

1     **Title:** Short-term reef changes in fish community metrics correlate with variability in large shark  
2     occurrence

3

4     **Running Head:** Short-term predator presence

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23      **Abstract**

24      Large predators exert control on lower trophic levels, often influencing long-term  
25      changes in community structure. Many large predators are highly mobile and occur along a  
26      continuum of presence and absence on habitats. In many natural systems, the movement of large  
27      predators through an area has been shown to lead to rapid changes in prey distribution through  
28      trait-mediated behavioral responses. To test whether a similar interaction also occurs for artificial  
29      habitats, we examined how reef fish community metrics (abundance, species richness,  
30      community composition) varied with the presence of a large coastal shark (sand tiger shark,  
31      *Carcharias taurus*). Remotely-operated vehicle surveys of large sharks and reef fishes on  
32      shipwrecks along the North Carolina, USA, continental shelf revealed that short-term shark  
33      presence correlated with changes in reef fish community metrics. Specifically, when sharks were  
34      present, fish species abundance and richness did not differ compared to when sharks were absent.  
35      Finer-scale analyses near sharks revealed similar abundance but elevated species richness  
36      proximate to sharks. We confirmed that this fine-scale pattern of similar abundance but higher  
37      richness near sharks held when the ROV was not in the water by repeating analyses using time-  
38      lapse videos from nearby shipwrecks. The detected differences in fish community metrics in the  
39      presence of sharks correlated with higher numbers of water-column associated species, such as  
40      jacks and barracuda, but lower numbers of benthic-associated species, including seabass and  
41      grouper. These findings suggest that the presence of large predators on artificial structures, as in  
42      natural systems, can drive short-term changes in community structure.

43

44      **Keywords:** artificial reef; elasmobranch; predator ecology; shipwreck; remotely-operated  
45      vehicle

46     **Introduction**

47     Large predators are ecologically important with roles ranging from the maintenance of  
48     biodiversity (Ripple et al. 2014; Dalerum et al. 2008), regulation of prey population size  
49     (Beschta & Ripple, 2009), alteration of prey behavior and habitat use (Heithaus et al. 2007;  
50     Brown et al. 1999; Werner & Peacor, 2003), to limitations of prey productivity and reproduction  
51     (Estes & Duggins, 1995; Creel et al. 2011). Because large predators often occupy upper trophic  
52     levels, they can exert top-down control on lower trophic levels through consumptive and non-  
53     consumptive effects (Ordiz et al. 2013; Baum & Worm, 2009). For example, large predators  
54     consume prey items, which can affect diversity and species behavior (Johnson et al. 2007;  
55     Johnson & VanDerWal, 2009; Pace et al. 1999; Barley et al. 2017) and stabilize prey oscillations  
56     (Morozov et al. 2012) within food webs. Even predation risk associated with predator presence  
57     can initiate behavior-mediated responses in lower trophic levels that can modify mesopredator  
58     abundance and distribution (Ritchie & Johnson, 2009; Preisser et al. 2005). Despite playing  
59     fundamental roles in ecosystems and their food webs, large predators are often highly mobile or  
60     migratory (Brown et al. 1996; Haskell et al., 2002; Harestad & Bunnell, 1979).

61     Many examinations of how predator presence versus absence affects communities, food  
62     webs, and ecosystems have focused on broad spatial or extended temporal scales (Mittelbach et  
63     al. 1995; Whitehead et al. 2008; Menge et al. 2016; Schultz et al. 2016). The majority of  
64     opportunities to examine large predator occurrence is through the lens of predator removal or  
65     loss (e.g. killer whale, sea otter (Estes & Duggins, 1995); freshwater piscivorous fish (Browne &  
66     Lutz, 2010; Ripple et al. 2014)). In general, the effects of predator decline and removal in food  
67     webs manifest over long time periods, as lower trophic levels gradually adjust to the absence of  
68     the largest, most functionally important individuals (Dulvy et al. 2017). This approach compares

69 community structure and function within healthy ecosystems containing predators to those  
70 without predators or with low predator densities, often attributable to overhunting, overfishing,  
71 or habitat degradation. For example, long-term fence exclusion of dingoes, a large terrestrial  
72 Australian predator, established an area where dingoes are functionally extinct and led to  
73 pronounced changes in sheep distributions (Allen & West, 2013). Dingo absence also triggered  
74 shifts in avian communities, including reduced species richness, whereas dingo presence  
75 maintained avian diversity, largely through regulation of mesopredators and herbivores (Rees et  
76 al. 2019), ultimately improving ecosystem resiliency (Letnic et al. 2009; Johnson et al. 2007). In  
77 marine systems, the presence and absence of sharks have been associated with long term changes  
78 in the distribution of sea turtles, dugongs, and seagrass as a result of predator avoidance and risk-  
79 based foraging (Burkholder et al. 2013, Wirsing et al. 2007).

80 Predator presence also affects lower trophic levels in the short-term. In natural systems,  
81 the movement of large predators through an area leads to rapid changes in prey distribution  
82 through behavior responses (Lima & Dill, 1990; Schmitz et al. 1997). Predator presence, for  
83 example, can alter prey species distribution as evidenced through colonization patterns of marsh  
84 decapod crustaceans (Dorn et al. 2006), seagrass habitat use of Australian salmon prey species  
85 (Smith et al. 2011), and vertical migration of copepods (Bollens & Frost, 1989). Studies  
86 explicitly and repeatedly support the theory that large predators relate to community structure in  
87 natural ecosystems (Estes et al. 2013; Myers et al. 2007). Despite the proliferation of examples in  
88 natural systems of predator presence being associated with variations in lower trophic levels,  
89 whether this pattern holds on artificial or human-made systems is less well studied. To test  
90 whether large predators exert short-term influences on communities requires an ecosystem where  
91 large predators exhibit both presence and absence over short temporal and spatial scales.

92        Here, we test how the short-term presence or absence of a large predator, the sand tiger  
93        shark (*Carcharias taurus*), correlates to the reef fish community metrics observed on artificial  
94        habitats (shipwrecks) off the southeastern US continental shelf. We specifically tested whether:  
95        1) Reef fish abundance and species richness differ when sand tiger sharks are present versus  
96        absent; 2) Reef fish abundance and species richness differ immediately surrounding sand tiger  
97        sharks versus farther from sharks; and 3) Reef fish community composition differs with sand  
98        tiger shark presence versus absence.

99

## 100 **Materials and Methods**

### 101 ***Model predator selection***

102        We selected a large coastal shark species, the sand tiger shark (*Carcharias taurus*), as a  
103        model large predator because they commonly aggregate on shipwrecks off the coast of North  
104        Carolina (NC), USA, the geographic area of our study. While the reason why sand tiger sharks  
105        occupy these shipwrecks remains undocumented, sand tiger sharks likely use the shipwrecks as  
106        “rest-stops” along their seasonal migration or, perhaps, as year-round habitat (Teter et al. 2015;  
107        Jorgensen et al. 2009). More recently, evidence of site fidelity of sand tiger sharks to the same or  
108        nearby shipwrecks has been documented (Paxton et al. 2019). Despite their affinity for  
109        shipwrecks, sand tiger shark abundances on shipwrecks fluctuate and a sand tiger can be present  
110        on a shipwreck one day or hour and absent the next. The highly mobile nature of sand tiger  
111        sharks, coupled with their alternating presence and absence on shipwrecks (Teter et al. 2015;  
112        Haulsee et al. 2018; Kneebone et al. 2012; Peterson et al. 2017) provides an opportunity to test  
113        the short-term or fine-scale association of a large predator and the reef fish community  
114        occupying coastal NC shipwrecks. Also, while other large predators do occur along the coast of

115 NC, sand tiger sharks are the largest fish predator that can be commonly observed on shipwrecks  
116 off NC (Paxton et al. 2017), making them the ideal model predator for this study since other  
117 large predators like white sharks (*Carcharodon carcharias*), sandbar sharks (*Carcharhinus*  
118 *plumbeus*), and nurse sharks (*Ginglymostoma cirratum*) occur infrequently on NC shipwrecks  
119 (Paxton, personal observation).

120

121 ***Remotely-operated vehicle surveys***

122 *Site selection*

123 Remotely-operated vehicle (ROV) surveys were conducted at seven shipwrecks located on  
124 the continental shelf of NC (Figure 1A; Table S1). These shipwrecks, which extend from the  
125 southwest to the northwest of Cape Lookout, NC, were selected because they are located in an  
126 area where sand tiger sharks are known to occur (Haulsee et al. 2016; Teter et al. 2015). The  
127 shipwrecks are 25-40 m deep, rest on sand, and all sank during 1942, except for one that sank in  
128 1918. These shipwrecks also provide an opportunity to understand how artificial habitats, such as  
129 artificial reefs, that are often installed to enhance, supplement, or restore fish habitat (Becker et  
130 al. 2018) may function for sharks and reef fish in the future.

131

132 *Data collection*

133 Each shipwreck was surveyed once between July and September 2018 using a Teledyne  
134 Benthos Stingray ROV. The survey period likely coincided with the seasonal migration period  
135 when male sand tigers are thought to move into areas off the NC coast (Teter et al. 2015),  
136 although it has been hypothesized that some sand tiger sharks may reside off NC year-round.

137 After the ROV descended and located a particular shipwreck, we completed a 45 to 60-minute  
138 survey of the fish community with the ROV facing the shipwreck and remaining down current of  
139 the wreck, to avoid entanglement of the ROV tether in the wreck. If the ROV pilot observed  
140 sharks via the topside video monitor, then the pilot steered the ROV toward the sharks, if  
141 possible, to provide a closer glimpse of the fish community near the shark. The ROV field of  
142 view was consistent across all surveys. Ethics approval was not required because this was an  
143 observational study involving visual identification and counts of fish.

144 During the shipwreck surveys, the ROV position was tracked using a dual Hemisphere  
145 GPS that recorded latitude, longitude, and heading, and a Tracklink 1505B ultra-short baseline  
146 acoustic tracking system. The position of the survey vessel and ROV were logged in Hypack  
147 (Xylem Inc. 2015). During surveys, Hypack also displayed the position of the ROV in real-time  
148 to assist in visually piloting the ROV around the shipwrecks. We also utilized multibeam  
149 bathymetry collected previously at the seven shipwrecks to aide in ROV navigation relative to  
150 the shipwreck structures. The umbilical transmitted ROV video from the ROV to the survey  
151 vessel during surveys, and this video footage was recorded by an HD recorder. On the front of  
152 the ROV, parallel with the ROV video camera, we mounted two GoPro Hero 6 video cameras  
153 (GoPro, USA), one as a primary video camera, and one as a backup video camera. The GoPro  
154 recorded higher quality (2.7K primary GoPro and 1080p backup GoPro) video than the onboard  
155 ROV video camera. We used videos collected by the primary GoPro with the highest video  
156 resolution to assess fish communities.

157 For each 45 to 60 minute video for the seven shipwrecks, we first recorded whether sand  
158 tiger sharks were present or absent at any point in the ROV dive. Second, we processed clips of  
159 video from each shipwreck survey. Specifically, we processed one full minute of video every

160 four minutes (e.g. three minutes between the end of one clip and the start of the next clip). In  
161 total, we processed 70 one-minute video clips, ranging from 6 to 17 clips per dive across the  
162 shipwrecks. In each video clip, we recorded whether sand tiger sharks were present or absent to  
163 help differentiate whether sand tigers were present on the wreck at all during the survey versus  
164 whether sand tigers were present in the one-minute processed video clips. We identified fish to  
165 the lowest taxonomic level possible and recorded their approximate location relative to the shark.  
166 We counted the maximum number (maxN) of each fish species visible within any frame during  
167 each one-minute clip. Large schools of fish were counted using the group-counting method in  
168 which we counted individuals within an arbitrarily drawn box and then multiplied by the number  
169 of boxes that fit within the frame (Labrosse et al. 2002). We excluded the portions of the video  
170 when the ROV ascended or descended from processing. Fish that were out of focus or otherwise  
171 unidentifiable were counted, but their species was recorded as “unknown fish.”

172

### 173 *Data analyses*

174 Statistical analyses were conducted in R version 3.5.3 (R Development Core Team, 2019)  
175 using an alpha value of 0.05. We first used generalized linear mixed models (GLMM) (Bolker et  
176 al. 2009) to model the relationship between a) reef fish abundance and shark occurrence and b)  
177 reef fish species richness and shark occurrence. The response variable reef fish abundance was  
178 the total fish abundance in each one-minute video clip. Similarly, the response variable for  
179 species richness was the total species richness in each one-minute clip. Abundance and species  
180 richness from each clip were treated as individual samples or replicates. Given the elapsed time  
181 between these one-minute clips, it is unlikely that we documented the same fish multiple times.  
182 Both models included shark occurrence (presence vs. absence) within an entire ROV survey as a

183 fixed effect. For example, if a shark was not observed during the entire duration of a dive at a  
184 particular shipwreck, then we designated the shipwreck and all ROV videos from that particular  
185 shipwreck survey as “shark absent.” Alternatively, if we spotted a shark or multiple sharks  
186 anywhere during any portion of the ROV dive, then we recorded the corresponding shipwreck  
187 and collected videos as “shark present” even if a shark was not immediately visible in a  
188 particular one-minute clip. The shipwreck was included in the GLMM as a random effect to help  
189 control for potential sources of variation in counts among the shipwrecks due to differing  
190 shipwreck characteristics (e.g., area, volume, vertical relief) not directly accounted for. We fit  
191 the models with the ‘glmmADMB’ package using Laplace parameter estimations (Fournier et al.  
192 2012). We used a negative-binomial error distribution with a log link to allow for overdispersion  
193 of the reef fish abundance and species richness counts. We used likelihood ratio tests (LRTs)  
194 between the full model and a model without the fixed effect for shark presence to generate a *p*-  
195 value for the fixed effect of shark presence. We then examined the fixed log-effects estimates to  
196 determine the magnitude and significance of changes in reef fish abundance with shark presence  
197 versus absence.

198 Second, we used GLMMs to again model the relationship between shark occurrence and  
199 response variables (reef fish abundance and reef fish species richness) but this time using a fixed  
200 effect called “shark visibility” that allowed a finer-scale analysis of the effect of shark  
201 occurrence. For GLMM models, we used reef fish abundances from only the video clips  
202 recorded on shipwrecks where we observed sharks at any point during the entire ROV survey.  
203 This approach allowed us to test for a response of reef fish abundance and species richness near a  
204 shark when a shark was visible in the clip versus farther away when a shark was not visible. We  
205 included shark visibility as a fixed effect and shipwreck as a random effect. As above, we fit the

206 GLMMs with negative-binomial error distributions and assessed evidence for patterns predicted  
207 by shark visibility with LRTs.

208 To examine whether shark presence influenced fish community composition, we used  
209 multivariate analyses, including nonmetric multidimensional scaling (nMDS) analysis,  
210 permutational analysis of dispersion (PERMDISP), permutational analysis of variance  
211 (PERMANOVA), and indicator species analysis. We performed all multivariate tests on square-  
212 root transformed reef fish species abundance data from each one-minute video clip within the  
213 ‘vegan’ package (Oksanen et al. 2015) with an alpha value of 0.05. We first used PERMANOVA  
214 (Anderson, 2001) with Bray-Curtis distances and 1,000 permutations to test whether fish  
215 community composition varied with shark presence versus absence on shipwrecks. Second,  
216 PERMDISP, a distance-based test for homogeneity of multivariate dispersion (Anderson, 2006)  
217 helped interpret PERMANOVA results by determining whether multivariate dispersion differed  
218 with shark presence versus absence. Together, PERMANOVA and PERMDISP permitted an  
219 evaluation of whether reef fish communities differed when sharks were present versus absent.  
220 Third, we performed nMDS with Bray-Curtis distances to visually summarize patterns in the  
221 structure of the reef fish community with and without sharks. The nMDS mapped samples into  
222 ordination space using ecological distances between samples ordered by rank. A Shepard  
223 diagram confirmed linearity between ordination distances and Bray-Curtis distance. Biplots  
224 illustrated the relationships among samples in ordination space with samples colored by shark  
225 presence/absence and superimposed ellipses indicating 50% confidence intervals. Fourth, we  
226 performed an indicator species analysis within the ‘indicspecies’ package (De Caceres &  
227 Legendre, 2009) to identify which reef fish species correlated with the presence or absence of

228 sharks on a shipwreck. The resulting indicator values represent the level of association between  
229 particular species and whether sharks are present or absent.

230

231 ***Time-lapse video surveys***

232 ***Site selection***

233 To confirm patterns of reef fish abundance and species richness with shark visibility  
234 when the ROV was not in the water, we repeated the shark visibility analyses using previously  
235 collected stationary time-lapse videos from two nearby shipwrecks (Figure 1B; Table S2). The  
236 nearby shipwrecks are two artificial reefs containing intentionally-sunk vessels located on soft  
237 sediment bottom in the same geographic vicinity and depth as the seven shipwrecks surveyed  
238 with the ROV. On each of the two additional shipwrecks, video footage collection occurred  
239 during three sampling periods over five months in 2016. The artificial reef *Spar* sampling  
240 spanned one to two weeks during the following periods: 1) November 2015; 2) January 2016;  
241 and 3) April 2016. The artificial reef *Aeolus* was sampled during the April 2016 period. The  
242 stationary camera field of view was consistent among the surveys, as the cameras were placed at  
243 the same location on each individual shipwreck.

244

245 ***Data collection***

246 Time-lapse videos were recorded at each of the two wrecks for 20 seconds every 20  
247 minutes using a stationary GoPro Hero 3+Black video camera (GoPro, USA) with  
248 intervalometers mounted in a cylindrical housing with dome port (Sexton Co, Oregon, USA). A  
249 total of 547 videos were processed, 332 from the *Spar*, and 215 from the *Aeolus*. In each of the  
250 stationary 20-second videos, the video analyst noted the presence or absence of sand tigers and

251 identified all visible reef fish (Pierce et al. 2018) and recorded their position relative to the shark,  
252 as well as the sharks' position relative to the reef. The analyst also counted the maximum  
253 number (maxN) of each fish species visible during each one-minute clip. The group-counting  
254 method was used to count large schools of fish (Labrosse et al. 2002), as detailed above.  
255 Additionally, for all 20-second clips within 60 minutes, we recorded whether a sand tiger shark  
256 was present in any of the 20-second clips.

257

#### 258 *Data analyses*

259 Analyses were conducted in R to test effects of shark presence on species abundance and  
260 richness. To ensure that our analytical approach matched the approach from the ROV videos as  
261 closely as possible, we used the subset of 20-second video clips from clock hours where sharks  
262 were present. We categorized each 20-second video clip as either having a shark visible or not,  
263 so using video clips where sharks were present enabled us to test whether the changes in  
264 communities proximal to versus farther away from sharks that we detected with ROV videos  
265 were preserved in the time-lapse video dataset. To conduct this test, we fit two GLMMs, one for  
266 the response variable reef fish abundance and one for the response variable reef fish species  
267 richness. Both were fit and assessed using the 'glmmADMB' package and negative-binomial  
268 error distribution, as described above (Fournier et al. 2012). The models included shark visibility  
269 as a fixed effect and the shipwreck as a random effect.

270

#### 271 **Results**

272 Reef fish abundance did not differ with shark presence or absence on shipwrecks  
273 surveyed with the ROV (Figure 2A;  $p = 0.64$ ; Table S3). On the three shipwrecks with sharks,

274 reef fish abundance was similar in the immediate vicinity of (several meters) and farther away  
275 from sharks (Figure 2B;  $p = 0.44$ ; Table S3). We confirmed that the lack of a pattern near sharks  
276 held when the ROV was not in the water by using time-lapse videos (Figure 2C;  $p = 0.17$ ; Table  
277 S3). Reef fish species richness was marginally, but not significantly lower, on shipwrecks with  
278 than without sharks (Figure 3A;  $p = 0.07$ ). On shipwrecks with sharks, however, there was a  
279 higher species richness near sharks than farther away from sharks (Figure 3B;  $p = 0.04$ ), and fish  
280 were observed swimming behind, above, under, or in sync with the predator movements. We  
281 confirmed that the pattern of elevated species richness near sharks held when the ROV was not  
282 in the water by using stationary, time-lapse videos (Figure 3C;  $p < 0.0001$ ).

283           Reef fish community composition differed on shipwrecks with and without sharks that  
284 were surveyed with the ROV (Figure 4; PERMANOVA  $p < 0.001$ ), and this was attributed to  
285 greater dispersion in community composition when sharks were absent than present (PERMDISP  
286  $p = 0.02$ ). These differences in community composition with shark presence versus absence  
287 correlated with prevalence of water-column associated species, such as banded rudderfish  
288 (*Seriola zonata*, indicator value = 0.36,  $p = 0.04$ ) and barracuda (*Sphyraena barracuda*, indicator  
289 value = 0.58,  $p = 0.008$ ), on shipwrecks with sharks. In contrast, benthic-associated species, like  
290 black sea bass (*Centropristes striata*, indicator value = 0.62,  $p = 0.004$ ) and gag grouper  
291 (*Myceteroperca microlepsis*, indicator value = 0.53,  $p = 0.008$ ) occurred in lower numbers on  
292 sites with sharks, instead frequenting shipwrecks without sharks.

293

## 294 **Discussion**

295           Our study provides evidence that large predator presence correlates with fine-scale  
296 changes in reef fish community metrics on artificial habitats, as in natural habitats. While reef

297 fish abundance did not vary with large predator presence, we found that species richness differed  
298 based on proximity to the large predator. Community composition varied with large predator  
299 presence versus absence, with water-column associated fish species indicative of large predator  
300 presence and benthic-associated species more often found when the large predator was absent.

301 Our finding that reef fish abundance did not vary with large predator presence but that  
302 species richness was lower when sharks were present is inconsistent with previous studies. For  
303 example, mesopredator abundance often positively correlates with predator presence (Masi et al.  
304 2018; Ritchie & Johnson, 2009). We posit that this difference between our findings and those  
305 from previous research may relate to the scale of our study. In particular, demonstrations of  
306 increased biodiversity around large predators are often over broad spatial scales (Ripple et al.  
307 2014; Dalerum et al. 2008), whereas our video collection occurred over short periods (45-60  
308 min) and small areas (shipwrecks). Therefore, our findings suggest that abundance, and likely by  
309 extension - species richness - may be spatially or temporally dependent and thus the response of  
310 fish community metrics to trophic interactions, such as predator presence, may differ across fine  
311 and broad scales.

312 The pattern that we observed of similar abundance but elevated species richness near  
313 sharks in both ROV and time-lapse video datasets supports previous food webs literature  
314 documenting that animals respond to predation risk in real-time and utilize avoidance and other  
315 behavioral strategies to reduce predator encounters (Burkholder et al. 2013; Lima & Dill, 1990;  
316 Madin et al. 2012; Wirsing et al. 2007; Gallagher et al. 2017). For example, even though the  
317 constant threat of predation can promote a heightened sensitivity in prey, the levels of predation  
318 risk experienced are largely species-specific and can depend on fine-scale changes in predator  
319 behavior (Schmidt & Kuijper, 2015; Hamilton, 1971; Stankowich, 2003; Creel et al. 2019).

320 Additionally, predation risk has a spatial component because closer proximity to large predators  
321 elevates risk. In our study, however, we observed species close to the large predators swimming  
322 behind, under, and in sync with the predator movements and we observed a greater number of  
323 species close to the predators. Finding more species near the predator may, at first, seem  
324 counterintuitive, but prey responses could be attributed to rapid, strategic maneuvers of prey  
325 species reacting to subtle changes in large predator movements, the benefits of polyspecific  
326 associations (Au, 1991), or reduced predation risks associated with forming multispecies groups  
327 (Scott et al. 2012). Further, this finding suggests that there may be a “halo-of-influence” around  
328 large predators, where elevated species richness occurs, driven largely by species that frequently  
329 associate with the predator.

330 The notion that a halo-of-influence may exist around large predators is further supported  
331 by our finding that reef fish community composition differed with and without sharks. When  
332 sharks were absent, the fish community exhibited higher multivariate dispersion, which we  
333 interpret to mean that the community composition was more variable. In contrast, when sharks  
334 were present, community composition was more consistent. When we examined species driving  
335 community composition patterns, we discovered that the dissimilarities in fish community  
336 composition with sharks were largely attributable to how benthic and water-column associated  
337 fish species and their trophic roles correlated with or without sharks.

338 The large reef-associated fish species that exhibited an association with reefs with sharks  
339 (barracuda, banded rudderfish) or without sharks (gag grouper, black sea bass) occupy high  
340 trophic levels but have smaller body sizes than sand tiger sharks. The location of fish within the  
341 water column relates to their feeding methods and diet (Young et al. 2015), which may explain  
342 the different association of water-column versus bottom-associated fishes to predators.

343 Barracuda and banded rudderfish consume prey in the water-column, whereas gag grouper and  
344 black seabass are benthic feeders. Sand tiger sharks are nocturnal feeders that have not been  
345 found to consume barracuda, banded rudderfish, gag grouper, or black seabass. Instead, sand  
346 tiger sharks often consume smaller-bodied prey. For example, sand tiger sharks gut content  
347 analyses in the Chesapeake Bight region, which is north of our study area, demonstrate that this  
348 shark preys upon teleosts (65% of diet), elasmobranchs (35% of diet), crustaceans (<0.1%),  
349 unidentified plant material (<0.1%), and molluscs (<0.1%) (Gelsleichter et al. 1999). The  
350 teleost prey items include water-column associated species, such as Atlantic menhaden  
351 (*Brevoortia tyrannus*) and bluefish (*Pomatomus saltatrix*), but also benthic-associated species,  
352 such as sea robin (*Prionotus carolinus*) and summer flounder (*Paralichthys dentatus*)  
353 (Gelsleichter et al. 1999). Elasmobranch prey include skates (Rajidae) and their eggs, as well as  
354 small sharks (Gelsleichter et al. 1999). As such, the four reef-associated predatory fish species  
355 (barracuda, banded rudderfish, gag grouper, black seabass) whose abundances varied with shark  
356 presence should not experience consumptive predation pressure from sand tiger sharks. We posit  
357 that the differential presence of predatory fish species in the presence or absence of sharks is  
358 likely not attributable to consumptive pressure, but instead that the ability of reef-associated  
359 fishes to optimize success in their differing modes of foraging (Au, 1991). It is also possible that  
360 water-column associated predators may perceive sharks as a threat or as competitors for prey.

361       Although we do not understand the exact mechanism, we suggest that benthic predators  
362 can maximize foraging success in the absence of sharks, whereas water-column predators may  
363 achieve higher foraging success in the presence of sharks. This likely relates to the landscape of  
364 fear and energy paradigms between predator and prey species that, respectively, dictate tradeoffs  
365 in optimizing survival and energetic costs (Gallagher et al. 2017). Banded rudderfish are

366 commonly referred to as “pilot fish,” reflecting their tendency to closely follow sharks and other  
367 large predators (Kells & Carpenter, 2011), which supports the notion that water-column  
368 associated species may reap foraging benefits from close associations with sharks. Also, we  
369 observed densely packed schools of baitfish with shark presence, and schooling formations could  
370 dilute predation pressure from sharks (Hamilton, 1971; Stankowich, 2003; Turner & Pitcher,  
371 1986).

372         Sharks likely resided on the shipwrecks before our ROV descended and began collecting  
373 video footage, but we do not know how long the sharks were present before our ROV surveys.  
374 We tried to control for the amount of time the shark was present by analyzing the time-lapse  
375 videos. Since the time-lapse cameras were stationary, they likely recorded footage closer to the  
376 moment that the sharks arrived on the wrecks. If, however, sharks and reef fish cohabited reefs,  
377 the reef fish response that we documented may not represent the immediate response of reef fish  
378 to the sharks but rather a post-arrival response. Future studies should monitor the habitat and  
379 conduct associated surveys before a shark arrives, at the moment of arrival, at intervals while the  
380 shark is present, and immediately after a shark leaves. It is also possible that fish community  
381 metrics may respond differently to first-time predator visits versus more frequent predator visits.  
382 While we did not observe this directly, predation pressure on younger sharks from more mature  
383 conspecifics, as has been demonstrated in another aggregating shark species, the lemon shark  
384 (*Negaprion brevirostris*; Guttridge et al. 2009) or complex social dynamics among predators  
385 (Guttridge et al. 2012; Haulsee et al. 2016) may relate to reef fish community metrics.  
386 Additionally, since the ROV video and time-lapse video footage demonstrated the same pattern  
387 in reef fish community metrics with shark presence, our findings were unlikely to have been  
388 influenced by the presence of the ROV in the water. It would be worthwhile to test whether these

389 patterns hold with diver-conducted surveys and whether a predator correction factor may be  
390 needed when for reef fish surveys when fish predators or human (diver) predators are present.  
391 We acknowledge that other rare predators may be present on these reefs and also relate to reef  
392 fish distributions. Future efforts should focus on teasing apart the relative influence of different  
393 large predators on reef fish.

394 Our study confirms that large predator occurrence not only relates to changes in  
395 community metrics in natural habitats but also in artificial habitats. In marine environments,  
396 artificial habitats, such as artificial reefs, are commonly deployed to enhance or supplement  
397 existing natural habitat or to restore degraded natural habitat (Becker et al. 2018). In this context,  
398 artificial reefs are intended to mimic functions of natural habitats. Whether artificial reefs  
399 provide functions similar to natural reefs is a topic of debate. It has been demonstrated, for  
400 example, that artificial reefs have different trophic structures than natural reefs (Burt et al. 2009;  
401 Simon et al. 2013) and can function differently than natural reefs by facilitating not only the  
402 spread of invasive species (Dafforn et al. 2012; Langhamer, 2012) but also the likely movement  
403 of tropical fish poleward (Paxton et al. 2019). Other studies, such as a meta-analysis of fish  
404 community metrics on artificial reefs relative to natural reefs, reveal performance similarities  
405 between these two reef types (Paxton et al. 2020). Our demonstration that large predator  
406 presence correlates with fine-scale changes in reef fish community metrics on artificial habitats,  
407 as in natural habitats, reveals that artificial habitats can provide similar ecosystem properties to  
408 natural habitats, increasing our understanding of how these novel habitats function ecologically  
409 within the context of food webs.

410 Our findings reveal that the presence of sand tiger sharks is associated with variations in  
411 reef fish community metrics. Specifically, elevated species richness occurred within a “halo of

412 influence" around the large predator, and community composition differed on reefs with and  
413 without sharks. The differences in community composition linked to species-specific responses  
414 to shark presence, where pelagic predatory fish associated with sharks but bottom-associated reef  
415 fish predators did not. Our study supports previous research on the role of large predators in  
416 structuring communities (i.e. Mittelbach et al. 1995, Myers et al. 2007) but also adds to the body  
417 of literature on predator ecology by providing evidence of short-term influences of a large  
418 predator on reef fish communities occupying artificial habitats.

419

## 420 **Acknowledgments**

421 We thank E. Ebert, C. Blawas, D. Day, R. Purifory, crew from Olympus Dive Center, and  
422 the UNCW Undersea Vehicles Program, for assistance with ROV surveys. For the time-lapse  
423 video surveys, we thank G. Safrit G. Sorg, H. Lemoine, R. Rosemond, J. Fleming, T. Courtney,  
424 M. Kenworthy, A. Poray, D. Keller, I. Kroll, C. Hamilton, J. Hughes, J. Bouton, T. Dodson, J.  
425 Purifoy, S. Davis, C. Lewis, E. Kromka, E. Ebert, K. Egan, J. Vander Pluym, B. Teer, B. Degan,  
426 J. Hackney, R. Muñoz, D.W. Freshwater, K. Johns, G. Compeau, J. Styron, D. Wells, S. Hall, M.  
427 Dionesotes, L. Bullock, A. Pickett, C. Marion, I. Conti-Jerpe, E. Weston, M. Wooster, J.  
428 McCord, D. Sybert, R. Purifoy and crew from Olympus Dive Center, T. Leonard and crew from  
429 Discovery Diving for diving and boating assistance. We thank Y. Azevedo, P. Oliviera, A.  
430 Requarth, L. Revels, S. Richardson, D. Rouse, T. Urugant, and K. Wiedbusch for assistance with  
431 time-lapse video processing. We thank R. Noble for mentorship and guidance of CB during the  
432 UNC IE Semester and as the chair of CB's honor's thesis committee. ABP was supported by a  
433 NSF Graduate Research Fellowship awarded under grant no. DGE-1144081, the P.E.O.  
434 Foundation, and the South-East Zoo Alliance for Reproduction & Conservation. The time-lapse

435 component of this research was supported by BOEM under cooperative agreement  
436 M13AC00006. The ROV component of this research was supported by funding from the North  
437 Carolina Aquarium Society, SeaWorld and Busch Gardens Conservation Fund, and NC Coastal  
438 Recreational Fishing License Grant (#6446). We also thank A. McDowell and L. Penfold for  
439 assistance in research funding acquisition. We thank R. Muñoz, M. Burton, J. Christensen, G.  
440 Piniak, C. Layman, and an anonymous reviewer for thoughtful feedback on this manuscript.

441

#### 442 **Author Contributions**

443 ABP conceptualized the ROV research. ABP and JCT conceptualized the time-lapse  
444 video research. ABP and JCT conducted ROV fieldwork. ABP, JCT, and RVV conducted  
445 fieldwork for time-lapse videos. CB processed ROV videos. RVV and ABP processed time-lapse  
446 videos. ABP and CB analyzed the data. CB and ABP wrote the manuscript. All authors discussed  
447 and interpreted the results and edited the manuscript. The views and conclusions contained in  
448 this document are those of the authors and should not be interpreted as representing the opinions  
449 or policies of the US Government, nor does mention of trade names or commercial products  
450 constitute endorsement or recommendation for use.

451

#### 452 **Data Availability**

453 Data are archived in Dryad Digital Repository (xxxx).

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456 **References**

457 Allen, B., West, P., 2013. Influence of dingoes on sheep distribution in Australia. *Australian*  
458 *Veterinary Journal*, 91(7), 261–267. doi: 10.1111/avj.12075

459 Anderson, M. J., 2001). A new method for non-parametric multivariate analysis of variance.  
460 *Aust. Ecology*. 26, 32–46.

461 Anderson, M. J., 2006). Distance-based tests for homogeneity of multivariate dispersions.  
462 *Biometrics* 62, 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.

463 Au, D. W., 1991). Polyspecific nature of tuna schools: shark, dolphin, and seabird associates.  
464 *Fishery Bulletin*, 89(3), 343-354. <https://swfsc.noaa.gov/publications/CR/1991/9104.PDF>

465 Barley, S. C., Meekan, M. G., Meeuwig, J. J., 2017). Species diversity, abundance, biomass, size  
466 and trophic structure of fish on coral reefs in relation to shark abundance. *Marine Ecology  
467 Progress Series*, 565, 163-179. <https://doi.org/10.3354/meps11981>

468 Baum, J. K., Worm, B., 2009). Cascading top-down effects of changing oceanic predator  
469 abundances. *Journal of Animal Ecology*, 78(4), 699-714. doi: 10.1111/j.1365-  
470 2656.2009.01531.x

471 Becker, A., M. D. Taylor, H. Folpp, M. B. Lowry, 2018. Managing the development of artificial  
472 reef systems: the need for quantitative goals. *Fish and Fisheries*, 19(4), 750-752. doi:  
473 10.1111/faf.12288.

474 Bellio, M. G., Kingsford, R. T., Kotagama, S. W., 2009. Natural versus artificial- wetlands and  
475 their waterbirds in Sri Lanka. *Biological Conservation*, 142(12), 3076-3085.  
476 <https://doi.org/10.1016/j.biocon.2009.08.007>

477 Beschta, R. L., Ripple, W. J., 2009. Large predators and trophic cascades in terrestrial  
478 ecosystems of the western United States. *Biological Conservation*, 142(11), 2401-2414.

479 doi:10.1016/j.biocon.2009.06.015.

480 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H.,  
481 White, J. S. S., 2009. Generalized linear mixed models: a practical guide for ecology and  
482 evolution. *Trends Ecol. Evol.* 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.

483 Bollens, S. M., Frost, B. W., 1989. Predator-induced diel vertical migration in planktonic  
484 copepod. *Jornal of Plankton Research* 11(5), 1047-1065. doi: 10.1093/plamkt/11.5.1047

485 Brown, J., Stevens, G., Kaufman, D., 1996. The geographic range: size, shape, boundaries, and  
486 internal structure. *Annual Review of Ecology and Systematics*, 27(1). 597-623. doi:  
487 10.1146/annurev.ecolsys.27.1.597

488 Brown, J. S., Laundré, J. W., Gurung M., 1999. The ecology of fear: Optimal foraging, game  
489 theory and trophic interactions. *Journal of Mammology*, 80(2), 385-399. doi:  
490 10.2307/1383287

491 Browne, R. A., Lutz, D., 2010. Lake ecosystem effects associated with top-predator removal due  
492 to selenium toxicity. *Hydrobiologia*, 655(1), 137-148. <https://doi.org/10.1007/s10750-010-0416-3>

493

494 Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A., Dill, L. M., 2013. Patterns  
495 of top-down control in a seagrass ecosystem: Could a roving apex predator induce a  
496 behaviour-mediated trophic cascade? *Journal of Animal Ecology*.  
497 <https://doi.org/10.1111/1365-2656.12097>

498 Burt, J., Bartholomew, A., Usseglio, P., Bauman, A., Sale, P. F., 2009. Are artificial reefs  
499 surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? *Coral  
500 Reefs*, 28(3), 663-675. doi:<http://dx.doi.org.libproxy.lib.unc.edu/10.1007/s00338-009-0500-1>

502 Creel, S., Becker, M., Dröge, E., M'soka, J., Matandiko, W., Rosenblatt, E., Mweetwa, T.,  
503 Mwape, H., Vinks, M., Goodheart, B., Markle, J., Mukula, T., Smit, D., Sanguinetti, C.,  
504 Dart, C., Christianson, D., Schuette, P., 2019. What explains variation in the strength of  
505 behavioral responses to predation risk? A standardized test with large carnivore and  
506 ungulate guilds in three ecosystems. *Biological Conservation* 232, 164-172. doi:  
507 10.1016/j.biocon.2019.02.012

508 Creel, S., Christianson, D. A., Winnie, J. A., 2011. A survey of the effects of wolf predation risk  
509 on pregnancy rates and recruitment in elk. *Ecological Applications*, 21(8), 2847-2853. doi:  
510 10.1890/11-0768.1

511 Dafforn, K. A., Glasby, T. M., Johnston, E. L., 2012. Comparing the invasibility of experimental  
512 "reefs" with field observations of natural reefs and artificial structures. *PLoS One*, 7(5).  
513 <http://dx.doi.org.libproxy.lib.unc.edu/10.1371/journal.pone.0038124>

514 Dalerum, F., Somers, M., Kunkel, K., Cameron, E., 2008. The potential for large carnivores to  
515 act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation*, 17(12),  
516 2939-2949. doi: 10.1007/s10531-008-9406-4

517 De Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices  
518 and statistical inference. *Ecology*, URL: <http://sites.google.com/site/miqueldecaceres/>

519 Defreitas, B., 2003. Estimating juvenile northern abalone (*Haliotis kamtschatkana*) abundance  
520 using artificial habitats. *Journal of Shellfish Research*, 22(3), 819-823.  
521 [https://www.researchgate.net/publication/266482848\\_Estimating\\_juvenile\\_northern\\_abalone\\_Haliotis\\_kamtschatkana\\_abundance\\_using\\_artificial\\_habitats](https://www.researchgate.net/publication/266482848_Estimating_juvenile_northern_abalone_Haliotis_kamtschatkana_abundance_using_artificial_habitats)

523 Dorn, N. J., Trexler, J. C., Gaiser, E. E., 2006. Exploring the role of large predators in marsh  
524 food webs evidence for a behaviorally-mediated cascade. *Hydrobiologia*, 569(1), 375-386.

525 doi: 10.1007/s10750-006-0143-y

526 Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N. K., Fordham, S. V., Brautigam, A., Sant,  
527 G., Welch, D. J., 2017. Challenges and Priorities in Shark and Ray Conservation. *Current  
528 Biology*, 27(11), R565–R572. doi: 10.1016/J.CUB.2017.04.038

529 Estes, J. A., Duggins, D. O., 1995. Sea otters and kelp forests in Alaska: Generality and variation  
530 in a community ecological paradigm. *Ecological Monographs*, 65(1), 75–100. doi:  
531 10.2307/2937159doi:10.2307/2937159

532 Estes, J. A., Steneck, R. S., Lindberg, D. R., 2013. Exploring the Consequences of Species  
533 Interactions Through the Assembly and Disassembly of Food Webs: A Pacific-Atlantic  
534 Comparison. *Bulletin of Marine Science*, 89(1), 11–29. doi: 10.5343/bms.2011.1122

535 Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A.,  
536 2012. AD Model Builder: using automatic differentiation for statistical inference of highly  
537 parameterized complex nonlinear models. *Optimum Methods Software*. 27, 233–249.

538 Gallagher, J., Creel, S., Wilson, R. P., Cooke, S. J., 2017. Energy landscapes and the landscape  
539 of fear. *Trends in Ecology and Evolution*, 32(2), 88-96. doi:10.1016/j.tree.2016.10.010

540 Gelsleichter, J., Musick, J. A., Nichols, S., 1999. Food habitats of the smooth dogfish, *Mustelus*  
541 *canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon*  
542 *terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean.  
543 Environmental Biology of Fishes 54, 205-217.

544 Guttridge, T. L., Gruber, S.H., Gledhill, K. S., Croft, D.P, Sims, D. W., Krause, J., 2009. Social  
545 preferences of juvenile lemon sharks, *Negaprion brevirostris*. *Animal Behavior*, 78, 543-  
546 548.

547 Guttridge, T. L., Gruber, S.H. Franks, B. R., Kessel, S. T., Gledhill, K. S., Uphill, J., Krause, J.,

548 Sims, D. W., 2012. Deep danger: intra-specific predation risk influences habitat use and  
549 aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology*  
550 *Progress Series*, 445, 279-291.

551 Hamilton, W. D., 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295-  
552 311.

553 Harestad, A. S., Bunnell, F. L., 1979. Home range and body weight--a reevaluation. *Ecology*,  
554 60(2), 389-402. doi: 10.2307/1937667

555 Haskell, J. P., Ritchie, M. E., Olff, H., 2002. Fractal geometry predicts varying body size scaling  
556 relationships for mammal and bird home ranges. *Nature*, 418(6897), 527-530. doi:  
557 10.1038/nature00840

558 Haulsee, D., Breece, M., Brown, L., Wetherbee, B., Fox, D., Oliver, M., 2018. Spatial ecology of  
559 *Carcharias taurus* in the northwestern Mid-Atlantic coastal ocean. *Marine Ecology Progress Series*  
560 *Series*, 597, 191–206. doi: 10.3354/meps12592

561 Haulsee, D. E., Fox, D. A., Breece, M. W., Brown, L. M., Kneebone, J., Skomal, G. B., Oliver,  
562 M. J., 2016. Social network analysis reveals potential fission–fusion behavior in a shark.  
563 *Scientific Reports*, 6:34087. doi: 10.1038/srep34087

564 Heithaus, M. R., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D.,  
565 Thomson, J., Bejder L., 2007. State-dependent risk-taking by green sea turtles mediates  
566 top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal  
567 Ecology*, 76, 837-844. doi: 10.1111/j.1365-2656.2007.01260.x

568 Johnson, C. N., Isaac, J. L., Fisher, D. O., 2007. Rarity of a top predator triggers continent-wide  
569 collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal  
570 Society B: Biological Sciences*, 274(1608), 341–346.

571                    <https://doi.org/10.1098/rspb.2006.3711>

572    Johnson, C. N., VanDerWal, J., 2009. Evidence that dingoes limit abundance of a mesopredator  
573                    in eastern Australian forests. *Journal of Applied Ecology*, 46(3), 641–646.

574                    <https://doi.org/10.1111/j.1365-2664.2009.01650.x>

575    Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R.,  
576                    Block, B. A., 2009. Philopatry and migration of Pacific white sharks. doi:  
577                    10.1098/rspb.2009.1155

578    Kells, V., Carpenter, K., 2011. *A Field Guide to Coastal Fishes from Maine to Texas*. Baltimore,  
579                    Maryland: John Hopkins University Press. ISBN: 9780801898389

580    Kneebone, J., Chisholm, J., Skomal, G., 2012. Seasonal residency, habitat use, and site fidelity of  
581                    juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. *Marine Ecology  
582                    Progress Series*, 471, 165–181. doi: 10.3354/meps09989

583    Labrosse, P., Kulbicki, M., Ferraris, J., 2002. Underwater visual fish census surveys: proper use  
584                    and implementation. SPC: Reef Resources Assessment Tools. Retrieved from  
585                    <https://www.researchgate.net/publication/282170595>

586    Langhamer, O., 2012. Artificial reef effect in relation to offshore renewable energy conversion:  
587                    state of the art. *The Scientific World Journal*, 2012: 386713.  
588                    <https://doi.org/10.1100/2012/386713>

589    Letnic, M., Koch, F., Gordon, C., Crowther, M. S., Dickman, C. R., 2009. Keystone effects of an  
590                    alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B:  
591                    Biological Sciences*, 276(1671), 3249–3256. <https://doi.org/10.1098/rspb.2009.0574>

592    Lima, S. L., Dill, L. M., 1990. Behavioral decisions made under the risk of predation: a review  
593                    and prospectus. *Burnaby*, B.C., 156(68), 619-640. Retrieved from

594                   www.nrcresearchpress.com

595   Madin, E. M. P., Gaines, S. D., Madin, J. S., Link, A.-K., Lubchenco, P. J., Selden, R. L.,

596   Warner, R. R., 2012. Do Behavioral Foraging Responses of Prey to Predators Function

597   Similarly in Restored and Pristine Foodwebs? *PLoS ONE*, 7(3), e32390. doi:

598   10.1371/journal.pone.0032390

599   Masi, M. D., Ainsworth, C. H., Kaplan, I. C., Schirripa, M. J., 2018. Interspecific Interactions

600   May Influence Reef Fish Management Strategies in the Gulf of Mexico. *Marine and*

601   *Coastal Fisheries*, 10, 24-39. doi: 10.1002/mcf2.10001

602   Menge, B. A., Cerny-Chipman, E. B., Johnson, A., Sullivan, J., Gravem, S., Chan. F., 2016. Sea

603   star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: Insights into

604   differential population impacts, recovery, predation rate, and temperature effects from long-

605   term research. *PLoS ONE* 11(5). doi: 10.1371/journal.pone.0153994

606   Mittelbach, G. G., Turner A. M., Hall, D. J., Rettig, J. E., Osenberg, C. W., 1995. Perturbation

607   and resilience: A long-term, whole-lake study of predator extinction and reintroduction.

608   *Ecology*, 76(8), 2347-2360. doi: 10.2307/2265812

609   Morozov, A., Sen, M., Banerjee, M., 2012. Top-down control in a patchy environment:

610   Revisiting the stabilizing role of food-dependent predator dispersal. *Theoretical Population*

611   *Biology*, 81(1), 9–19. <https://doi.org/10.1016/j.tpb.2011.10.003>

612   Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., Peterson, C. H., 2007. Cascading

613   effects of the loss of apex predatory sharks from a coastal ocean. *Science*. doi:

614   10.1126/science.1138657

615   Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B.,

616   Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H., 2015. vegan: Community

617                   Ecology Package R Package.

618   Ordiz, A., Bischof, R., Swenson, J. E., 2013. Saving large carnivores, but losing the apex  
619                   predator? *Biological Conservation*, 168, 128-133. doi: 10.1016/J.BIOCON.2013.09.024

620   Pace, M. L., Cole, J. J., Carpenter, S. R., Kitchell, J. F., 1999. Trophic cascades revealed in  
621                   diverse ecosystems. *Trends in Ecology & Evolution*, 14(12), 483–488. Retrieved from  
622                   <http://www.ncbi.nlm.nih.gov/pubmed/10542455>

623   Paxton, A. B., Pickering, E. A., Adler, A. M., Taylor, J. C., Peterson, C. H., 2017. Flat and  
624                   complex temperate reefs provide similar support for fish: evidence for a unimodal species-  
625                   habitat relationship. *PLOS ONE*, 12(9): e0183906.

626   Paxton, A. B., Blair, E., Blawas, C., Fatzinger, M., Marens, M., Holmberg, J., Kingen, C.,  
627                   Houppermans, T., Keusenkothen, M., McCord, J., Silliman, B. R., Penfold, L. M., 2019.  
628                   Citizen science reveals female sand tiger sharks (*Carcharias taurus*) exhibit signs of site  
629                   fidelity on shipwrecks. *Ecology* 100(8): e02687. doi: 10.1002/ecy.2687.

630   Paxton, A. B., Peterson, C. H., Taylor, J. C., Adler, A. M., Pickering, E. A., Silliman, B. R.,  
631                   2019. Artificial reefs facilitate tropical fish at their range edge. *Communications Biology*  
632                   2:168. doi:10.1038/s42003-019-0398-2.

633   Paxton, A. B., Shertzer, K. W., Bacheler, N. W., Kellison, G. T., Riley, K. L., Taylor, J. C.,  
634                   2020. Meta-analysis reveals artificial reefs can be effective tools for fish habitat  
635                   enhancement but are not one-size-fits-all. *Frontiers in Marine Science*, 7:282.  
636                   doi:10.3389/fmars.2020.00282.

637   Peterson, C. D., Belcher, C. N., Bethea, D. M., Driggers, W. B., Frazier, B. S., Latour, R. J.,  
638                   2017. Preliminary recovery of coastal sharks in the south-east United States. *Fish and*  
639                   *Fisheries*, 18(5), 845–859. doi: 10.1111/faf.12210

640 Pierce, S. J., Homberg, J., Kock, A. A., Marshall, A. D., 2018. Photographic identification of  
641 sharks. *Shark Research: Emerging Technologies and Applications for the Field and*  
642 *Laboratory*: Chapter 12.

643 Preisser, E. L., Bolnick, D. I., Benard, M. F., 2005. Scared to death? The effects of intimidation  
644 and consumption in predator-prey interactions. *Ecology*, 86(2), 501–509. doi: 10.1890/04-  
645 0719

646 R Development Core Team, 2019. R: A language and environment for statistical computing.

647 Rees, J. D., Kingsford, R. T., Letnic, M., 2019. Changes in desert avifauna associated with the  
648 functional extinction of a terrestrial top predator. *Ecography*, 42(1), 67–76.  
649 <https://doi.org/10.1111/ecog.03661>

650 Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., 2014. Status and  
651 ecological effects of the world's largest carnivores. *Science*, 343(6167) . doi:  
652 10.1126/science.1241484

653 Ritchie, E. G., Johnson, C. N., 2009. Predator interactions, mesopredator release and biodiversity  
654 conservation. *Ecology Letters*, 12(9), 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>

656 Schmidt, K., Kuijper, D. P., 2015. A “death trap” in the landscape of fear. *Mammal Research*,  
657 60(4), 275-284. doi: 10.1007/s13364-015-0229-x

658 Schmitz, O. J., Beckerman, A. P., O'Brien, K. M., 1997. Behaviorally mediated trophic  
659 cascades: Effects of predation risk on food web interactions. *Ecology*, 78(5), 1388–1399.  
660 [https://doi.org/10.1890/0012-9658\(1997\)078\[1388:BMCEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1388:BMCEO]2.0.CO;2)

661 Schultz, J. A., Cloutier, R. N., Cote, I. M., 2016. Evidence for a trophic cascade on rocky reefs  
662 following sea star mass mortality in British Columbia. *PeerJ*, 4. doi: 10.7717/peerj.1980

663 Scott, M. D., Chivers, S. J., Olson, R. J., Fiedler, P. C., Holland, K., 2012. Pelagic associations:  
664 tuna and dolphins in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series*,  
665 458, 283-302. <https://doi.org/10.3354/meps09740>

666 Simon, T., Joyeux, J., Pinheiro, H. T., 2013. Fish assemblages on shipwrecks and natural rocky  
667 reefs strongly differ in trophic structure. *Marine Environmental Research* 90: 55-65.

668 Smith, J. A., Lowry, M. B., Champion, C. Suthers, I. M., 2016. A designed artificial reef is  
669 among the most productive marine fish habitats: new metrics to address 'productivity versus  
670 attraction'. *Marine Biology*, 163(188), <https://doi.org.libproxy.lib.unc.edu/10.1007/s00227-016-2967-y>

672 Smith, T. M., Hindell, J. S., Jenkins, G. P., Connolly, R. M., Keough, M. J., 2011. Edge effects  
673 in patchy seagrass landscapes: The role of predation in determining fish distribution. *Journal  
674 of Experimental Marine Biology and Ecology*, 399(1), 8-16.  
675 <https://doi.org/10.1016/j.jembe.2011.01.010>

676 Stankowich, T., 2003. Marginal predation methodologies and the importance of predator  
677 preferences. *Animal Behavior*, 66, 589–599. <https://doi.org/10.1006/anbe.2003.2232>

678 Teter, S. M., Wetherbee, B. M., Fox, D. A., Lam, C. H., Kiefer, D. A., Shivji, M., 2015.  
679 Migratory patterns and habitat use of the sand tiger shark (*Carcharias taurus*) in the western  
680 North Atlantic. *Marine and Freshwater Research*, 66, 158-169. doi: 10.1071/MF14129

681 Turner, G. F., Pitcher, T. J., 1986. Attack abatement: A model for group protection by combined  
682 avoidance and dilution. *The American Naturalist*, 128(2), 228-240.  
683 <https://www.jstor.org/stable/2461547>

684 Werner, E. E., Peacor, S. D., 2003. A review of trait-mediated indirect interactions in ecological  
685 communities. *Ecology*, 84(5), 1083–1100. <https://doi.org/10.1890/0012->

686 9658(2003)084[1083:AROTII]2.0.CO;2

687 Werry, J. M., Lee, S. Y., Lemckert, C. J., Otway N. M., 2012. Natural or artificial? Habitat-use  
688 by the bull shark, *Carcharhinus leucas*. *PLoS One*, 7(11). doi:10.1371/journal.pone.0049796

689 Whitehead, A. L., Edge, K., Smart, A. F., Hill, G. S., Willans, M. J., 2008. Large scale predator  
690 control improves productivity of a rare New Zealand riverine duck. *Biological Conservation*,  
691 141(11), 2784-2794. doi: 10.1016/j.biocon.2008.08.013

692 Wirsing, A. J., Heithaus, M. R., Dill, L. M., 2007. Fear factor: do dugongs (Dugong dugon)  
693 trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia*, 153(4), 1031–1040.  
694 <https://doi.org/10.1007/s00442-007-0802-3>

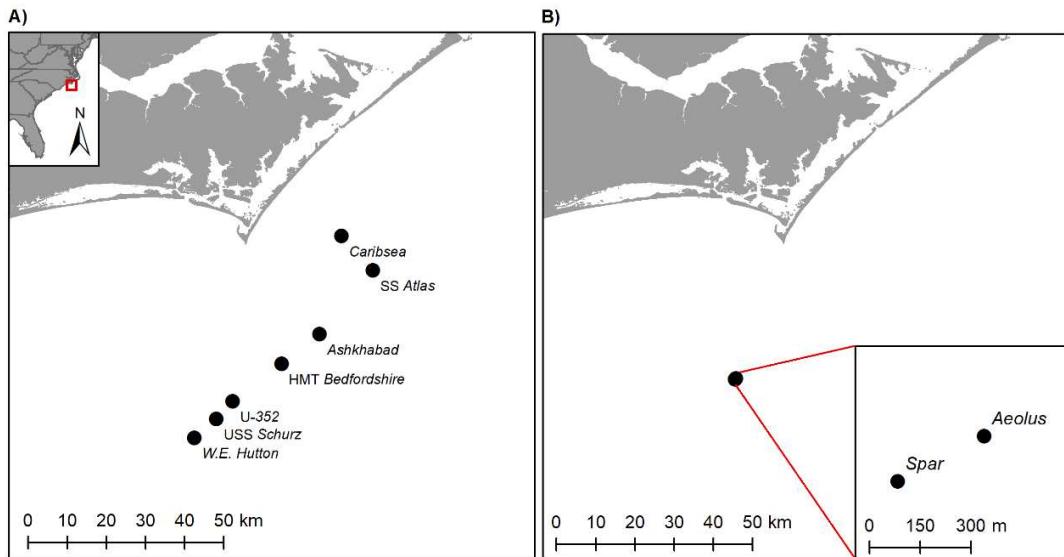
695 Xylem Analytics, 2015. NYSE: XYL Hypack. <http://www.hypack.com>

696 Young, J. W., Hunt, B. PV., Cook, T. R., Llopiz, J. K., Hazen, E. L., Pethybridge, H. R.,  
697 Ceccarelli, D., Lorrain, A., Olson, R. J., Allain, V., Menkes, C., Patterson, T., Nicol, S.,  
698 Lehodey, P., Kloser, R. J., Arrizabalaga, H., Choy, C. A., 2015. The trophodynamics of  
699 marine top predators: Current knowledge, recent advances and challenges. *Deep Sea  
700 Research Part II: Tropical Studies in Oceanography*, 113, 170-187. doi:  
701 10.1016/j.dsr2.2014.05.015

702

703 **Figures**

704



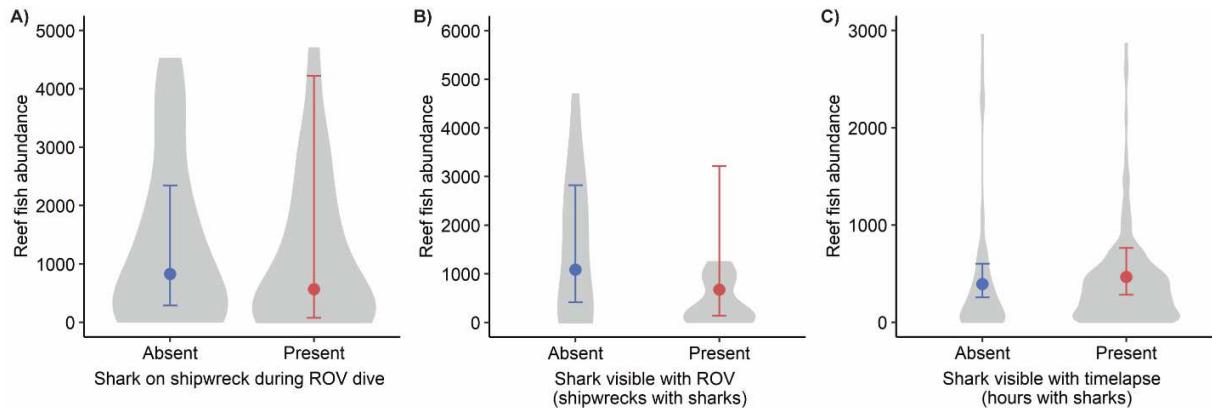
705

706 **Figure 1:** A) Location of seven shipwrecks surveyed using a remotely-operated vehicle (ROV).

707 B) Location of two shipwrecks surveyed without an ROV using stationary time-lapse

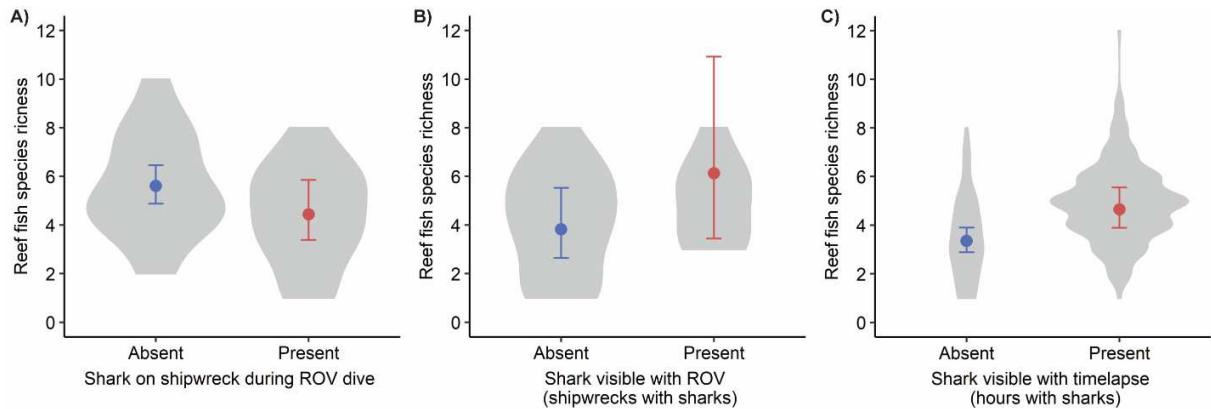
708 videography.

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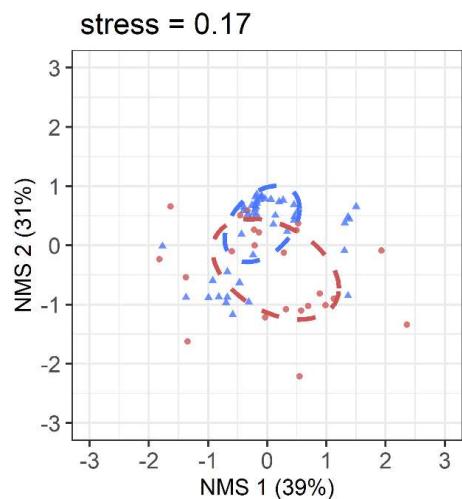
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711 **Figure 2:** Reef fish abundance per video clip when A) sharks are present versus absent on  
 712 shipwrecks during ROV surveys, B) sharks are visible versus not visible on shipwrecks occupied  
 713 by sharks during ROV surveys, and C) sharks are visible versus not visible on shipwrecks  
 714 occupied by sharks during each hour of stationary time-lapse video. Violin plots display the  
 715 observed data, where the shaded area is proportional to the number of observations. Predicted  
 716 values of reef fish abundance and corresponding confidence intervals from generalized linear  
 717 mixed models are shown inside the violin plots as colored points and lines.



718 **Figure 3:** Reef fish species richness per video clip when A) sharks are present versus absent on  
 719 shipwrecks during ROV surveys, B) sharks are visible versus not visible on shipwrecks occupied  
 720 by sharks during ROV surveys, and C) sharks are visible versus not visible on shipwrecks  
 721 occupied by sharks during each hour of stationary time-lapse video. Observed data are displayed  
 722 as violin plots, where the shaded area is proportional to the number of observations. Predicted  
 723 values of reef fish richness and corresponding confidence intervals from generalized linear  
 724 mixed models are shown inside the violin plots as colored points and lines.  
 725

726



729 **Figure 4:** Nonmetric multidimensional scaling ordination of community composition when  
730 sharks are present (red circles) versus absent (blue triangles). Each point represents the  
731 community in a one-minute video clip from ROV surveys. Ellipses represent 50% confidence  
732 intervals.

733 **Supplementary Materials**

734

735 **Table S1:** Descriptions of shipwrecks surveyed with remotely-operated vehicles.

Shipwreck	Description	Depth (m)	Latitude	Longitude	Date Sunk	Survey Date	Video clips	Sharks Present
<i>Caribsea</i>	Freighter	27	34.6069	-76.3146	1942	2018-07-16	17	Yes
<i>SS Atlas</i>	Tanker	38	34.5285	-76.2422	1942	2018-08-06	6	Yes
<i>Ashkhabad</i>	Tanker	18	34.3815	-76.3650	1942	2018-08-06	11	No
<i>HMT Bedfordshire</i>	Converted	32	34.3141	-76.4525	1942	2018-08-06	10	No
<i>U-352</i>	German U-boat	35	34.2280	-76.5649	1942	2018-08-07	8	No
<i>USS Schurz</i>	US Navy	33	34.1873	-76.6022	1918	2018-08-07	7	No
<i>W.E. Hutton</i>	Tanker	38	34.1437	-76.6524	1942	2018-08-07	11	Yes

736

737 **Table S2:** Description of artificial reef shipwrecks surveyed with time-lapse videography.

Shipwreck	Description	Depth (m)	Latitude	Longitude	Video clips	Sharks Present
<i>Spar</i>	US Coast Guard Buoy Tender	34	34.2771	-76.6455	332	Yes
<i>Aeolus</i>	US Navy Cable Layer	35	34.2783	-76.6432	215	Yes

738

739 **Table S3:** Generalized linear mixed model (GLMM) results for models corresponding to each  
 740 survey approach and response variable. The fixed and random effects, as well as the data used to  
 741 fit the model, are specified. Deviance and *p*-values from the likelihood ratio test (LRT) between  
 742 the full model and reduced model without the fixed effect are provided, as are the GLMM  
 743 estimates for the mean reef fish abundance when sharks are absent and present.

Survey approach	Response variable	Data	Fixed effect	Random effect	Deviance	<i>p</i> -value	$\mu_{\text{absent}}$	$\mu_{\text{present}}$
ROV	Reef fish abundance	All	Shark presence vs. absence	Shipwreck	0.214	0.64	826	565
ROV	Reef fish abundance	Shipwrecks with sharks	Shark visible vs. not	Shipwreck	0.60	0.44	1084	676
Time lapse	Reef fish abundance	Hours with sharks	Shark visible vs. not	Shipwreck	1.88	0.17	393	465
ROV	Reef fish species richness	All	Shark presence vs. absence	Shipwreck	3.22	0.07	5.61	4.45
ROV	Reef fish species richness	Shipwrecks with sharks	Shark visible vs. not	Shipwreck	4.15	0.04	3.82	6.13
Time lapse	Reef fish species richness	Hours with sharks	Shark visible vs. not	Shipwreck	47.56	<0.0001	3.36	4.65

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