season-averaged) longline samples that contained more than one species, and on telemetry samples

264   averaged for each combination of station and calendar month (not season). Longline habitat variables

265   included water temperature, water clarity, depth (as a continuous variable), salinity, dissolved oxygen,

266   seafloor slope, distance from shore, and latitude. Acoustic telemetry variables also included water

267   temperature, clarity, depth, seafloor slope, distance from shore, and latitude, as well as sediment percent

268   fines and percent organics. When necessary, habitat variables were log transformed to reduce skewness

269   and normalized to remove the effect of differing measurement scales prior to running the BEST routine in

270   PRIMER.

271

Results

Longline overview

274   A total of 978 longline sets (455 shallow, 445 deep, 78 targeted) were completed on or adjacent

275   to the Canaveral Shoals from October 2012 through September 2017. Coastal sharks dominated samples,

276   comprising 90% of all fish caught. Bony fish, primarily adult red drum, comprised 7% of catch, and benthic

277   and pelagic rays represented 3%. In total, 2,595 sharks from 16 species were recorded (Table 2). Sharks

278   were collected on 65% of sets with a maximum of four species occurring on any single set. Atlantic

279   sharpnose shark alone accounted for 55% of shark captures, with blacknose (19%), blacktip (11%), and

280   finetooth sharks (6%) also relatively common. For most species, catch was dominated by adults and large

281   juveniles. All lemon sharks (n = 24) and bull sharks (n =7) were juveniles but only 3% of sharks were

282   classified as neonates including most spinner sharks and some scalloped hammerhead and sharpnose

283   sharks. Notably, while catches of adult sharpnose shark were male-dominated, catches of blacknose,

284   blacktip, and finetooth shark were female-dominated (Table 2). This female-skewed distribution was most

285   apparent from December through March, well before the typical spring pupping period, although gravid

286   blacknose (n = 20), blacktip (n = 12), and finetooth (n = 26) were encountered over a wider timeframe

287   from January to April or May each year.

288   Shark longline CPUE was significantly greater in the deeper troughs vs. shallow shoal ridges (two-

289   way ANOVA, 10.6 vs. 6.0 sharks per 100 hook-hours; $F_{1,107}$ = 6.72, p = 0.011; Fig. 2). There was also a

290   significant seasonal difference ($F_{3,107}$ = 15.28, p < 0.001) with CPUE highest in summer (13.8), moderate in

291   spring (6.6) and fall (8.8), and low in winter (4.0). These effects were due almost exclusively to the elevated

292   abundance of sharpnose sharks in deeper water adjacent to the shoals, particularly in summer and fall

293   (Fig. 3). When sharpnose were excluded from this comparison, shark CPUE was modestly but significantly

294   greater in shallow water (4.0 vs 3.1 sharks per 100 hook-hours; p = 0.031) but did not differ across seasons

295   (p = 0.387). No depth by season interactions were detected. Besides sharpnose shark, other common

296   warm season species included nurse and spinner sharks while cool-season species included finetooth,

297   lemon, sandbar, and to some extent blacktip sharks (Fig. 3). Catch of bonnethead and scalloped

298   hammerheads suggested possible winter-spring abundance peaks while blacknose sharks were present in

299   relatively even numbers year-round.

300

301

302

Table 2. Numbers and sizes of sharks captured on longlines. CPUE is expressed as fish per 100 hook hours and size as total length in cm. Targeted (i.e., non-random) longline sets are not included in Grand CPUE estimates.

Species	Total	CPUE Shallow	CPUE Deep	CPUE Targeted	CPUE Grand	Mean Length (Range)	Female %	Adult / Juvenile / YOY %
Sharpnose Shark *Rhizoprionodon terraenovae*	1436	2.73	8.06	0.00	5.37	85 (30–105)	24.5	84 / 13 / 3
Blacknose Shark *Carcharhinus acronotus*	488	1.29	1.17	1.58	1.23	113 (73–155)	66.3	73 / 27 / 0
Blacktip Shark *Carcharhinus limbatus*	277	0.87	0.43	0.99	0.65	132 (63–190)	72.5	46 / 54 / 0
Finetooth Shark *Carcharhinus isodon*	157	0.45	0.15	0.80	0.30	132 (70–156)	75.7	77 / 23 / 0
Nurse Shark *Ginglymostoma cirratum*	52	0.18	0.18	0.03	0.18	213 (135–278)	36.8	56 / 44 / 0
Bonnethead Shark *Sphyrna tiburo*	40	0.09	0.09	0.21	0.09	105 (80–120)	92.3	95 / 5 / 0
Spinner Shark *Carcharhinus brevipinna*	34	0.09	0.14	0.04	0.12	99 (64–210)	47.1	18 / 6 / 77
Scalloped Hammerhead *Sphyrna lewini*	29	0.04	0.17	0.02	0.10	134 (47–200)	22.2	11 / 82 / 7
Lemon Shark *Negaprion brevirostris*	24	0.12	0.02	0.01	0.07	149 (115–189)	65.0	0 / 100 / 0
Sandbar Shark *Carcharhinus plumbeus*	22	0.04	0.10	0.03	0.07	168 (78–220)	66.7	32 / 68 / 0
Great Hammerhead *Sphyrna mokarran*	13	0.05	0.03	0.03	0.04	265 (174–400)	66.7	46 / 54 / 0
Bull Shark *Carcharhinus leucas*	7	0.02	0.01	0.00	0.01	188 (171–210)	83.3	0 / 100 / 0
Sand Tiger Shark *Carcharias taurus*	5	0.02	0.01	0.05	0.02	183 (138–268)	100.0	20 / 80 / 0
Tiger Shark *Galeocerdo cuvier*	5	0.01	0.03	0.00	0.02	191 (89–320)	80.0	20 / 60 / 20
Smooth Hammerhead *Sphyrna zygaena*	1	0.01	0.00	0.00	<0.01	152	100.0	0 / 100 / 0
Dusky Shark *Carcharhinus obscurus*	1	0.00	0.01	0.00	<0.01	259	0.0	0 / 100 / 0
Unknown Carcharhinid	4	0.01	0.02	0.00	0.02	150 (100–200)	-	-
Total	2595	6.02	10.62	3.79	8.30			

303

304 **Fig. 2. Boxplots of shark longline CPUE across water depth zones and seasons for (A) all species, and (B)**

305 **excluding Atlantic sharpnose shark**. Horizontal black lines represent the group median, boxes represent

306 the interquartile range, and whiskers represent the full data range. Seasonal differences were only

307 detected for the all-species ANOVA test with pairwise differences denoted with lowercase letters.

308

309 **Fig. 3. Longline CPUE (+/- SE) by month and depth zone for ten most common shark species averaged**

310 **across all five years of the study**. Note the differing y-axis scale for each species.

311

Acoustic telemetry overview

313   A total of 567 acoustically tagged sharks across 16 species were detected within the Canaveral

314 Array from December 2013 through February 2020. These included 219 sharks tagged on the Canaveral

315 Shoals including blacknose (n = 57), finetooth (55), scalloped hammerhead (39), sharpnose (38), and

316 lemon sharks (30), plus 348 sharks from twelve species tagged by researchers over a wide area from

317 south Florida and the Bahamas to Nova Scotia, Canada (Table 3). Blacktip shark was the most commonly

318 detected species (n = 114), and all species recorded in the Canaveral Array were also collected on

319 longlines with the exception of white sharks (48) and common thresher shark (1). Acoustic telemetry

320 better documented the presence of larger species relative to longline catches. Specifically, while sharks

321 in the US small coastal management complex (e.g., sharpnose, blacknose, finetooth, bonnethead)

322 represented 82% of the longline catch, they represented only 33% of sharks detected in the Canaveral

323 Array, and the majority of these were tagged locally.

324

Table 3. Acoustically tagged sharks detected at Cape Canaveral December 2013–February 2020.

326 The number of acoustic receivers deployed in each habitat subset is listed in parentheses. Tagging

327 organization designations are ordered based on number of individuals detected.

Species	Acoustic Receiver Station Groups					
	All (62)	Deep (30)	Shallow (27)	Dredge (12)	Control (12)	Reef (5)
Blacktip Shark *Carcharhinus limbatus* [6,15,3,2,14]	114	112	85	93	83	103
Lemon Shark *Negaprion brevirostris* [2,1,3]	73	58	64	35	27	28
Blacknose Shark *Carcharhinus acronotus* [1]	57	57	38	47	48	47
Finetooth Shark *Carcharhinus isodon* [1]	55	53	52	49	38	44
White Shark *Carcharodon carcharias* [9,11]	48	45	15	12	13	30
Bonnethead Shark *Sphyrna tiburo* [15,16,7]	39	38	19	11	18	30
Scalloped Hammerhead *Sphyrna lewini* [1]	39	27	21	10	8	3
Bull Shark *Carcharhinus leucas* [2,3,12,14,4,8]	38	35	20	20	22	26
Sharpnose Shark *Rhizoprionodon terraenovae* [1]	38	38	20	14	28	26
Tiger Shark *Galeocerdo cuvier* [12,15,2,11]	20	20	6	9	8	17
Great Hammerhead *Sphyrna mokarran* [2,12]	14	12	6	4	4	6
Nurse Shark *Ginglymostoma cirratum* [2,8]	10	10	2	3	4	8
Sand Tiger Shark *Carcharias taurus* [5,9,10,17]	9	9	5	2	2	3
Sandbar Shark *Carcharhinus plumbeus* [3,10]	7	7	1	2	4	4
Spinner Shark *Carcharhinus brevipinna* [1]	5	5	2	3	1	-
Common Thresher Shark *Alopias vulpinus* [13]	1	1	1	-	1	1
Total	567	527	357	314	309	376

[1]Current Project, [2]Bimini Biological Field Station, [3]Coastal Carolina Univ., [4]Cape Eleuthera Inst., [5]Delaware State Univ., [6]Florida Atlantic Univ., [7]Florida State Univ., [8]Harbor Branch Oceanographic Inst., [9]Massachusetts Div. of Marine Fisheries, [10]Monmouth Univ., [11]Ocearch, [12]Rosenstiel School of Marine and Atmospheric Science, [13]Stony Brook Univ., [14]Smithsonian Environmental Research Center, [15]South Carolina Dept. Natural Resources, [16]Univ. North Carolina Chapel Hill, [17]Univ. North Carolina Wilmington

328   More individuals were detected in deep vs. shallow depth zones for all species except the lemon

329   shark (Table 3), although this comparison is complicated by the superior detection range of acoustic

330   receivers in deeper water. While seven species were recorded in every month of the year, there were

331   clear seasonal trends that closely mirrored longline catch trends for most species (Fig. 4). Cool season

332   sharks included blacktip, bonnethead, finetooth, lemon, sandbar, and white sharks, while warm season

333   sharks included sharpnose, nurse and great hammerheads. Combined across years, winter was an

334   especially productive season for acoustic telemetry monitoring with > 200 individual sharks detected

335   each calendar month from November through April (peak 294 sharks in January) with a rapid decline in

336   sharks detected from May-October (minimum 70 sharks in September).

337

338   **Fig. 4. Number of acoustically-tagged sharks detected in the Canaveral Array, December 2013 –**

339   **February 2020.** The total number of individuals detected in each calendar month is listed in the bottom

340   row.

341

Community differences across depths and seasons

343   Both longline and acoustic telemetry documented differences in the shark community through

344   space and time (Fig. 5). A PERMANOVA test of longline catch confirmed that *Season* explained over twice

345   the variance as *Depth Zone* although both factors were significant ($p < 0.001$, Table S3). Pairwise

346   comparisons confirmed that all four seasons had unique shark assemblages with the greatest differences

347   detected between summer and winter, whose samples were only 37% similar on average. A significant

348   follow-up PERMDISP test for the factor *Season* ($p = 0.013$) suggests that community differences are due,

349   in part, to uneven sample variation across seasons, not just differing species complements. Specifically,

350   the shark catch in summer was more uniform than during other seasons due to the reliable presence of

351   sharpnose sharks (Fig. 5A).

352

353   **Fig. 5. MDS plots of the shark community observed in (A) longline samples and (B) the Canaveral Array.**

354   Points represent the shark community for every combination of depth zone and season, with points closer

355   together having more similar communities. Replicates within each longline group are drawn from each of

356   the five years of the study while those in the Canaveral Array samples are drawn once from each acoustic

357   receiver station.

358

359   The shark community documented by the Canaveral Array also differed more across seasons than

360   depth zones, with *Season* explaining nearly five times the variance as *Depth Zone* but both were again

361   significant (PERMANOVA, $p < 0.001$, Table S4). Interpretation is complicated by a significant season-by-

362   depth interaction although examination of the MDS plot shows that the direction of the effects to be

363   rather consistent across both factors (Fig. 5B). The random effect of *Station* was also important ($p < 0.001$),

364   explaining about as much variability as *Depth Zone* and demonstrating that differences in the shark

365   community were detectable across individual receiver stations. As with longlines, the shark assemblage

366   was distinct for each season, and with summer and winter samples again the most divergent (only 44%

367   similar on average). PERMDISP tests again found that sample variability was unequal across seasons but

368   not depths, but in contrast to longline catches, the species assemblage in the Canaveral Array was

369   decidedly more uniform during winter than in other seasons.

370   Results of the longline SIMPER routine found that sharpnose shark alone, with its preference for

371   deeper and warmer water, accounted for 28% of the dissimilarity in shark community across *Depth Zone*

372   and 42% across *Season* (Fig. 6A and B, respectively). Blacktip and blacknose sharks contributed moderately

19

373   to community differences across depths (11-14%) while the nurse shark also helped discriminate across

374   seasons (11%). In the telemetry dataset, blacknose sharks contributed most to differences across depths

375   (21%) while finetooth, blacknose, and sharpnose sharks appeared similarly important (18-20%) in

376   discriminating across seasons.

377

378   **Fig. 6. A SIMPER routine to determine which species contribute most to the dissimilarity (%) in the shark**

379   **community across (A) Depth Zones and (B) Seasons for longline and telemetry datasets.**

380

Shark use of dredge and control sites, nearshore waters, and reefs

382   Combined across the six-year study, a similar number of shark species (15 vs. 16) and individuals

383   (314 vs. 309) were detected by acoustic receivers at the sand dredge site vs. nearby control site (Table 3).

384   Rarefaction curves also suggest that after standardizing for unequal receiver coverage, overall species

385   richness at the dredge and control sites were similar to that of other offshore shoal sites, nearshore shoal

386   sites, and reef sites (Fig. 7A). Nonetheless, a PERMANOVA test and follow-on pairwise comparisons

387   confirmed subtle but significant community differences between the dredge and control site as well as

388   other receiver groups ($p < 0.001$; Fig. 7B, Table S5). The greatest contrasts were observed between

389   nearshore shoal vs. offshore shoal stations and nearshore shoal vs. reef stations (samples 74% similar

390   when averaged across the study), confirming that the shark community changes with increasing distance

391   from shore. This transition was not dramatic, however, and numerous tagged finetooth, blacknose,

392   blacktip, and lemon sharks, amongst the most common species in shallow longline samples, were

393   routinely detected on the offshore reef tract well beyond the bounds of the Canaveral Shoals.

394

395 **Fig. 7. Shark assemblage comparisons across dredge and control sites, other nearshore and offshore**

396 **shoal sites, and reefs**. (A) Rarefaction curves comparing relative species richness after accounting for

397 uneven numbers of acoustic receivers, and (B) MDS plot of the shark community detected at each receiver

398 station in the Canaveral Array averaged across the study.

399

Habitat factors influencing the shark community

401 Longlines and acoustic telemetry documented similar habitat associations for most shark species

402 in the project area. In both datasets, for example, the lemon shark was encountered in shallower water

403 (mean 5.4-6.7 m) and closer to shore (mean 1.2-1.5 km) on average than any other species. Finetooth

404 sharks also showed similar preferences for shallow nearshore habitat across datasets while blacknose

405 and blacktip sharks had intermediate depth and distance preferences. Conversely, sharpnose sharks

406 exhibited a consistent preference for deeper water farther offshore (mean 10.3-11.9 m deep, 6.5-7.6 km

407 from shore), as did sandbar, tiger, and great hammerhead sharks. The mean and range of habitat

408 conditions for which each species as observed in longline samples and the Canaveral Array are provided

409 in Tables S1 and S2.

410 At the community level, the BEST procedure identified water temperature and water clarity as

411 the habitat conditions most strongly correlated with the shark community in both longline and telemetry

412 samples (Fig. 8). The high rank of these two factors across both datasets reinforces their importance to

413 shark distribution in the project area. Distance from shore and water depth also explained some

414 community variation in both datasets. For longlines, the combination of water clarity (i.e., Secchi depth),

415 water temperature, and distance from shore had the greatest overall correlation (BEST, $\rho_s = 0.280$). For

416 telemetry samples, a combination of just sea surface temperature and water clarity (i.e., K490 irradiance),

21

417   both obtained from satellite-based measurements, produced an even stronger correlation (ρ_s = 0.510).

418   Notably, seafloor slope, a quality that helps distinguish sand shoals from adjacent shelf habitats, appeared

419   uninformative (ρ_s = 0.02) in both datasets. Salinity and dissolved oxygen—available only for longline

420   samples—and sediments % fines and % organics—available only for telemetry samples—also did not

421   correlate with shark community structure.

422

423   **Fig. 8. A BEST procedure to determine which measured habitat variables correlate most strongly with**

424   **the shark community.** Correlation values (Spearman ρs) for the top overall combination plus all individual

425   variables are included.

426

Discussion

428   This study was the first to directly sample a shark community associated with offshore sand

429   shoals, dynamic but poorly surveyed features of continental shelves whose sand deposits are valued for

430   shoreline restoration projects and increasingly for renewable energy development. Our results confirmed

431   that sharks as a group are abundant on shoals in east Florida and presumably analogous shoal sites in

432   other regions. The opportunity to monitor spatial and seasonal changes in the local shark assemblage with

433   both traditional longline gear and acoustic telemetry—perhaps the most unique aspect of this study—

434   was made possible by working in a region of active shark research with a strong culture of researcher

435   collaboration. Both approaches documented a similar suite of shark species (14 of 18 were held in

436   common), improving confidence in the observed abundance and community trends, and providing a

437   means to compare the strengths and limitations of each approach.

438

Community differences across depths and seasons

440   Longlines and acoustic telemetry independently documented real but modest differences in the

441 shark community between shallow shoal ridges and deeper water along shoal flanks and troughs. This

442 finding was partly due to the rather narrow depth range sampled, out to a maximum of only 25 meters.

443 Study objectives precluded sampling much deeper outer shelf waters where additional species would be

444 encountered and community contrasts with shallow shoals would be more dramatic. Drymon et al. [10]

445 for example, reported substantial changes in the shark assemblage across a 364-m depth gradient

446 offshore Alabama with deep water samples producing nearly twice as many species. Distinct shark

447 communities are also commonly associated with areas of extreme vertical relief such as seamounts and

448 coral reef drop-offs [37,38]. Nonetheless, the present findings do appear to corroborate recent modeling

449 by Pickens and Taylor [39] who found that proximity to sand shoals and seafloor slope are not strong

450 abundance predictors for several shark species in shelf waters of the US South Atlantic and Gulf of Mexico.

451   All common species in this study were widely distributed in the project area suggesting that

452 community differences across depths are due to each shark species using habitat on and adjacent to the

453 Canaveral Shoals in different ways. For example, shallow water is often utilized by small sharks to reduce

454 predation risk [40]. This strategy is adopted locally by young lemon sharks who aggregate each winter

455 along the shoreline and inner shoals in water only 1-2 meters deep with only infrequent excursions farther

456 offshore [41]. Finetooth shark, a small coastal species, also preferred shallower water than other species.

457 In contrast, Atlantic sharpnose shark, the smallest species in the region, clearly selected for deeper water

458 suggesting it has an alternative strategy to mitigate predation risk. Shallow shoals may also offer a

459 temporary respite from adverse environmental conditions. Summer cold-water upwellings in east Florida

460 often coincide with the formation of short-lived giant manta ray (*Manta birostris*) aggregations on shoal

461 ridges, presumably to thermoregulate [27] although the behavior of sharks during these events is not well

462   documented. In the northern Gulf of Mexico, certain shoals also serve as refugia for benthic fish and

463   invertebrates when deeper water becomes hypoxic [42,43], events which also undoubtedly influence

464   shark distribution.

465   Deeper troughs between and adjacent to shoal ridges may serve as high value foraging grounds for many

466   sharks and other large marine predators. The prominent sand waves, invertebrate burrows, and fine

467   sediments that are routinely scoured away by waves and strong currents on ridges, persist in deeper

468   water, offering complex microhabitats that are preferred by many small benthic fishes and invertebrates

469   [17]. Previous trawl and camera sled surveys suggest that deep water near shoals exhibit greater

470   abundance of benthic fauna than shoal ridges themselves [19,20]. At Cape Canaveral, a trawl survey

471   performed concurrently with the present study documented over double the fish density and biomass,

472   and higher species richness in deeper troughs (10-18 m) than on ridges (<10 m) [44]. Moreover, space use

473   analyses of several priority species tagged at Cape Canaveral found that blacknose and finetooth sharks,

474   as well as benthic feeding red drum and loggerhead turtles, spent considerable time in deeper water

475   between and adjacent to the shoals, and particularly in the Canaveral Bight, suggesting that these areas

476   are important foraging grounds [27]. Even so, most coastal sharks also opportunistically feed on pelagic

477   prey whose movements are not closely linked to water depth. Pelagic forage fishes, particularly the

478   regionally abundant menhaden (*Brevoortia* spp.), are important prey for sharpnose, blacktip, spinner, and

479   finetooth sharks [45], a preference which may explain why most sharks range widely through the project

480   area including excursions to offshore reefs.

481   Changes in the shark assemblage across seasons were pronounced and somewhat anticipated.

482   Long distance migrations, while only now being resolved in detail for many coastal sharks thanks to

483   improved tagging technology (see [46–50]), have been broadly recognized for decades in the US Atlantic

484   and many other regions of the world. Although not presented in detail here, a majority of blacknose,

finetooth, sharpnose, and lemon sharks acoustically tagged at Cape Canaveral undertook northward

spring migrations before returning to east Florida in fall [27,41], and over 200 sharks tagged by other

researchers from South Florida and Bahamas to Canada migrated through the project area. These

migrations result in a shark community that is in constant flux throughout the year. Thus far, seasonal

variations in shark communities have been best described for estuaries (see [51–55]), habitats where

annual variation in environmental conditions can be dramatic. Shark community surveys over the open

continental shelf—especially those that include year-round sampling—are uncommon but similar

patterns should be expected and may be particularly stark at mid-latitudes where seasonal changes in

water temperature and primary productivity are pronounced.

Habitat influencing the shark community

Shifts in the shark community across depths and seasons are the culmination of sharks reacting

to multiple cues in their local environment. Oceanographic conditions, prey abundance, competition, and

predation risk (among other factors) all influence the distribution and behavior of each species. Of the

measured environmental and habitat variables, changes in water temperature and water clarity were two

factors that best matched changes in the shark community. As ectotherms, temperature directly

influences shark metabolism and growth [56], embryonic development [57], and swimming speed [58],

and mediates interspecies competition and predatory-prey relationships [59]. Consequently, water

temperature is recognized as a primary factor dictating the geographic distribution, migrations, and

community structure of sharks worldwide [60]. The role of temperature in structuring fish communities

may be especially important east Florida where water temperature varies nearly 15°C across the year and

where the shifting edge of the Florida Current can lead to rapid swings in coastal ocean temperatures and

periodic upwellings [27].

508 Water clarity also influenced the shark assemblage in acoustic telemetry and particularly longline samples,

509 where it appeared even more influential than temperature. Water over and adjacent to the Canaveral

510 Shoals is often quite turbid due to waves breaking over the shallow seabed and resuspending fine

511 sediments that accumulate in the lee of the shoals. Sharpnose shark strongly preferred clearer offshore

512 water but other species, particularly finetooth, lemon, blacktip and blacknose sharks, were abundant in

513 turbid conditions. Water clarity has also been shown to structure shark communities in other regions

514 including Australia [61] , South Africa [62], and the Gulf of Mexico [11]. Pelagic sharks often select for clear

515 water [63] but several coastal species have been shown to select for high turbidity including sand tiger

516 [49] and scalloped hammerheads [64]. Small fish and crustaceans often prefer elevated turbidity since it

517 reduces individual risk of predation [65,66]. Foraging coastal sharks may move in concert with these prey

518 species and thus spend more time foraging in turbid conditions; small sharks may themselves experience

519 reduced predation risk in turbid water. Therefore, while there was no obvious association of sharks with

520 shallow shoal ridges, these features may still serve an important function by introducing greater local

521 variation in water clarity that are exploited by small coastal fishes and the sharks that depend on them.

522 Distance from shore was also moderately influential in structuring the local shark community.

523 Common species including lemon, finetooth, and blacknose sharks were encountered relatively close to

524 the beach in both datasets (1-3 km on average) while others such as sharpnose, nurse, and great

525 hammerhead sharks were more abundant farther offshore (4-8 km on average). Notably, the visit duration

526 of several sharks to stations in the Canaveral Array increases when near the beach [27] suggesting reduced

527 swim speeds or more tortuous swimming paths, perhaps linked to foraging. These findings are consistent

528 with a review by Sequeira et al. [67] who demonstrated that movement of marine vertebrates become

529 more complex and less directed near the coast, regardless of taxonomy or body size, a convergence they

530 link to increased microhabitat complexity in nearshore waters.

531

Nursery function of shoals

533   Many coastal sharks rely on spatially discrete nursery grounds where females give birth and young

534   spend their first months or years of life. Nurseries are defined as areas that support high densities of

535   young sharks, sustain individuals for extended periods, and are used repeatedly across years [68]. These

536   sites are likely selected for the high productivity, reduced predation risk, and optimal temperature and

537   salinity [68]. While some small coastal species including sharpnose and blacknose shark—the two most

538   abundant species in longline samples—may forego the use of nurseries altogether [40], identifying

539   nursery locations for sharks that require them is important because these sites often occur in shallow

540   coastal waters that experience elevated human habitat degradation and fishing pressure.

541   Nearshore waters of east-central Florida have been recognized as a nursery for the scalloped

542   hammerhead [69], spinner [70], and lemon shark [71]. Longline catches support these earlier

543   assessments; all captured lemon sharks were immature, and most neonates were either spinner or

544   scalloped hammerhead sharks. Nonetheless, anecdotal observations suggest that this gear was

545   underestimating the density of young sharks. From 2012–2016 for example, YOY scalloped hammerheads

546   (n = 369, mean FL = 39 cm) comprised 40% of all sharks collected in gill net sampling off Cape Canaveral

547   in support of tagging and genetic studies ([30]; authors' unpublished data). In February 2017, nearly 1800

548   immature (~0.75-2.0 m TL) lemon sharks were video documented along a 29 km aerial survey along the

549   Canaveral shoreline, roughly one shark every 16 meters (authors' unpublished data). None of these

550   species strongly associated with offshore shoal ridges. Most YOY spinner sharks and hammerheads were

551   collected in deeper water adjacent to the shoals while juvenile lemon sharks aggregate in the surf zone.

552   Moreover, declining CPUE of finetooth, blacktip, and blacknose in March and April each year, and

553   confirmed northward migrations of many tagged females at this time [27] suggest that pupping primarily

554   occurs north of Cape Canaveral. Gill nets, which better target small sharks and avoid biases from bait type

555　and hook size, are likely a more effective gear for shark nursery studies on sand shoals but can be more

556　labor-intensive, reducing the replication needed to evaluate shark community patterns and habitat

557　preferences. Regardless, this study did not document evidence that the shallow shoals themselves served

558　a unique shark nursery function or that other species pupped nearby in especially large numbers.

559

Implications for dredging

561　　　Sharks as a group are thought to face reduced direct risk from sand dredging compared to benthic

562　rays and teleost fishes. As large and mobile predators, sharks are unlikely to suffer direct mortality from

563　the dredge itself [72] and many coastal species have been shown to maintain large home ranges and

564　exhibit low site fidelity, although reef-associated sharks are important exceptions. Sand dredge sites will

565　represent a small fraction of an individual shark's overall activity space in most instances. Moreover, while

566　many sharks forage on the seafloor, others feed primarily or opportunistically in the water column and

567　may better tolerate disruption to benthic communities resulting from dredging operations. In this study,

568　only modest differences between the shark assemblage were detected at the active dredge site versus

569　the nearby control site. Moreover, behavioral assessments of the five shark species tagged at Cape

570　Canaveral (detailed in [27]) demonstrated that individuals remained near a given receiver station for less

571　than an hour on average, made regular inshore-offshore movements, and commonly undertook

572　migrations spanning several hundred kilometers, all behaviors which minimize the effects of localized

573　dredging disturbances. One major limitation of the present study is that the shark community comparison

574　at the dredge vs. control site was purely descriptive and complicated by the repeated disturbance of the

575　dredge site over the past 20 years. More rigorous study designs such as Before-After-Control-Impact

576　(BACI) protocols are viable options when evaluating proposed sand borrow sites and would better reveal

577　causal links between dredging to shark community structure.

578   Amongst the most significant impacts to sharks from dredging may occur beyond the boundaries

579   of a dredge site itself. Dredging along shallow shoal ridges, for example, will increase water depth and can

580   alter local wave field dynamics, sediment grain size, turbidity, and benthic communities in unpredictable

581   ways [73,74]. The deeper troughs adjacent to and between shoals, particularly in the Canaveral Bight,

582   were regularly utilized by most shark species. Exposing these areas of fine sediment to more powerful

583   waves and ocean currents could degrade the quality of local shark nurseries and foraging grounds. Altered

584   turbidity and sedimentation processes are also a recognized threat to reef habitat [75] and the sharks that

585   rely on them. At Cape Canaveral, this risk is low because the main reef tract occurs several km east of the

586   active dredge site, and sand is dredged from the leading edge and trough (not ridge) of the shoal. In areas

587   where reefs lie closer to a dredge site, are dominated by sensitive corals, or where water clarity is naturally

588   high, minimizing changes in turbidity and sedimentation during and after dredging should be a principal

589   concern.

590   Offshore sand dredging is almost always accompanied by redeposition of the same sand along the

591   shoreline to counteract beach erosion or rebuild marshes. These nourishment activities can themselves

592   disrupt fish communities through burial and sedimentation of nearshore hardbottom [76]. Locally, lemon

593   sharks may be the species of greatest risk from beach placement of sand. Young sharks gather each winter

594   in semi-isolated runnels between the shoreface and offshore sandbar, in concentrations sufficient for

595   east-central Florida to be classified as a Habitat Area of Particular Concern (one of only three shark species

596   in the US to benefit from this designation). Beach renourishment activity, which also commonly occurs in

597   winter to avoid impact on nesting sea turtles and shorebirds, would temporarily fill these runnels. The

598   effect on lemon shark aggregations is hard to predict although the species experienced declines in survival

599   after shoreline dredging operations in the Bahamas [77].

600   **Longline vs. acoustic telemetry comparison**

601   Bottom longlines and acoustic telemetry separately documented similar single species and

602   community trends in east Florida but each has limitations for surveying offshore sand shoals. Longlines

603   are easily quantifiable and thus widely used for population assessments but with known biases related to

604   shark size and behavior, hook size, and bait choice [78]. Bonnetheads, for example, feed primarily on blue

605   crabs (*Callinectes* spp.) [79] and were likely underrepresented in the catch locally. Longlines will also miss

606   rare species. While not a shark, acoustically tagged smalltooth sawfish (*Pristis pectinata*), now protected

607   under the US Endangered Species Act, were regularly detected by the Canaveral Array in summer [80] but

608   none were collected despite being prone to capture on baited hooks. Finally, longline sampling here was

609   conducted during the day to maximize safety when working on the shoals. Studies have found that shoal

610   fish assemblages can vary over a diel cycle [17], and day-night differences in catches rates have been

611   reported for several coastal shark species [54,81].

612   Acoustic telemetry monitoring of shark communities are less influenced by these sampling biases

613   but are only realistic in regions where multiple species are being tracked and researcher coordination is

614   occurring. Due to varying management effort across nations as well as cost and logistical constraints, this

615   approach remains unrealistic in many parts of the world. Moreover, acoustic telemetry cannot easily

616   assess single species abundance or explore interannual community patterns since the number of tagged

617   animals is in constant flux and represents an unknown fraction of the population. Finally, it is challenging

618   to collect the needed environmental variables (e.g., temperature, turbidity, chlorophyll) at acoustic

619   telemetry stations for which to rank habitat value although improvements in environmental data loggers

620   and remote sensing capabilities are addressing this limitation.

621

622

623

Conclusions

624

625   As a group, sharks are a prominent and year-round component of sand shoal fish community in east

626   Florida and presumably in similar habitats in other regions. Nonetheless, most common species were

627   widely distributed with relatively subtle differences in community composition observed between shallow

628   shoal ridges and nearby deeper water, and across an inshore-offshore gradient, at least out to a depth of

629   25 meters. With their naturally high mobility and low site fidelity, sharks may be better able to avoid or

630   overcome direct dredging disturbances, and no major community differences were observed between a

631   previously dredged site and a nearby undisturbed site. Despite no strong affinities for shallow shoal ridges,

632   shoals on the whole offer elevated habitat complexity when compared to much of the continental shelf.

633   Coastal sand dredging operations and wind energy development projects, which already focus on

634   minimizing disturbance to nearby reef habitat, should also consider impacts to soft-bottom substrates

635   directly adjacent to shoals, and strive to preserve natural variation in seafloor bathymetry, sediments, and

636   turbidity that likely sustain the most diverse shark community.

637

638

639

640

641

Acknowledgements

References

1. Davidson LNK, Krawchuk MA, Dulvy NK. Why have global shark and ray landings declined: Improved management or overfishing? Fish and Fisheries. 2016;17. doi:10.1111/faf.12119

2. Pacoureau N, Rigby CL, Kyne PM, Sherley RB, Winker H, Carlson JK, et al. Half a century of global decline in oceanic sharks and rays. Nature. 2021;589. doi:10.1038/s41586-020-03173-9

3. Sherman CS, Digel ED, Zubick P, Eged J, Haque AB, Matsushiba JH, et al. High overexploitation risk due to management shortfall in highly traded requiem sharks. Conserv Lett. 2023;16: e12940. doi:https://doi.org/10.1111/conl.12940

4. Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, et al. Extinction risk and conservation of the world's sharks and rays. Elife. 2014;3. doi:10.7554/elife.00590

5. Latour RJ, Gartland J. Dynamics of the shark community in the Mid-Atlantic Bight. Mar Biol. 2020;167: 100. doi:10.1007/s00227-020-03720-y

6. Peterson CD, Belcher CN, Bethea DM, Driggers WB, Frazier BS, Latour RJ. Preliminary recovery of coastal sharks in the south-east United States. Fish and Fisheries. 2017;18: 845–859. doi:10.1111/faf.12210

7. NMFS. Final Consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MD. Public Document. pp. 1600. 2006.

8. Hueter RE, Tyminski JP. Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off Peninsular Florida and Texas. In: C. McCandless, N. Kohler HPJr, editor. Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. Bethesda, Maryland: American Fisheries Society; 2007. pp. 193–223.

9. Ulrich GF, Jones CP, Driggers WB, Drymon JM, Oakley D, Riley C. Habitat utilization, relative abundance, and seasonality of sharks in the estuarine and nearshore waters of South Carolina. In: McCandless CT, Kohler NE, Pratt Jr. HL, editors. Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. Bethesda, Maryland: American Fisheries Society; 2007. pp. 125–139.

10. Drymon JM, Powers SP, Dindo J, Dzwonkowski B, Henwood TA. Distributions of Sharks across a Continental Shelf in the Northern Gulf of Mexico. Marine and Coastal Fisheries. 2010;2: 440–450. doi:10.1577/c09-061.1

11. Bethea DM, Ajemian MJ, Carlson JK, Hoffmayer ER, Imhoff JL, Grubbs RD, et al. Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. Environ Biol Fishes. 2014;98: 1233–1254. doi:10.1007/s10641-014-0355-3

12.   Pickens BA, Taylor JC, Finkbeiner M, Hansen D, Turner L. Modeling sand shoals on the U.S. Atlantic shelf: Moving beyond a site-by-site approach. J Coast Res. 2021;37: 227–237. doi:10.2112/JCOASTRES-D-20-00084.1

13.   Rutecki D, Dellapenna T, Nestler E, Scharf F, Rooker J, Glass C, et al. Understanding the Habitat Value and Function of Shoals and Shoal Complexes to Fish and Fisheries on the Atlantic and Gulf of Mexico Outer Continental Shelf. Literature Synthesis and Gap Analysis. Prepared for the U.S. Dept. of the Interior, Bureau of Ocean Energy Management. Contract # M12PS00009. BOEM 2015-012. 176 pp. 2014.

14.   Michel J, Bejarano A, Peterson C, Voss C. Review of Biological and Biophysical Impacts from Dredging and Handling of Offshore Sand. U.S. Department of the Interior, Bureau of Ocean Energy Management, Herndon, VA. OCS Study BOEM 2013-0119. 258 pp. 2013.

15.   Knorr PA. Searching for sand in Florida: Exploiting sea floor morphology as a reconnaissance tool. Shore & Beach. 2017;85: 1–11.

16.   Stenberg C, Støttrup JG, van Deurs M, Berg CW, Dinesen GE, Mosegaard H, et al. Long-term effects of an offshore wind farm in the North Sea on fish communities. Mar Ecol Prog Ser. 2015;528. doi:10.3354/meps11261

17.   Diaz RJ, Cutter GR, Able KW. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries. 2003;26: 12–20. doi:10.1007/BF02691689

18.   Kaiser MJ, Bergmann M, Hinz H, Galanidi M, Shucksmith R, Rees EIS, et al. Demersal fish and epifauna associated with sandbank habitats. Estuar Coast Shelf Sci. 2004;60: 445–456. doi:10.1016/j.ecss.2004.02.005

19.   Vasslides JM, Able KW. Importance of shoreface sand ridges as habitat for fishes off the northeast coast of the United States. Fishery Bulletin. 2008;106: 93–107.

20.   Slacum HW, Burton WH, Methratta ET, Weber ED, Llansó RJ, Dew-Baxter J. Assemblage Structure in Shoal and Flat-Bottom Habitats on the Inner Continental Shelf of the Middle Atlantic Bight, USA. Marine and Coastal Fisheries. 2010;2: 277–298. doi:10.1577/c09-012.1

21.   de Jong MF, Baptist MJ, van Hal R, de Boois IJ, Lindeboom HJ, Hoekstra P. Impact on demersal fish of a large-scale and deep sand extraction site with ecosystem-based landscaped sandbars. Estuar Coast Shelf Sci. 2014;146: 83–94. doi:10.1016/j.ecss.2014.05.029

22.   Wenger AS, Harvey E, Wilson S, Rawson C, Newman SJ, Clarke D, et al. A critical analysis of the direct effects of dredging on fish. Fish and Fisheries. 2017;18. doi:10.1111/faf.12218

23.   Pickens B, Taylor J, Hansen D. Volume 1: Fish habitat associations and the potential effects of dredging on the Atlantic and Gulf of Mexico Outer Continental Shelf, literature synthesis and gap analysis. In: Pickens, BA, Taylor JC, editors. Regional Essential Fish Habitat geospatial assessment and framework for offshore sand features. Sterling (VA): US Department of the Interior, Bureau of Ocean Energy Management. OCS Study BOEM 2020-002 and NOAA NCCOS Technical Memorandum 270. https://doi.org/10.25923/akzd-8556 122 pp. 2020.

24. McArthur C, Parsons M. Spatial analysis of sediment grain size in the vicinity of the Canaveral Harbor Ocean Dredged Material Disposal Site. Atlanta, Georgia; 2005. Report No.: EPA-904-R-05-002.

25. Valle-Levinson A, Adams P, Paniagua-Arroyave J, Parr S, Yousif A, So S. Chapter 2: Physical oceanography surveys. Pages 10-102 in Ecological Function and Recovery of Biological Communities within Dredged Ridge-Swale Habitats in the South-Atlantic Bight. Murie DJ and Smith GH Jr (editors). Sterling (VA): U.S. Department of the Interior, Bureau of Ocean Energy Management. Report No.: OCS Study BOEM 2022. Contract No.: M13AC00012. 2022.

26. Gilmore RG. Environmental and Biogeographic Factors Influencing Ichthyofaunal Diversity: Indian River Lagoon. Bull Mar Sci. 1995;57: 153–170.

27. Iafrate J, Watwood S, Reyier E, Ahr B, Scheidt D, Holloway-Adkins K, et al. Behavior, Seasonality, and Habitat Preferences of Mobile Fishes and Sea Turtles Within a Large Sand Shoal Complex: Insights from Traditional Sampling and Emerging Technologies. Sterling (VA): US Department of the Interior, Bureau of Ocean Energy Management. OCS Study BOEM 2019-043. 183 pp. 2019.

28. Young JM, Bowers ME, Reyier EA, Morley D, Ault ER, Pye JD, et al. The FACT Network: Philosophy, Evolution, and Management of a Collaborative Coastal Tracking Network. Marine and Coastal Fisheries. 2020;12: 258–271. doi:10.1002/mcf2.10100

29. Davis MM, Suárez-Moo P de J, Daly-Engel TS. Genetic structure and congeneric range overlap among sharpnose sharks (Genus *Rhizoprionodon*) in the northwest Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences. 2019;76. doi:10.1139/cjfas-2018-0019

30. Barker AM, Frazier BS, Adams DH, Bedore CN, Belcher CN, Driggers WB, et al. Distribution and relative abundance of scalloped (*Sphyrna lewini*) and Carolina (*S. gilberti*) hammerheads in the western North Atlantic Ocean. Fish Res. 2021;242. doi:10.1016/j.fishres.2021.106039

31. NOAA CoastWatch ERDDAP. https://coastwatch.noaa.gov//erddap/index.html. 17 Dec 2022.

32. Mendelssohn R. rerddapXtracto: Extracts Environmental Data from "ERDDAP" Web Services. 2020. Available: https://github.com/rmendels/rerddapXtracto

33. Clarke K, Gorley R, Somerfield P, Warwick R. Change in marine communities: an approach to statistical analysis and interpretation, 3nd edition. Plymouth, UK: PRIMER-E; 2014.

34. Anderson DR. Model based inference in the life sciences: A primer on evidence. New York: Springer; 2008.

35. Clarke K. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 1993;18: 117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

36. Clarke KR, Ainsworth M. A method of linking multivariate community structure to environmental variables. Marine Ecology-Progress Series. 1993;92: 205.

37. Friedlander AM, Sandin SA, DeMartini EE, Sala E. Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. Mar Ecol Prog Ser. 2010;410. doi:10.3354/meps08634

38. Dunn N, Savolainen V, Weber S, Andrzejaczek S, Carbone C, Curnick D. Elasmobranch diversity across a remote coral reef atoll revealed through environmental DNA metabarcoding. Zool J Linn Soc. 2022. doi:10.1093/zoolinnean/zlac014

39. Pickens B, Taylor J. Volume 3: Predicting the Distribution of Select Fish Species of the Gulf of Mexico, South Atlantic, and Greater Atlantic. In: Pickens, BA, Taylor JC (eds.). Regional Essential Fish Habitat Geospatial Assessment and Framework for Offshore Sand Features. Sterling (VA): US Department of the Interior, Bureau of Ocean Energy Management. OCS Study BOEM 2020-002, NOAA NCCOS Technical Memorandum 270. https://doi.org/10.25923/akzd-8556 67 pp. 2020.

40. Knip DM, Heupel MR, Simpfendorfer CA. Sharks in nearshore environments: models, importance, and consequences. Marine Ecology-Progress Series. 2010;402: 1–11. doi:10.3354/meps08498

41. Reyier EA, Franks BR, Chapman DD, Scheidt DM, Stolen ED, Gruber SH. Regional-scale migrations and habitat use of juvenile lemon sharks (*Negaprion brevirostris*) in the US South Atlantic. PLoS One. 2014;9. doi:10.1371/journal.pone.0088470

42. Craig J. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar Ecol Prog Ser. 2012;445: 75–95. doi:10.3354/meps09437

43. Dubois S, Gelpi CG, Condrey RE, Grippo MA, Fleeger JW. Diversity and composition of macrobenthic community associated with sandy shoals of the Louisiana continental shelf. Biodivers Conserv. 2009;18: 3759–3784. doi:10.1007/s10531-009-9678-3

44. Murie D, Smith G. Chapter 4: Habitat classification of the shoals and surrounding area based on direct sampling using sediment grabs. In Ecological Function and Recovery of Biological Communities within Dredged Ridge-Swale Habitats in the South-Atlantic Bight. Murie DJ and Smith GH Jr (editors). Sterling (VA): U.S. Department of the Interior, Bureau of Ocean Energy Management. Report No.: OCS Study BOEM 2022. Contract No.: M13AC00012. 2023.

45. Bethea DM, Buckel JA, Carlson JK. Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser. 2004;268: 245–264. doi:10.3354/meps268245

46. Kessel ST, Chapman DD, Franks BR, Gedamke T, Gruber SH, Newman JM, et al. Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). Mar Ecol Prog Ser. 2014;514: 175–190. doi:10.3354/meps10966

47. Kneebone J, Chisholm J, Skomal G. Movement patterns of juvenile sand tigers (*Carcharias taurus*) along the east coast of the USA. Marine Biology 2014 161:5. 2014;161: 1149–1163. doi:10.1007/S00227-014-2407-9

48. Skomal GB, Braun CD, Chisholm JH, Thorrold SR. Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. Mar Ecol Prog Ser. 2017;580: 1–16. doi:10.3354/meps12306

49.   Haulsee DE, Breece MW, Brown LM, Wetherbee BM, Fox DA, Oliver MJ. Spatial ecology of *Carcharias taurus* in the northwestern Mid-Atlantic coastal ocean. Mar Ecol Prog Ser. 2018;597: 191–206. doi:10.3354/meps12592

50.   Legare B, DeAngelis B, Skomal G. After the nursery: Regional and broad-scale movements of sharks tagged in the Caribbean. Marine Ecology. 2020;41. doi:10.1111/maec.12608

51.   Heithaus MR, Burkholder D, Hueter RE, Heithaus LI, Pratt HL, Carrier JC. Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. Canadian Journal of Fisheries and Aquatic Sciences. 2007;64: 1302–1313. doi:10.1139/F07-098

52.   Wiley TR, Simpfendorfer CA. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bull Mar Sci. 2007;80: 171–189.

53.   Ward-Paige CA, Britten GL, Bethea DM, Carlson JK. Characterizing and predicting essential habitat features for juvenile coastal sharks. Marine Ecology. 2015;36: 419–431. doi:10.1111/maec.12151

54.   Bangley CW, Rulifson RA. Habitat partitioning and diurnal-nocturnal transition in the elasmobranch community of a North Carolina estuary. Bull Mar Sci. 2017;93: 319–338. doi:10.5343/bms.2016.1038

55.   Plumlee JD, Dance KM, Matich P, Mohan JA, Richards TM, TinHan TC, et al. Community structure of elasmobranchs in estuaries along the northwest Gulf of Mexico. Estuar Coast Shelf Sci. 2018;204: 103–113. doi:10.1016/j.ecss.2018.02.023

56.   Zhou C. Multidecadal daily resolved growth increments reveal climate effect on the growth of a highly migratory shark in the North Atlantic. ICES JOURNAL OF MARINE SCIENCE. 2021;78: 2496–2505. doi:10.1093/icesjms/fsab130

57.   Hume JB. Higher temperatures increase developmental rate & reduce body size at hatching in the small-eyed skate Raja microocellata: implications for exploitation of an elasmobranch in warming seas. J Fish Biol. 2019;95: 655–658. doi:10.1111/jfb.13997

58.   Gervais CR, Huveneers C, Rummer JL, Brown C. Population variation in the thermal response to climate change reveals differing sensitivity in a benthic shark. Glob Chang Biol. 2021;27: 108–120. doi:10.1111/gcb.15422

59.   Arnes-Urgelles C, Salinas-de-Leon P, Rastoin-Laplane E, Vaca-Pita L, Suarez-Moncada J, Paez-Rosas D. The Effects of Climatic Variability on the Feeding Ecology of the Scalloped Hammerhead Shark (Sphyrna lewini) in the Tropical Eastern Pacific. Front Mar Sci. 2021;8. doi:10.3389/fmars.2021.625748

60.   Birkmanis CA, Freer JJ, Simmons LW, Partridge JC, Sequeira AMM. Future Distribution of Suitable Habitat for Pelagic Sharks in Australia Under Climate Change Models. Front Mar Sci. 2020;7. doi:10.3389/fmars.2020.00570

61.   Birkmanis CA, Partridge JC, Simmons LW, Heupel MR, Sequeira AMM. Shark conservation hindered by lack of habitat protection. Glob Ecol Conserv. 2020;21. doi:10.1016/j.gecco.2019.e00862

62.	Wintner SP, Kerwath SE. Cold fins, murky waters and the moon: what affects shark catches in the bather-protection program of KwaZulu-Natal, South Africa? Mar Freshw Res. 2018;69. doi:10.1071/MF17126

63.	Lisney TJ, Theiss SM, Collin SP, Hart NS. Vision in elasmobranchs and their relatives: 21st century advances. Journal of Fish Biology. 2012. doi:10.1111/j.1095-8649.2012.03253.x

64.	Holland KN, Wetherbee BM, Peterson JD, Lowe CG. Movements and Distribution of Hammerhead Shark Pups on Their Natal Grounds. Copeia. 1993;1993: 495. doi:10.2307/1447150

65.	Abrahams M, Kattenfeld M. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behav Ecol Sociobiol. 1997;40: 169–174. doi:10.1007/s002650050330

66.	de Robertis A, Ryer CH, Veloza A, Brodeur RD. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences. 2003;60: 1517–1526. doi:10.1139/f03-123

67.	Sequeira AMM, Rodríguez JP, Eguíluz VM, Harcourt R, Hindell M, Sims DW, et al. Convergence of marine megafauna movement patterns in coastal and open oceans. Proc Natl Acad Sci U S A. 2018;115: 3072–3077. doi:10.1073/pnas.1716137115

68.	Heupel MR, Carlson JK, Simpfendorfer CA. Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology-Progress Series. 2007;337: 287–297. doi:10.3354/meps337287

69.	Adams DH, Paperno R. Preliminary Assessment of a Nearshore Nursery Ground for the Scalloped Hammerhead off the Atlantic Coast of Florida. In: McCandless N.E.; Pratt, H.L., Jr. CT; K, editor. Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. Bethesda, Maryland: American Fisheries Society; 2007. pp. 165–174.

70.	Aubrey CW, Snelson Jr. FF. Early life history of the spinner shark in a Florida nursery. In: McCandless CT, Kohler NE, Pratt HL, editors. Shark nursery grounds of the Gulf of Mexico an the east coast waters of the United States. Bethesda, Maryland: American Fisheries Society Symposium 50; 2007. pp. 175–189.

71.	Reyier EA, Adams DH, Lowers RH. First Evidence of a High Density Nursery Ground for the Lemon Shark, *Negaprion brevirostris*, Near Cape Canaveral, Florida. Florida Scientist. 2008;71: 134–148.

72.	Reine K, Clarke D. Entrainment by hydraulic dredges-A review of potential impacts. Technical Note DOER-E1. Vicksburg, MS; 1998.

73.	Byrnes MR, Hammer RM, Thibaut TD, Snyder DB. Physical and biological effects of sand mining offshore Alabama, USA. J Coast Res. 2004;20: 6–24. doi:10.2112/1551-5036(2004)20\{[\}6:PABEOS]2.0.CO;2

74.	Nairn R, Johnson JA, Hardin D, Michel J. A Biological and Physical Monitoring Program to Evaluate Long-term Impacts from Sand Dredging Operations in the United States Outer Continental Shelf. J Coast Res. 2004;20: 126–137. doi:10.2112/1551-5036(2004)20[126:ABAPMP]2.0.CO;2

75. Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA. Environmental impacts of dredging and other sediment disturbances on corals: A review. Mar Pollut Bull. 2012;64: 1737–1765. doi:10.1016/j.marpolbul.2012.05.008

76. Lindeman KC, Snyder DB. Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging. Fishery Bulletin. 1999;97: 508–525.

77. Jennings DE, Gruber SH, Franks BR, Kessel ST, Robertson AL. Effects of large-scale anthropogenic development on juvenile lemon shark (Negaprion brevirostris) populations of Bimini, Bahamas. Environ Biol Fishes. 2008;83: 369–377. doi:10.1007/s10641-008-9357-3

78. Gilman E, Chaloupka M, Bach P, Fennell H, Hall M, Musyl M, et al. Effect of pelagic longline bait type on species selectivity: a global synthesis of evidence. Rev Fish Biol Fish. 2020;30. doi:10.1007/s11160-020-09612-0

79. Plumlee JD, Wells RJD. Feeding ecology of three coastal shark species in the northwest Gulf of Mexico. Mar Ecol Prog Ser. 2016;550: 163–174. doi:10.3354/meps11723

80. Graham J, Kroetz A, Poulakis G, Scharer R, Carlson J, Lowerre-Barbieri S, et al. Large-scale space use of large juvenile and adult smalltooth sawfish *Pristis pectinata*: implications for management. Endanger Species Res. 2021;44: 45–59. doi:10.3354/esr01088

81. Driggers WB, Campbell MD, Hoffmayer ER, Ingram GW. Feeding chronology of six species of carcharhinid sharks in the western North Atlantic Ocean as inferred from longline capture data. Mar Ecol Prog Ser. 2012;465: 185–192. doi:10.3354/meps09901

Supporting information

S1 Table. Habitat conditions under which each shark species was collected on longline sets. Values are mean with range in parentheses. The mean and range across all longline sets is also provided.

S2 Table. Habitat conditions under which acoustically tagged sharks were detected on the Canaveral Shoals. Detections from offshore reef stations are excluded. Values are mean with range in parentheses.

S3 Table. PERMANOVA test for shark community differences in the longline catch across seasons and depth zones. Variance values estimate the amount of variation in the dataset explained by the factor while SD gives the square root of these values, and thus is in Bray–Curtis units. Pairwise tests of community similarity across seasons are also provided.

S4 Table. PERMANOVA test for shark community differences in Canaveral Array detections across seasons and depth zones. Variance estimates the amount of variation in the dataset explained by the factor while SD gives the square root of these values, and thus is in Bray–Curtis units. Pairwise tests of shark community similarity across seasons are also provided.

S5 Table. PERMANOVA test for shark community differences in Canaveral Array detections across station groupings. Groups include the offshore dredge site, offshore control site, all other offshore shoal stations (>1.5 km from shore), offshore reef stations, and nearshore shoal stations (< 1.5 km from shore).
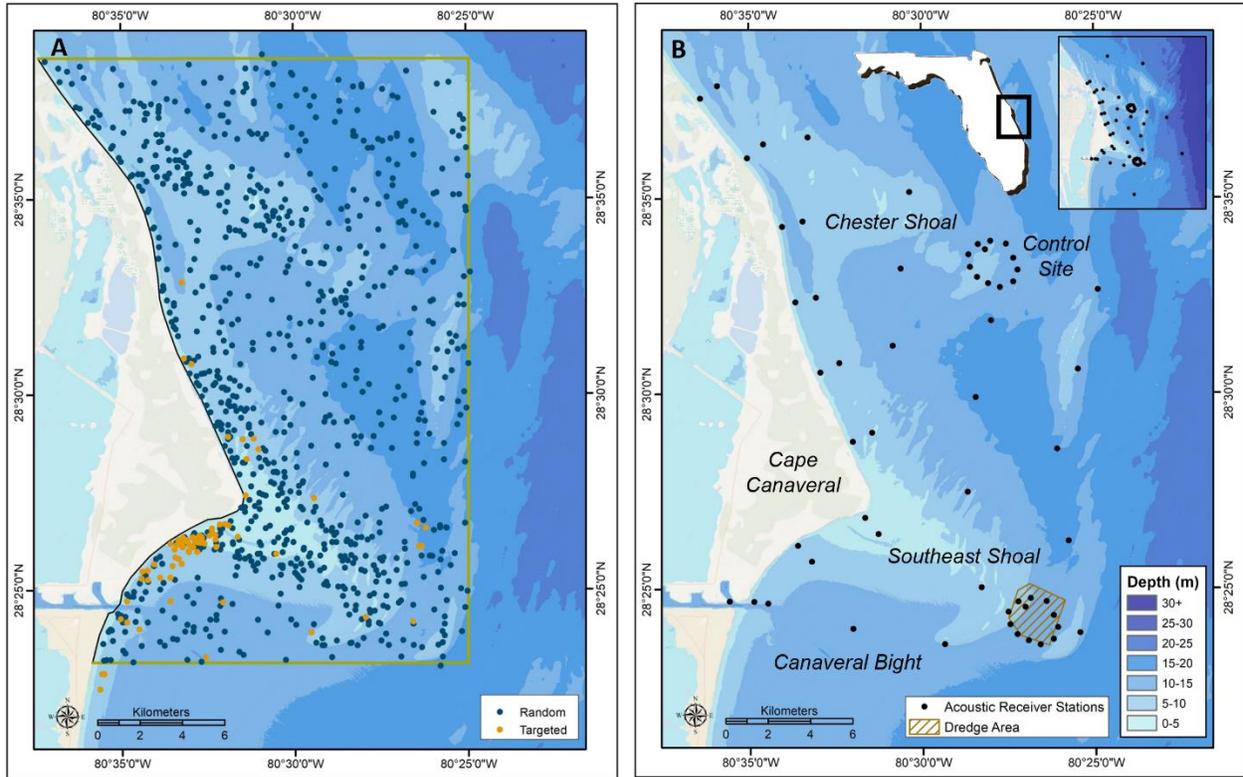
Fig. 1. Canaveral Shoals study area. (A) Locations of all longline sets 2012-2017. (B) Map of acoustic receiver stations 2013-2020 as well as the active sand dredge site and nearby control site. Map B inset includes locations of five reef receiver stations established farther offshore.
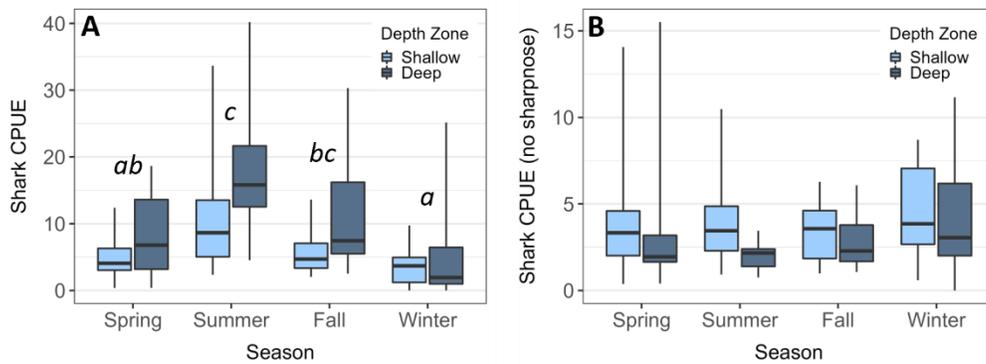

Fig. 2. Boxplots of shark longline CPUE across water depth zones and seasons for (A) all species, and (B) excluding Atlantic sharpnose shark. Horizontal black lines represent the group median, boxes represent the interquartile range, and whiskers represent the full data range. Seasonal differences were only detected for the all-species ANOVA test with pairwise differences denoted with lowercase letters.
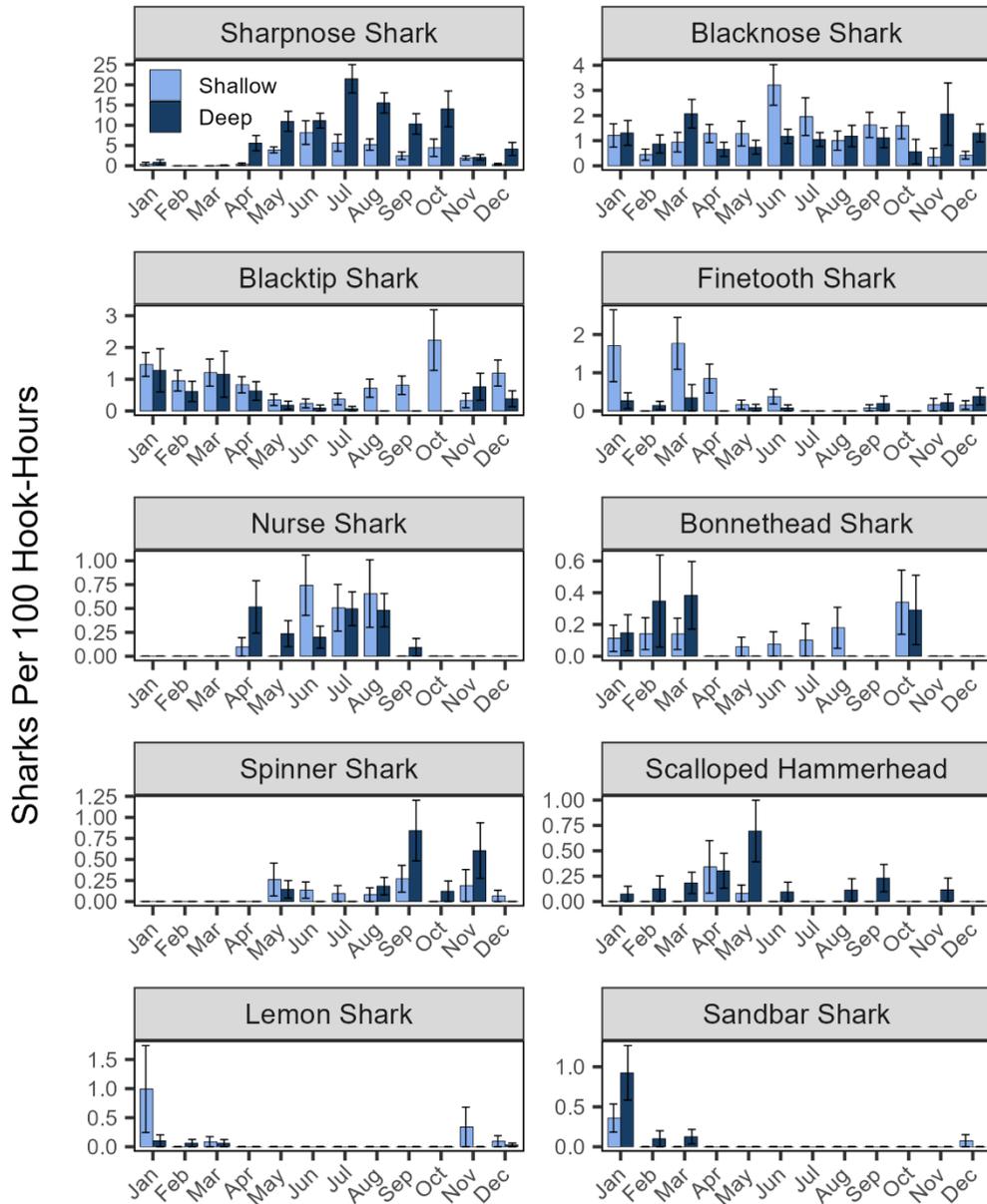
Fig. 3. Longline CPUE (+/- SE) by month and depth zone for ten most common shark species averaged across all five years of the study. Note the differing y-axis scale for each species.
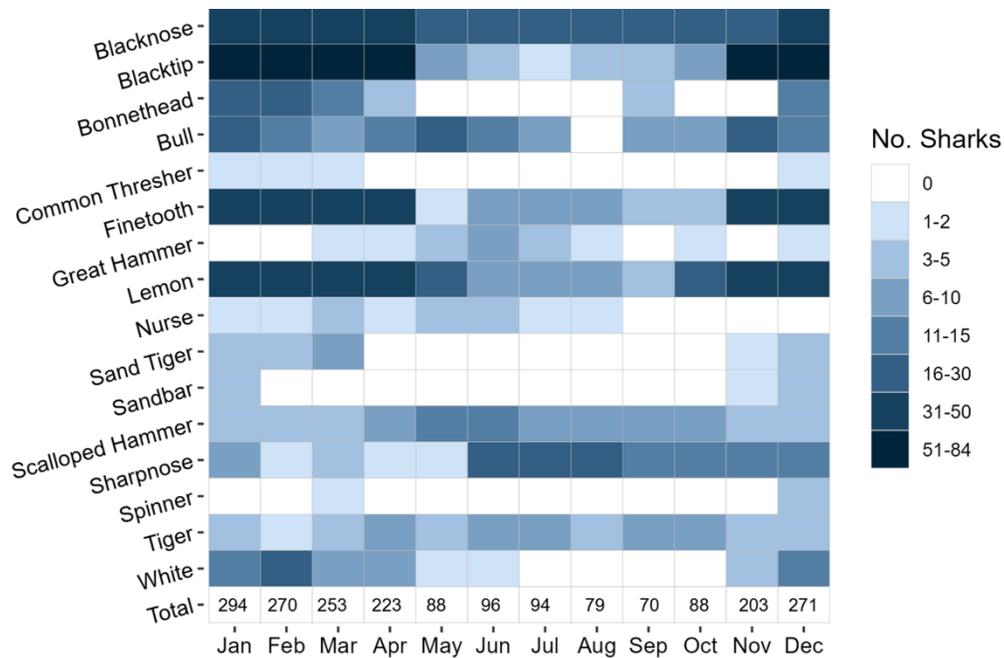
Fig. 4. Number of acoustically-tagged sharks detected in the Canaveral Array, December 2013 – February 2020. The total number of individuals detected in each calendar month is listed in the bottom row.
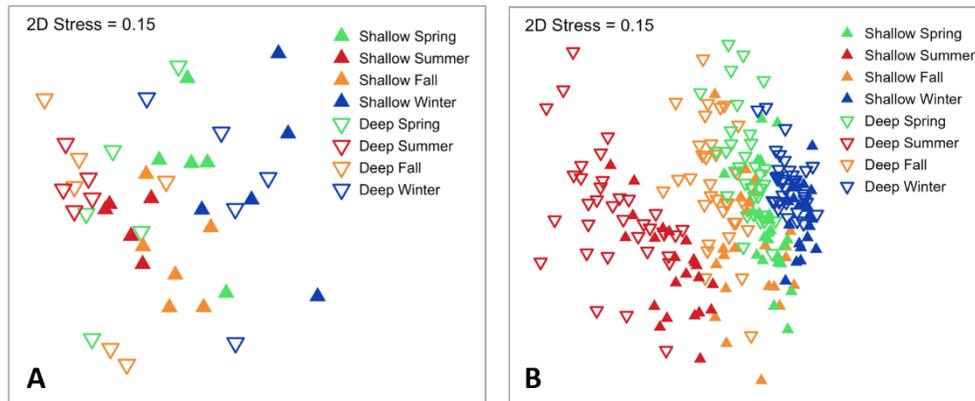

Fig. 5. MDS plots of the shark community observed in (A) longline samples and (B) the Canaveral Array. Points represent the shark community for every combination of depth zone and season, with points closer together having more similar communities. Replicates within each longline group are drawn from each of the five years of the study while those in the Canaveral Array samples are drawn once from each acoustic receiver station.
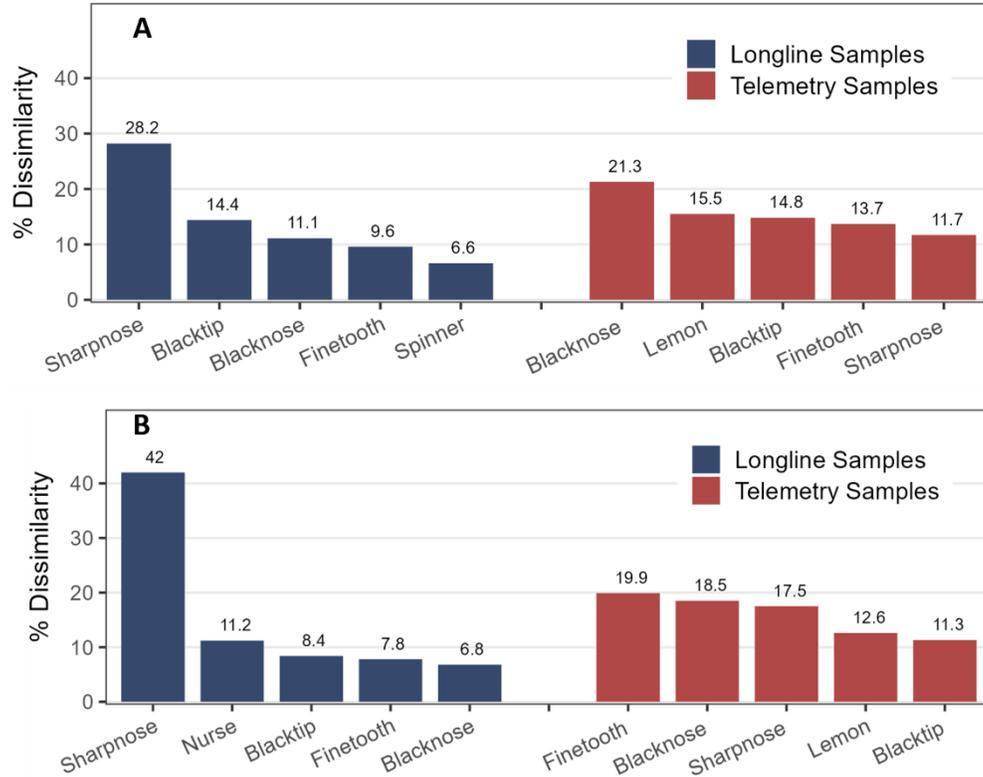
Fig. 6. A SIMPER routine to determine which species contribute most to the dissimilarity (%) in the shark community across (A) Depth Zones and (B) Seasons for longline and telemetry datasets.
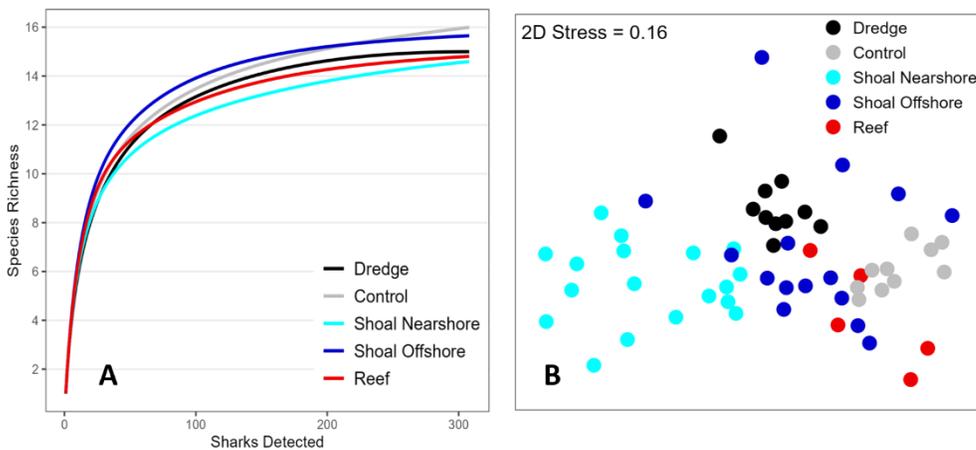
Fig. 7. Shark assemblage comparisons across dredge and control sites, other nearshore and offshore shoal sites, and reefs. (A) Rarefaction curves comparing relative species richness after accounting for uneven numbers of acoustic receivers, and (B) MDS plot of the shark community detected at each receiver station in the Canaveral Array averaged across the study.
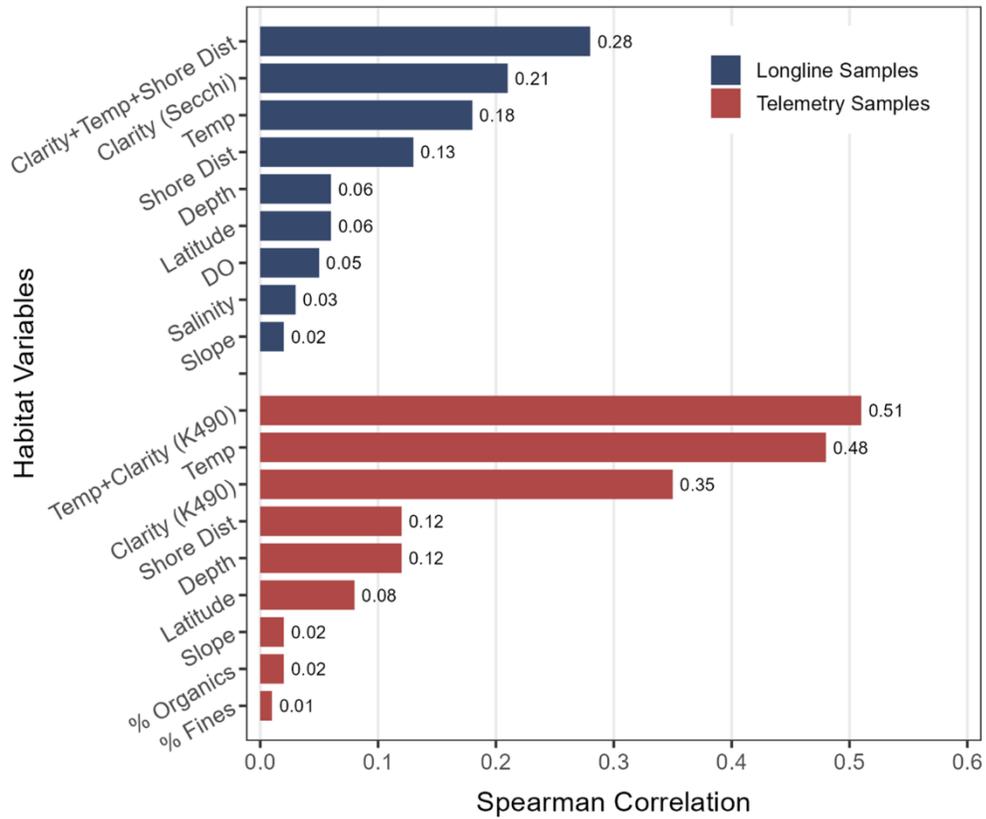
Fig. 8. A BEST procedure to determine which measured habitat variables correlate most strongly with the shark community. Correlation values (Spearman ρs) for the top overall combination plus all individual variables are included.