Association behavior between sand tiger sharks and round scad is driven by mesopredators

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Abstract

16   Underwater videos (n = 216) from SharkCam, a camera installation sited beneath Frying Pan

17   Tower on a natural, hard bottom site off Cape Fear, North Carolina, were used to investigate

18   association behavior of round scad *Decapterus punctatus* around sand tiger sharks *Carcharias*

19   *taurus*. Videos containing sand tiger sharks were analyzed for the simultaneous presence of

20   round scad, and six species of scad mesopredators, with scad-shark interactions assigned to one

21   of three categories of association: no visible interaction, loosely associated, or tightly associated.

22   The likelihood of scad being loosely or tightly associated with sharks was significantly higher in

23   the presence of scad mesopredators, suggesting that sharks provide a predation refuge for scad.

24   This behaviorally-mediated indirect interaction has important implications for trophic energy

25   transfer and mesopredator control on hard bottoms, as scad are one of the most important

26   planktivorous fish in the western Atlantic Ocean. Although we were not able to provide

27   statistical evidence that sand tiger sharks also benefit from this association behavior, we have

28   strong video evidence that round scad association provides concealment and attraction of

29   mesopredators that enhances predation opportunities for sand tiger sharks. This likely possibility

30   adds further trophic consequences to this unique interaction and highlights the value of exploring

31   behaviorally mediated interactions in marine communities.

Introduction

34   Hard bottom reefs, or "live bottoms" are conspicuous geological features on the mainly soft

35   sediment-dominated continental shelf within the South Atlantic Bight (SAB). In the Carolina

36   Capes region of the SAB (offshore of North and South Carolina) (Riggs et al., 1996) estimates of

37   areal coverage for this habitat vary on both latitudinal and longitudinal bases, with reports of the

38 greatest areal proportions of hard bottom habitat of the shelf to the south of Cape Lookout, North

39 Carolina (Parker, Colby & Willis, 1983; SAFMC, 1998). Hard bottoms provide structural habitat

40 for the settlement of benthic sessile foundation species, including rich assemblages of sponges,

41 scleractinian and octocorallian corals, ascidians, and macroalgae (Struhsaker, 1969; Miller &

42 Richards, 1980; Wenner et al., 1983). The growth of these sessile organisms contributes to hard

43 bottom reef structural complexity. Compared to adjacent soft-sediment dominated areas of the

44 sea floor, hard bottoms create a striking contrast in habitat that attracts and supports high

45 richness and abundance of fishes (Sedberry & Van Dolah, 1984; Hopkinson, Jansson &

46 Schubauer-Berigan, 1991), invertebrates (Wenner et al., 1983; Peckol & Searles, 1984), and

47 macroalgae (Schneider & Searles, 1973, 1991; Schneider, 1976; Freshwater & Idol, 2013).

48 Specifically, hard-bottom reefs attract aggregations of small pelagic schooling fishes that serve

49 as important prey resources for many pelagic and demersal piscivorous fishes (Kracker, Kendall

50 & McFall, 2008).

51   The abundance and taxonomic richness of species on hard bottoms facilitate unique

52 interspecies interactions that are often driven by enhanced feeding opportunities or decreased

53 vulnerability to predators (McFarland & Kotchian 1982, Diamant and Shpigel 1985, Baird

54 1993). For example, associations between blue runner (*Caranx crysos* (Mitchill, 1815)), greater

55 amberjack (*Seriola dumerili* (Risso, 1810)), and other large piscivorous fishes have been

56 observed during coordinated predatory foraging (Auster et al., 2009). Effects of such

57 associations containing multiple predators on prey mortality has been heavily debated and

58 several studies have reported both additive and reduced predation effects (reviewed in Sih,

59 Englund & Wooster, 1998).

60   Multispecies interactions highlight the underlying interdependency between organisms that

61   exist in all communities (Hutchinson, 1959; Paine, 1984; Beard & Dess, 1988). These

62   interactions are often categorized as direct, between two species, or indirect, where the

63   interaction between two species ultimately affects a third species (Wootton, 1993). Behaviorally

64   mediated indirect interactions (BMIIs) are a further classification of trait mediated indirect

65   interactions (TMIIs) that are regulated by changes in a species' behavior (Dill, Heithaus &

66   Walters, 2003). Both direct and indirect interactions produce changes in a species' density or

67   behavior and are useful in understanding food webs and trophic exchanges. Indeed, indirect

68   affects alter the risk landscapes of prey, including mesopredators which are prey species for apex

69   carnivores (Ritchie & Johnson, 2009), especially in aquatic ecosystems (Preisser, Bolnick &

70   Benard, 2005), and can initiate trophic cascades (Schmitz, Krivan & Ovadia, 2004; Creel &

71   Christianson, 2008). However, BMIIs are less commonly investigated than other ecologic

72   interactions because of the difficulty attributed to quantifying changes in behavior, especially

73   within marine habitats. Competitor facilitation has been used to refer to BMIIs where the

74   presence of one species of predator causes a change in the behavior of a prey species that makes

75   that prey species more accessible for a second species of predator (Dill, Heithaus & Walters,

76   2003).

77   On hard bottoms off the coast of Georgia, competitive facilitation was observed as schools of

78   round scad (*Decapterus punctatus* (Cuvier, 1829)) and tomtate (*Haemulon aurolineatum* Cuvier

79   in Cuvier and Valenciennes, 1830) retreated from multispecies associations of pelagic

80   piscivorous fish toward the seafloor, increasing predation opportunities for demersal piscivorous

81   fishes (Auster et al., 2009, 2013) Furthermore, Auster et al. (2009) observed round scad and

82   tomtate responding to the presence of pelagic predators by reducing nearest neighbor distance

83   and forming more polarized aggregations. Increased polarization is a common response to

84   predators for many prey species that form aggregations and has been found to reduce the

85   vulnerability of prey aggregations (reviewed in Lima & Dill, 1990). In addition to increasing

86   polarization, prey fishes use several other strategies to reduce vulnerability to predators.

87   Alternative strategies include forming aggregations around physical objects, which is

88   hypothesized to be advantageous to prey by serving as a "schooling companion" (Klima &

89   Wickham, 1971). During diving observations analyzing the attraction of pelagic fishes to fish

90   aggregation devices (FADs), the removal of artificial structure initiated immediate multispecies

91   predation attempts by large, pelagic, piscivorous fish on small bait fishes (Wickham, Jr & Ogren,

92   1973).

93   *Sand tiger sharks (STs)*

94   Sand tiger sharks, *Carcharias taurus* Rafinesque, 1810, are large (to >4 m), heavy-bodied

95   sharks found in coastal and continental shelf waters of warm-temperate and tropical seas

96   worldwide. Individuals and aggregations occur especially in coastal areas of Australia (where

97   they are known locally as grey nurse sharks), the east coast of South Africa (raggedtooth sharks),

98   and the east coast of the United States (sand tiger sharks). Sand tiger shark aggregations are

99   associated with migratory behavior, feeding, and reproduction (Compagno, 2001), and complex

100   social networks and behaviors are present in this species (Haulsee et al., 2016). Year-to-year site

101   fidelity on shipwrecks and other artificial structures has been reported in North Carolina (Paxton

102   et al., 2019) and animals tagged in Delaware Bay undergo long-distance migrations to

103   overwinter in continental shelf waters of North Carolina (Teter et al., 2015). Additionally, sand

104   tiger sharks are one of the few large-bodied sharks commonly housed in captivity (Govender,

105   Kistnasamy & Van Der Elst, 1991; Gordon, 1993; Smale et al., 2012).

106   The diet of *C. taurus* is diverse and dominated by bony fishes and other elasmobranchs

107   (Gelsleichter, Musick & Nichols, 1999). The conservation status of *C. taurus* is listed as globally

108   vulnerable with regional populations considered endangered or critically endangered (Pollard &

109   Smith, 2009). Assessment of *C. taurus* in the northwestern Atlantic suggests that populations

110   have declined to a minor extent in recent decades (Carlson et al., 2009), much less dramatically

111   than for other large sharks (Ferretti et al., 2010), but that conservative management is warranted

112   due to the very low productivity for this species (Goldman, Branstetter & Musick, 2006; Carlson

113   et al., 2009).

114   *Round scad (RS)*

115   Round scad, *Decapterus punctatus* (Cuvier, 1829), are small-bodied (<300 mm) carangids

116   found in the western Atlantic Ocean southward from Nova Scotia, at Bermuda, and in the Gulf of

117   Mexico, Caribbean Sea, and along continental shores of South America to Rio de Janiero

118   (Naughton, Saloman & Vaught, 1986). In the South Atlantic Bight, round scad (typically 60–170

119   mm) are abundant in continental shelf waters in summer and fall, and move to hard bottoms in

120   deeper, warmer areas of the mid- and outer shelf in winter (Hales Jr., 1987). Throughout their

121   range, adult round scad are diurnal zooplankton specialists with the diet dominated by pelagic

122   species and life stages (for meroplankton), as opposed to demersal plankton (Hales Jr., 1987;

123   Donaldson & Clavijo, 1994).

124   Round scad are very frequently reported as stomach contents of pelagic and demersal

125   piscivores (Matheson, Huntsman & Manooch, 1986; Naughton, Saloman & Vaught, 1986), and

126   are often the most abundant species on FADs (Rountree, 1990), wrecks (Lindquist & Pietrafesa,

127   1989), and natural live bottoms (Parker, Chester & Nelson, 1994; Kendall, Bauer & Jeffrey,

128   2009; Burge et al., 2012) in portions of the South Atlantic Bight. Round scad schooling

129   behaviors have been described (Rountree, 1989, 1990; Lindquist & Pietrafesa, 1989; Rountree &

130   Sedberry, 1991). Observed abundances of round scad at FADs and other structures accentuates

131   this species' affinity for physical objects which can include larger fishes and elasmobranchs.

132   In the Gulf of Mexico, Fuller and Parsons (2019) report aggregations of round scad and

133   another carangid, Atlantic bumper (*Chloroscombrus chrysurus* (Linnaeus, 1766)), associating

134   with blacktip sharks (*Carcharhinus limbatus* (Müller and Henle, 1839)), spinner sharks

135   (*Carcharhinus brevipinna* (Müller and Henle, 1839)), and blacknose sharks (*Carcharhinus*

136   *acronotus* (Poey, 1860)). In situ observations with sand tiger sharks have not been previously

137   reported prior to the current study, but photographs document associations between round scad

138   and sand tiger sharks on North Carolina reefs (this study) and wrecks

139   (https://ncaquariums.wildbook.org/gallery.jsp), and are mentioned by Fuller and Parsons (2019).

140   Many different examples of commensal and mutualistic heterospecific fish associations have

141   been described. Reasons for heterospecific association behavior are typically categorized as

142   cleaner-client interactions, protection from predation, increased foraging opportunities, and

143   hydrodynamic or transportation efficiencies. For example, the mackerel scad *Decapterus*

144   *macarellus* (Cuvier in Cuvier and Valenciennes, 1833), an ecologically similar and sympatric

145   relative of round scad *D. punctatus*, associated with goliath grouper *Epinephelus itajara*

146   (Lichtenstein, 1822) to reduce their vulnerability to predation by the horse-eye jack *Caranx latus*

147   Agassiz in Spix and Agassiz, 1831. Mackerel scad were described as forming a dense

148   aggregation around the grouper while under threat by jacks, and the school of scad moved with

149   the grouper as one unit. The authors conclude that this behavior was likely advantageous for

150   mackerel scad by reducing their risk of predation by a mesopredator (jack) that was itself

151   potential prey for the grouper (Macieira et al., 2010).

152   *Mesopredators (MPs)*

153   Mesopredators are traditionally defined as intermediate trophic level predators relative to a

154   smaller group of apex carnivores that occupy top trophic positions within a food web.

155   Assignment of any given species to its role as a mesopredator is, of course, context dependent, as

156   the removal of apex predators affects the trophic position of others within the web (reviewed in

157   Prugh et al., 2009). From a practical perspective, mesopredator species richness is typically

158   higher under apex predator control (Terborgh, 2015), although the relative effects of

159   competition, facilitation, and indirect effects are difficult to assess broadly. There are also

160   instances in which mesopredator abundance and species richness are controlled by their lower

161   taxonomic level prey. In such scenarios, commonly referred to as wasp-waisted ecosystems, a

162   lack of species diversity at the primary consumer level (i.e. planktivorous fish) allows several or

163   even a single species to control trophic exchange from primary producers to higher level

164   consumers (Cury et al., 2000). Therefore, the abundance and diversity of mesopredators is

165   dependent on their ability to capture this essential primary consumer group. In many wasp-waist

166   ecosystems, mesopredator predation success is conventionally controlled by the abundance of the

167   essential primary consumer which is influenced by seasonal environmental factors (e.g. El

168   Niño/La Niña) and predator abundance (Bakun, 2006). However, it is also important to consider

169   other factors that might influence predation success and ultimately mesopredator abundance and

170   diversity. Primary consumer association with higher level apex predators and similar anti-

171   predation behaviors could reduce predation success for mesopredators and be an overlooked

172   factor that contributes to the control of mesopredators in wasp-waisted ecosystems.

173   A diverse assemblage of pelagic and demersal piscivorous mesopredatory fishes inhabit hard

174   bottom habitats of the South Atlantic Bight (Chester et al., 1984; Sedberry & Van Dolah, 1984;

175   Kendall, Bauer & Jeffrey, 2009; Burge et al., 2012; Burge, O'Brien & jon-newbie, 2020).

176   Pelagic mesopredators include medium to large-sized jacks (greater amberjack *Seriola dumerili,*

177   almaco jack *Seriola rivoliana* Valenciennes in Cuvier and Valenciennes, 1833, blue runner

178   *Caranx crysos*, crevalle jack *Caranx hippos* (Linnaeus, 1766)) and scombrids (little tunny

179   *Euthynnus alletteratus* (Rafinesque, 1810), and Atlantic bonito *Sarda sarda* (Bloch, 1793)). All

180   are reported to prey on round scad or similar small fishes (Manooch III & Haimovici, 1983;

181   Saloman & Naughton, 1984; Manooch III, Mason & Nelson, 1985; Campo et al., 2006; Sley et

182   al., 2009; Fletcher, Batjakas & Pierce, 2013). Interestingly, some demersal mesopredators alter

183   their behavior in the presence of pelagic mesopredators feeding on round scad that blurs the line

184   between pelagic and demersal (Auster et al., 2009, 2013).

185   *Underwater video*

186   Underwater videography using stationary cameras is an efficacious method to conduct in-situ

187   marine observations, including surveying marine fish assemblages for species richness and

188   abundance, and behavioral observations (reviewed in Mallet & Pelletier, 2014). Video

189   observations are non-extractive and can be depth and time independent, relative to in person (i.e.

190   SCUBA diver) observations.

191   Potential bias associated with SCUBA surveys can be introduced as fish react to the presence

192   of divers, sometimes for long periods post-survey (Emslie et al., 2018), and this effect has been

193   observed to be species specific (Cole, 1994; Kulbicki, 1998; Burge et al., 2012; Lindfield et al.,

194   2014). For example, sand tiger sharks display increased respiration and movement in the

195   presence of SCUBA divers (Barker, Peddemors & Williamson, 2011), providing evidence that

196   underwater videography may be a better alternative to observe the behavior of this species. Once

197   recorded, videos can be reviewed multiple times to optimize the amount of data collected from a

198   single event, and can potentially increase recognition of behaviors that would otherwise be

199   difficult to assess during SCUBA diving observations.

200   In this study, we examined association behavior between sand tiger sharks (STs), round scad

201   (RS), and scad mesopredators (MPs) using a unique, long-term underwater video installation

202   sited on a hard bottom reef off the coast of Cape Fear, North Carolina. Based on video

203   observations collected to assess the fish species assemblage (E Burge, 2020, unpublished data)

204   and in situ observations by Burge and others, we repeatedly noticed the unusual association

205   between STs and RS. Consequently, we hypothesized that association behaviors between round

206   scad and sand tigers were more frequent in the presence of pelagic mesopredators than in their

207   absence because the presence of mesopredators represents a potential predation threat for round

208   scad. Strength of the association behavior was believed to be a response to mesopredators that

209   reflects round scad vulnerability. We also suspect that aggregations of round scad may be

210   mutually beneficial to sand tiger sharks by providing camouflage and increasing predation

211   opportunities on mesopredators. Direct, visual observations of wild behavior of sand tiger sharks

212   are very limited (but see Smith, Scarr & Scarpaci, 2010; Barker, Peddemors & Williamson,

213   2011), and this species is currently IUCN Red listed as Vulnerable, making conservation and

214   research efforts necessary for protection of this species. Investigating this association behavior

215   may be insightful for a deeper understanding of predation strategies of sand tiger sharks,

216   protective behaviors of a common prey species, and contribute knowledge of trophic dynamics

217   on hard bottom reefs in the South Atlantic Bight.

218

219   **Materials & Methods**

220

Study site and infrastructure

221

222   Video collected in this project are from SharkCam, an underwater, live-streaming camera,

223   publicly-viewable from https://explore.org/livecams/oceans/shark-cam (Explore.org, Los

224   Angeles, CA). The camera is sited beneath Frying Pan Tower (33º29'N, 77º35'W) which is

225   located at the seaward edge of Frying Pan Shoals, approximately 60 km off the coast of Cape

226   Fear, North Carolina. Frying Pan Shoals lies near the northern edge of a marine biogeographic

227   transition zone between a tropical and warm-temperate zone to the south (Caribbean

228   Biogeographic Province) and cold-temperate and polar waters to the north (Western Atlantic

229   Biogeographic Province) (Floeter et al., 2008; Toonen et al., 2016). The camera is attached to a

230   horizontal support at the base of Frying Pan Tower in about 15 m of water and is surrounded by

231   an expansive area of natural hard bottom (Riggs et al., 1996; NC Division of Marine Fisheries,

232   2020) and anthropogenic debris

233   (https://www.youtube.com/playlist?list=PLK1g13VpyT6oYUJL7U3hRPlt2U5L_mcKL). To

234   date, videos from SharkCam have been used to identify 116 temperate and tropical marine fish

235   species (November 2014–February 2020) (Burge, O'Brien & jon-newbie, 2020).

236   View Into The Blue® (Boulder, CO) cameras with CleanSweep™ hardware were used for all

237   footage captured (https://www.viewintotheblue.com/). The cameras used (six during the span of

238   this project) featured HD 720p (November 2014–July 2016 footage) or HD 1080p (after October

239   2016) video resolution, 360° pan-tilt-zoom that rotated on a pre-determined schedule, or with

240   manual remote control, and a field of view of 62° × 37° (horizontal × vertical). Automatic white

241   balance (color control) was enabled in April 2017 to more closely approximate surface light for

242   color correction. Power is provided by a solar installation atop Frying Pan Tower and data

243   transmission used a line-of-sight radio to shore (Burge, O'Brien & jon-newbie, 2020)

244   *Video analysis*

245   SharkCam video files containing sand tiger sharks *Carcharias taurus* (STs, n = 216) were

246   extracted from a larger video database of all fish species occurrences gathered from non-

247   consecutive, 20-min clips (n=1024) analyzed as part of a larger community analysis project (E

248   Burge 2020, unpublished data). Video files were recorded during local daylight hours between

249   November 2014 and January 2019. All videos containing STs were re-analyzed for the

250   simultaneous presence of round scad *Decapterus punctatus* (RS) and STs within the frame of the

251   camera view. Duration of the STs on screen (seconds) was recorded to obtain average

252   observation time.

253   Videos containing simultaneous co-occurrences of both species were assigned a descriptive

254   category of the association behavior between RS and STs using the following categories: no

255   visible interaction (NVI), loosely associated (LA), and tightly associated (TA) (Figure 1). No

256   visible association was defined as both species moving independently of each other or in

257   opposing directions and with their heads oriented in different directions. Loosely associated

258   aggregations were defined as both species moving in a similar direction, their heads oriented in a

259   similar direction, and RS maintaining an estimated distance of five body lengths or more from

260   STs and other school members. Tightly associated aggregations were defined as both species

261   moving as one entity, their heads oriented in the same direction, and RS maintaining less than

262   five estimated body lengths from STs and other school members. These behaviors represent a

263   spectrum of association that we hypothesize correlates with the vulnerability of RS to predation

264   in response to the presence of pelagic mesopredators (MPs); NVI representing the least

265   vulnerable and TA representing the most vulnerable. Video files with multiple sightings of STs

266   were treated as independent occurrences if shark observations were separated by 10-min or

267   greater. Multiple association observations within a 10-min interval were assigned a descriptive

268   category that best described the general association behavior of the recurring individuals. We

269   were not able to individually identify observed STs, however, we have no reason to believe that

270   this association behavior was limited to individual sharks given the multi-year duration over

271   which videos were collected.

272   In order to assess the behaviorally-mediated responses of RS to the presence of

273   mesopredators (MPs), we documented the presence, species composition, and relative abundance

274   of six selected MPs within all 20-min video segments that also contained STs and RS.

275   Mesopredators considered to be mediators of RS and STs association behavior were selected

276   based on similarities in their predation style and size, and observations from SharkCam that

277   documented or suggested feeding on RS. Almaco jack (*Seriola rivoliana*, AJ), Atlantic bonito

278   (*Sarda sarda*, AB), blue runner (*Caranx crysos*, BR), crevalle jack (*Caranx hippos*, CJ), greater

279   amberjack (*Seriola dumerili*, GA), and little tunny (*Euthynnus alletteratus*, LT) were used as

280   representatives of pelagic mesopredators (individual body size approximately 0.5 m–1.5 m)

281   because of their highly active feeding behavior, including predation attempts documented on

282   SharkCam (data not shown), literature confirming their predation on RS or a similar species

283   (Manooch III & Haimovici, 1983; Saloman & Naughton, 1984; Manooch III, Mason & Nelson,

284   1985; Campo et al., 2006; Sley et al., 2009; Fletcher, Batjakas & Pierce, 2013), and their co-

285   occurrence in videos that suggest facilitated, or even cooperative, hunting (Auster et al., 2013,

286   2019).

287   *Data analysis*

288   Hierarchical cluster analysis using Bray-Curtis similarity was used to illustrate the strength of

289   co-occurrences between STs, RS, and each species of mesopredator in all recorded instances of

290   sharks (n=216). Presence or absence data within 20-min video segments for all analyzed videos

291   were square root transformed, Bray-Curtis similarity values were calculated, and a hierarchical

292   cluster analysis was performed with statistical significance tested with 1000 simulation

293   permutations by Simprof (α=0.05) in Primer-E 6.x (Plymouth Marine Laboratory UK).

294   Pearson's chi-squared test (χ^2) was used to further investigate whether the frequency of

295   association behaviors between STs and RS were more commonly observed than expected if each

296   category of association had an equal chance of occurring (33%). Equal likelihoods of each

297   association category occurring were assumed to represent a condition in which RS did not

298   benefit from a close physical association with STs. Pearson's χ^2 was also used to test the

299   frequency of association behaviors in the presence of one or more species of mesopredator. The

300   behavior categories were used to represent a continuum of association that reflected the relative

301   vulnerability of RS to pelagic MPs.

302   Multinomial logistic regression ('multinom', R version 3.5.1) was used to calculate the log-

303   odds of association behavior (i.e. LA and TA behaviors) in the presence or absence of one or

304   more species of mesopredator. This analysis expanded on the results from the χ^2 analysis, which

305   only compared the frequency of association behavior in the presence of MPs, by making

306   predictions of the frequency of association behavior in the presence and absence of MPs. Odds

307   ratios were exponentially transformed to obtain percentage values. We hypothesized that MPs

308   facilitated association behavior between STs and RS, therefore presence or absence data of MPs

309   was used as the independent variable and the association behavior was the dependent variable for

310   this analysis. We expected to see the log-odds of association behavior increase in the presence of

311   mesopredators, therefore the association category that represented the least degree of round scad

312   vulnerability, NVI, was used as the baseline in the analysis.

313

Results

315   Of the 1024, 20-min intervals of video analyzed, 216 clips (21%) contained one or more

316   occurrences of STs and were used for hierarchical cluster analysis with Bray-Curtis similarity.

317   Among clips that contained STs, 186 (86%) included simultaneous observations of RS and STs

318   and were used in multinomial logistic regression. Of the videos that contained STs and RS, 159

319   (85%) contained one or more species of MPs and were used in the Pearson's χ^2. Average

320   observation time of STs and RS association behavior within clips was 36 ± 37.5 s (mean $\pm$ SD),

321   range 3–254 s, median 26 s.

322   *Visual observations*

323   In the absence of MPs and STs, RS were commonly observed swimming in unpolarized,

324   distributed schools as they foraged for plankton. Foraging and plankton feeding were inferred

325   from a commonly seen behavior where individuals flex their bodies slightly upward while

326   simultaneously opening the mouth (head-tipping), often with slight lateral adjustments,

327   presumably to ingest individual plankters (https://youtu.be/7_i8hoQXeAU).

328   When STs were not observed and MPs were actively foraging on RS, RS responded by

329   forming denser schools (i.e. reducing nearest neighbor distance), and often retreated to the sea

330   floor or associated with the structure of Frying Pan Tower (https://youtu.be/IesLMb9OStw,

331   https://youtu.be/CTwih5UYaqw, https://www.youtube.com/watch?v=CIFLIu2FVfA).

332   During LA behavior with STs, RS exhibited unpolarized schooling behaviors, but maintained

333   proximity and speed with the STs (https://www.youtube.com/watch?v=_CIqWVUprmU).

334   During TA aggregation behavior, RS decreased distance to nearest neighbor and STs, and moved

335   with the STs as one entity (https://youtu.be/P37lg7iiDJo).

336   Distinct transitions between behavioral categories were rarely observed, and the few

337   observed transitions captured the movement from LA aggregations to TA aggregations. During

338   these observations, RS displayed an immediate response (less than one second) to MPs. In some

339   of these occurrences, RS can be described as "pulsating" around the shark, as they transitioned

340   constantly between a LA and TA state (https://youtu.be/9WuEyByf_Pw, https://youtu.be/1Ss-

341   AvAMkVg).

342   *Predation attempts*

343   Regardless of the species involved, apparently successful piscivorous predation seen on

344   SharkCam is exceedingly rare (E Burge, 2020, unpublished data). During data collection from

345   1024, 20-min intervals of video (>340 h), we recorded all likely successful fish-on-fish predation

346   events and noted the species involved. Only a small number of observations of STs predation

347   attempts on MPs or other species were made (see examples https://youtu.be/cfGFAq1cQtI,

348   https://youtu.be/PllHZr-ioeo, https://youtu.be/i5wO7ILbbd8, https://youtu.be/P37lg7iiDJo), and

349   these were always on prey species much larger than round scad (LT, gag *Mycteroperca*

350   *microlepis* (Goode and Bean, 1879), red drum *Sciaenops ocellatus* (Linnaeus, 1766)).

351   Additionally, STs were only observed making predation attempts on other fishes when tightly

352   associated with RS. During these rare phenomena, sand tiger sharks made quick lunges toward

353   approaching fishes that appeared oblivious to the presence of the STs, presumably due to shrouds

354   of RS tightly associated with the shark. Although STs were never observed capturing prey during

355   these attempts, it appeared that schools of RS concealed the presence of STs and attracted scad

356   predators to the STs.

357   *Descriptive frequencies*

358   Sand tiger sharks are fall-winter-spring visitors seen most frequently during cool months

359   (21.3% overall frequency of occurrence, n=1024; Figure 2). Round scad are ubiquitous during

360   cool months and appear to depart in May–June and September–October (64.8% overall

361   frequency of occurrence, n=1024; Figure 2), but are most frequently seen during periods of STs

362   residency. The combinatorial frequency of occurrence for these two species (co-occurrence) was

363   13.8% within the 1024 videos. Additionally, the frequency of videos (of 1024) that contained

364   STs, RS, and one or more species of up to six different MPs was 16.3% (combinatorial

365   frequency of occurrence for 3+ species).

366   However, in videos selected because they contained STs (100% frequency of occurrence,

367   n=216), RS were much more likely to be seen (86.1% frequency of occurrence), and the

368   likelihood of this co-occurrence was strongly clustered with the presence of one or more MPs

369   species (83.7%, combinatorial frequency of occurrence for 3+ species). Of the six species of

370   MPs selected for this study, four species (almaco jack, blue runner, little tunny, and Atlantic

371   bonito) were more frequently observed within the data set of only STs videos (n=216) than the

372   SharkCam occurrence data set (n=1024) (Table 1).

373   *Association behavior*

374   Sand tiger sharks and RS clustered together the strongest (92.5%), while MPs had lower

375   similarities (Figure 3). Among MPs, GA was significantly clustered with RS and STs and had

376   the highest similarity value of all MPs (63.4%). Almaco jack (54.2% similarity) and BR (37.9%

377   similarity) were also significantly clustered with STs, RS, and GA, while LT, CJ, and AB were

378   not significantly clustered within the group.

379   Analysis of the 186 videos containing co-occurrence of STs and RS resulted in 40

380   observations of NVI, 58 observations of LA behavior, and 88 observations of TA behavior

381   without regard to the presence or absence of MPs (Figure 4). In the presence of MPs the

382   frequency of LA and TA behaviors increased. NVI was least frequently observed (n=33), and TA

383   behavior was most frequently observed (n=79). There was a significant difference in the

384   observed occurrences of behavioral categories compared to their expected frequencies, assuming

385   equal likelihoods of occurrence in the presence of MPs (Pearson's χ^2 = 20.981; df 2; p < 0.000).

386   Compared to no visible association, the log-odds of round scad being loosely associated with

387   STs was 82.9% greater, and tightly associated behavior was 196% greater in the presence of

388   mesopredators, but this result was not statistically significant (p>0.05), likely due to the number

389   of NVI behaviors seen even when MPs were present.

390

Discussion

392   Based on SharkCam underwater video observations conducted over more than 5 years and

393   representing over 340 hours of underwater footage, we demonstrate that round scad (RS) are

394   significantly more likely to be associated with sand tiger sharks (STs) in the presence of potential

395   scad mesopredators (MPs), than in their absence. This example of a behaviorally-mediated

396   indirect interaction (BMII) has important implications for trophic energy transfer on hard

397   bottoms in the SAB.

398   Round scad are the most abundant pelagic, planktivorous fish species observed on these hard

399   bottom habitats (Lindquist & Pietrafesa, 1989; Rountree, 1990; Burge et al., 2012), and high

400   densities of RS are especially apparent on mid-shelf live-bottoms of the SAB in winter (Hales

401   Jr., 1987). Under these circumstances, MPs are likely dependent on RS as a primary prey

402   resource, especially in cooler months, therefore, the ecosystem as a whole depends on round scad

403   for the transfer of energy up the food chain. Given this, it is important to investigate round scad

404   association behavior with sand tiger sharks and be aware that this interaction may have effects on

405   trophic transfer and mesopredator control. We have no reason to believe this STs and RS

406   association behavior is unique to the hard bottom habitat off Cape Fear, North Carolina,

407   therefore describing this behavior and its motivation aids in understanding trophic interactions

408   and prey strategies that influence predation success for pelagic predators. While the possibility of

409   benefit to STs in the form of increased predation opportunities remains an open question,

410   available observations provide evidence that STs use this association to perform an

411   undocumented predation strategy. The concealment provided to STs by RS and the attraction of

412   MPs to the shark suggest that this association behavior facilitates the feeding behavior of sand

413   tiger sharks.

414   Underwater videography has often been used to survey marine fish assemblages for diversity

415   and abundance in many locations (reviewed in Mallet & Pelletier, 2014). For example, video has

416   revealed that hard bottom habitat near Frying Pan Tower supports a diverse assemblage of both

417   temperate and tropical reef fish species that fluctuates seasonally (Burge et al., 2012; Burge,

418   O'Brien & jon-newbie, 2020). With few exceptions, underwater video to assess multispecies

419   behavior that includes large and highly mobile predators, is much more limited (but see Davis et

420   al., 1999; Dunbrack & Zielinski, 2003; Barker, Peddemors & Williamson, 2011; Bond et al.,

421   2012; Kanno et al., 2019; Brown et al., 2020), despite evidence that video may be an

422   advantageous survey method (McCauley et al., 2012).

423   Admittedly, the limited field of view of SharkCam served as a constraint to fully observe

424   behavior between STs, RS, and MPs because interactions occurred rapidly and in three-

425   dimensional space. In this study, occurrences of MPs outside the perspective of SharkCam

426   undoubtedly influenced events captured on camera, and this is likely responsible for many of the

427   observations of loosely associated (LA) and tightly associated (TA) behaviors that occurred in

428   the absence of MPs (STs+RS-MPs, n= 27). One or more species of selected MPs occurred in

429   approximately 84% of videos containing STs and RS (Table 1). Additionally, many other species

430   of potential scad mesopredators are also present at Frying Pan Tower, including a diverse

431   assemblage of demersal piscivores, and other pelagic species not designated as MPs in analyses

432   (Table S1). Recent work by Brown et al. (2020), also on sand tiger sharks in North Carolina, has

433   revealed that the presence of the sharks alters short-term reef fish community richness on

434   shipwrecks, with the prevalence of pelagic mesopredators elevated, and those of demersal

435   mesopredators depressed. They suggest that these differences in richness may be behaviorally-

436   mediated responses attributed to mesopredator optimization of foraging strategy, with sharks as a

437   threat to or competitor with pelagic mesopredators. Given this, it is likely that there are few

438   circumstances when aggregations of round scad are not exposed to potential predators. The

439   inclusion of STs+RS-MPs videos in the multinomial logistic regression likely resulted in the lack

440   of statistical significance (p>0.05), despite the relatively large increases in the odds of

441   association behavior as association strength increased (82.9% for LA and 196% for TA). This

442   pattern is supported by the results of the chi-square analysis that show the frequency of

443   occurrence of association behavior increased with association strength (p<0.00, Figure 4).

444   In similar research analyzing predator influence on prey behavior, Seghers (1974)

445   hypothesized that guppies formed schools because they were always exposed to predation

446   threats. Constant exposure to predators provides a strong explanation for why round scad are

447   observed forming associations with sand tiger sharks when designated MPs are not seen on

448   SharkCam. While observations of round scad association with sand tiger sharks in the absence of

449   MPs observations may be a result of sampling bias, it suggests that aggregation behavior is

450   driven by perceived predation risk assessed by the scad, and further suggests near constant

451   exposure to mesopredators. Experimental manipulation of mesopredators, their prey, and apex

452   predator presence have tested perceived predation risk to prey and mesopredators in marine (del

453   Mar Palacios et al. 2016) and terrestrial (Gordon et al., 2015) settings—one commonality that

454   emerges is that the presence of an apex predator alleviates perceived risk to prey by providing a

455   "refuge effect" associated with behavioral changes in prey.

456   Behavioral descriptions of RS and STs association were created to classify three distinct

457   levels of association based on preliminary observations. Inclusion of a continuous, quantitative

458   variable to measure aggregation strength would have increased the accuracy of identifying round

459   scad responses to mesopredators but was not necessary given how distinct existing behavioral

460   categories were. Nearest neighbor distance is a structural measurement used for fish aggregations

461   to calculate the positional preference of individual fish within an aggregation based on the

462   positions and movements of adjacent fish (Parrish, Viscido & Grunbaum, 2002). Evidence

463   supports that synchronization and group coordination are mediated by an individual's

464   interactions with nearest group members (Ballerini et al., 2008; Niizato & Gunji, 2011). We

465   visually estimated nearest neighbor distance of round scad to other aggregation members and to

466   sand tiger sharks to incorporate a measure of aggregation structure into our behavioral

467   descriptions to reduce observer bias. Conventionally, model simulations have been effectively

468   used to understand the mechanisms that influence strength, response to stimulus, and

469   coordination of fish schools (Huth & Wissel, 1992; Parrish, Viscido & Grunbaum, 2002).

470   In-situ experiments analyzing fish aggregation dynamics are far less common given the

471   difficulty to track individual fish. High resolution acoustic sonar (DIDSON) has recently become

472   a reliable alternative to conduct in-situ analysis of fish schooling behavior and has the capability

473   of monitoring the movement of individual fish (Moursund, Carlson & Peters, 2003; Boswell,

474   Wilson & Cowan, 2008; Rieucau et al., 2016). Auster et al. (2013) used DIDSON techniques to

475   effectively analyze prey distribution during predator-prey interactions similar to those observed

476   in this study on hard-bottoms in the SAB. DIDSON analysis would support more quantitative

477   data on the structure of associations between RS and STs, but was not necessary to understand

478   interactions between RS and MPs and would introduce additional cost for support and

479   maintenance.

480   Observations of RS becoming more aggregated in response to perceived predation threats are

481   consistent with prior literature (Rountree & Sedberry, 1991; Auster et al., 2009, 2013).

482   Reduction in nearest neighbor distance (i.e. increase in polarity) facilitates more efficient

483   communication between school members which enhance group synchrony and coordination

484   (Rieucau et al., 2015).

485   Sharks were always the nucleus of associations in our study and proximity to sharks we

486   hypothesized served as an additive predation defense against mesopredators. Although we

487   focused on association as protective for round scad with sharks, it is important to consider other

488   potential explanations for this behavior. Fuller and Parsons (2019) report observations of

489   association between RS and several species of sharks. Their potential explanations for this

490   behavior include protection from mesopredator predation, optmotor responses (Shaw & Tucker,

491   1965), and scatophagy on shark fecal clouds. We did not document the frequency of round scad

492   feeding during associations or observe foraging on fecal clouds, but round scad foraging for

493   plankton was common during observations. As fish forage, especially pelagic planktivores like

494   round scad, they become more vulnerable to predation; therefore, future studies should consider

495   foraging benefits and how associations with sharks reduced vulnerability during foraging. It is

496   also important to continue to explore the possible benefit of this association to sand tiger sharks

497   to fully understand how this association influences trophic interactions.

498

Conclusions

500   Based on in situ and underwater video observations from SharkCam, we hypothesized that

501   association behaviors between round scad and sand tigers were more frequent in the presence of

502   pelagic mesopredators than in their absence because the presence of mesopredators represents a

503   potential predation threat for round scad. Scad were shown to be significantly more likely to be

504   tightly associated with sand tiger sharks in the presence of mesopredators, compared to in their

505   absence. This example of a behaviorally mediated indirect interaction suggests that presence of

506   an apex predator alleviates perceived risk to prey from mesopredators. These results illuminate a

507   previously undescribed interaction with important consequences for trophic transfer and

508   mesopredator control on hard bottom habitats, and support the usage of long-term underwater

509   camera installations for addressing questions in marine ecology.

510

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542   **References**

543   Auster PJ, Cortés J, Alvarado JJ, Beita-Jiménez A, Auster PJ, Cortés J, Alvarado JJ, Beita-

544   Jiménez A. 2019. Coordinated hunting behaviors of mixed-species groups of piscivores and

545   associated species at Isla del Coco National Park (Eastern Tropical Pacific). *Neotropical*

546   *Ichthyology* 17:e180165. DOI: 10.1590/1982-0224-20180165.

547

548   Auster PJ, Godfrey J, Watson A, Paquette A, McFall G. 2009. Behavior of prey links midwater

549   and demersal piscivorous reef fishes. *Neotropical Ichthyology* 7:109–112.

550

551   Auster PJ, Kracker L, Price V, Heupel E, McFall G, Grenda D. 2013. Behavior webs of

552   piscivores at subtropical live-bottom reefs. *Bulletin of Marine Science* 89:377–396. DOI:

553   10.5343/bms.2011.1123.

554

555   Baird T. 1993. A new heterospecific foraging association between the puddingwife wrasse,

556   *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: Evaluation of the foraging consequences.

557   *Environmental Biology of Fishes* 38:393–397. DOI: 10.1007/BF00007535.

558

559   Bakun A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the

560   "predator pit" topographies. *Marine Ecosystem Structure and Dynamics* 68:271–288. DOI:

561   10.1016/j.pocean.2006.02.004.

562

563   Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Lecomte V, Orlandi A,

564   Parisi G, Procaccini A, Viale M, Zdravkovic V. 2008. Interaction ruling animal collective

565   behavior depends on topological rather than metric distance: Evidence from a field study.

566   *Proceedings of the National Academy of Sciences* 105:1232–1237. DOI:

567   10.1073/pnas.0711437105.

568

569   Barker SM, Peddemors VM, Williamson JE. 2011. A video and photographic study of

570   aggregation, swimming and respiratory behaviour changes in the Grey Nurse Shark (*Carcharias*

571   *taurus*) in response to the presence of SCUBA divers. *Marine and Freshwater Behaviour and*

572   *Physiology* 44:75–92. DOI: 10.1080/10236244.2011.569991.

573

574   Beard DW, Dess GG. 1988. Modeling organizational species' interdependence in an ecological

575   community: An input-output approach. *Academy of Management Review* 13:362–373. DOI:

576   10.5465/amr.1988.4306941.

577

578   Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD. 2012. Reef

579   sharks exhibit site-fidelity and higher relative abundance in marine reserves on the

580   Mesoamerican Barrier Reef. *PLOS ONE* 7:e32983. DOI: 10.1371/journal.pone.0032983.

581

582   Boswell KM, Wilson MP, Cowan JH. 2008. A semiautomated approach to estimating fish size,

583   abundance, and behavior from Dual-Frequency Identification Sonar (DIDSON) data. *North*

584   *American Journal of Fisheries Management* 28:799–807. DOI: 10.1577/M07-116.1.

585

586   Brown CM, Paxton AB, Taylor JC, Van Hoeck RV, Fatzinger MH, Silliman BR. 2020. Short-

587   term changes in reef fish community metrics correlate with variability in large shark occurrence.

588   *Food Webs* 24:e00147. DOI: 10.1016/j.fooweb.2020.e00147.

589

590   Burge EJ, Atack JD, Andrews C, Binder BM, Hart ZD, Wood AC, Bohrer LE, Jagannathan K.

591   2012. Underwater video monitoring of groupers and the associated hard-bottom reef fish

592   assemblage of North Carolina. *Bulletin of Marine Science* 88:15–38. DOI:

593   info:doi/10.5343/bms.2010.1079.

594

595   Burge EJ, O'Brien CE, jon-newbie. 2020. *SharkCam fishes: A guide to nekton at Frying Pan*

596   *Tower*. Los Angeles: Explore.org Ocean Frontiers, https://explore.org/livecams/oceans/shark-

597   cam.

598

599   Campo D, Mostarda E, Castriota L, Scarabello MP, Andaloro F. 2006. Feeding habits of the

600   Atlantic bonito, *Sarda sarda* (Bloch, 1793) in the southern Tyrrhenian sea. *Fisheries Research*

601   81:169–175. DOI: 10.1016/j.fishres.2006.07.006.

602

603 Carlson JK, McCandless CT, Cortés E, Grubbs RD, Andrews KI, Musick JA. 2009. *An update*
604 *on the status of the sand tiger shark,* Carcharias taurus*, in the northwest Atlantic Ocean*. NOAA
605 Technical Memorandum NMFS-SEFSC-585: U.S. Department of Commerce, National Oceanic
606 and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science
607 Center, Panama City Laboratory, Panama City, FL.
608
609 Chester AJ, Huntsman GR, Tester PA, Manooch CS. 1984. South Atlantic Bight reef fish
610 communities as represented in hook-and-line catches. *Bulletin of Marine Science* 34:267–279.
611
612 Cole RG. 1994. Abundance, size structure, and diver-oriented behaviour of three large benthic
613 carnivorous fishes in a marine reserve in Northeastern New Zealand. *Biological Conservation*
614 70:93–99. DOI: 10.1016/0006-3207(94)90276-3.
615
616 Compagno LJ. 2001. *Sharks of the world. An annotated and illustrated catalogue of shark*
617 *species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes,*
618 *Lamniformes and Orectolobiformes)*. Rome, p 55–62: Food & Agriculture Organization of the
619 United Nations.
620
621 Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. *Trends in*
622 *Ecology & Evolution* 23:194–201. DOI: 10.1016/j.tree.2007.12.004.
623
624 Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM. 2000.
625 Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-
626 waist" ecosystems. *ICES Journal of Marine Science* 57:603–618. DOI: 10.1006/jmsc.2000.0712.
627
628 Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning
629 M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–
630 996. DOI: 10.1126/science.283.5404.993.
631

632   Diamant A, Shpigel M. 1985. Interspecific feeding associations of groupers (Teleostei:

633   Serranidae) with octopuses and moray eels in the Gulf of Eilat (Agaba). *Environmental Biology*

634   *of Fishes* 13:153–159. DOI: 10.1007/BF00002584.

635

636   Dill LM, Heithaus MR, Walters CJ. 2003. Behaviorally mediated indirect interactions in marine

637   communities and their conservation implications. *Ecology* 84:1151–1157. DOI: 10.1890/0012-

638   9658(2003)084[1151:BMIIIM]2.0.CO;2.

639

640   Donaldson PL, Clavijo IE. 1994. Diet of round scad (*Decapterus punctatus*) on a natural and an

641   artificial reef in Onslow Bay, North Carolina. *Bulletin of Marine Science* 55:501–509.

642

643   Dunbrack R, Zielinski R. 2003. Seasonal and diurnal activity of sixgill sharks (*Hexanchus*

644   *griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. *Canadian Journal of*

645   *Zoology* 81:1107–1111. DOI: 10.1139/z03-087.

646

647   Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HPA. 2018. Reef fish communities

648   are spooked by scuba surveys and may take hours to recover. *PeerJ* 6:e4886. DOI:

649   10.7717/peerj.4886.

650

651   Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010. Patterns and ecosystem

652   consequences of shark declines in the ocean. *Ecology Letters* 13:1055–1071. DOI:

653   10.1111/j.1461-0248.2010.01489.x@10.1111/(ISSN)1461-0248.oceans-to-mountains.

654   Fletcher N, Batjakas IE, Pierce GJ. 2013. Diet of the Atlantic bonito *Sarda sarda* (Bloch, 1793)

655   in the Northeast Aegean Sea. *Journal of Applied Ichthyology* 29:1030–1035. DOI:

656   10.1111/jai.12164.

657

658   Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, Edwards AJ,

659   Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G. 2008.

660   Atlantic Reef Fish Biogeography and Evolution. *Journal of Biogeography* 35:22–47.

661

662 Ford JR, Swearer SE. 2013. Shoaling behaviour enhances risk of predation from multiple

663 predator guilds in a marine fish. *Oecologia* 172:387–397. DOI: 10.1007/s00442-012-2508-4.

664

665 Freshwater DW, Idol JN. 2013. Studies of North Carolina marine algae XIII. First reports of the

666 genus *Cottoniella* (Rhodophyta, Sarcomeniaceae). *Marine Biodiversity Records* 6. DOI:

667 10.1017/S1755267213000651.

668

669 Fuller LN, Parsons GR. 2019. A note on associations observed between sharks and teleosts.

670 *Southeastern Naturalist* 18:489–498. DOI: 10.1656/058.018.0314.

671

672 Gelsleichter J, Musick JA, Nichols S. 1999. Food habits of the smooth dogfish, *Mustelus canis*,

673 dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*,

674 and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. *Environmental*

675 *Biology of Fishes* 54:205–217. DOI: 10.1023/A:1007527111292.

676

677 Goldman KJ, Branstetter S, Musick JA. 2006. A re-examination of the age and growth of sand

678 tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing

679 protocols and use of multiple back-calculation techniques. *Environmental Biology of Fishes*

680 77:241. DOI: 10.1007/s10641-006-9128-y.

681

682 Gordon I. 1993. Pre-copulatory behaviour of captive sandtiger sharks, *Carcharias taurus*. In:

683 Demski LS, Wourms JP eds. *The reproduction and development of sharks, skates, rays and*

684 *ratfishes*. Developments in environmental biology of fishes. Dordrecht: Springer Netherlands,

685 159–164. DOI: 10.1007/978-94-017-3450-9_14.

686

687 Gordon CE, Feit A, Grüber J, Letnic M. 2015. Mesopredator suppression by an apex predator

688 alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B:*

689 *Biological Sciences* 282:20142870. DOI: 10.1098/rspb.2014.2870.

690

691   Govender A, Kistnasamy N, Van Der Elst RP. 1991. Growth of spotted ragged-tooth sharks

692   *Carcharias taurus* (Rafinesque) in captivity. *South African Journal of Marine Science* 11:15–19.

693   DOI: 10.2989/025776191784287718.

694

695   Hales Jr. SL. 1987. Distribution, abundance, reproduction, food habits, age and growth of round

696   scad, *Decapterus punctatus*, in the South Atlantic Bight. *Fish. Bull.* 85:251–268.

697

698   Haulsee DE, Fox DA, Breece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ. 2016.

699   Social network analysis reveals potential fission-fusion behavior in a shark. *Scientific Reports*

700   6:1–9. DOI: 10.1038/srep34087.

701

702   Hopkinson C, Jansson B-O, Schubauer-Berigan J. 1991. Community metabolism and nutrient

703   cycling at Gray's Reef, a hard bottom habitat in the Georgia Bight. *Marine Ecology Progress*

704   *Series* 73:105–120. DOI: 10.3354/meps073105.

705

706   Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The*

707   *American Naturalist* 93:145–159.

708

709   Huth A, Wissel C. 1992. The simulation of the movement of fish schools. *Journal of Theoretical*

710   *Biology* 156:365–385. DOI: 10.1016/S0022-5193(05)80681-2.

711

712   Kanno S, Schlaff AM, Heupel MR, Simpfendorfer CA. 2019. Stationary video monitoring

713   reveals habitat use of stingrays in mangroves. *Marine Ecology Progress Series* 621:155–168.

714   DOI: 10.3354/meps12977.

715   Kendall MS, Bauer LJ, Jeffrey CFG. 2009. Influence of hard bottom morphology on fish

716   assemblages of the continental shelf off Georgia, southeastern USA. *Bulletin of Marine Science*

717   84:265–286.

718

719   Klima EF, Wickham DA. 1971. Attraction of coastal pelagic fishes with artificial structures.

720   *Transactions of the American Fisheries Society* 100:86–99. DOI: 10.1577/1548-

721   8659(1971)100<86:AOCPFW>2.0.CO;2.

722

723   Kracker L, Kendall M, McFall G. 2008. Benthic features as a determinant for fish biomass in

724   Gray's Reef National Marine Sanctuary. *Marine Geodesy* 31:267–280. DOI:

725   10.1080/01490410802466611.

726

727   Kulbicki M. 1998. How the acquired behaviour of commercial reef fishes may influence the

728   results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology*

729   222:11–30. DOI: 10.1016/S0022-0981(97)00133-0.

730

731   Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and

732   prospectus. *Canadian Journal of Zoology* 68:619–640. DOI: 10.1139/z90-092.

733

734   Lindfield SJ, Harvey ES, McIlwain JL, Halford AR. 2014. Silent fish surveys: bubble-free diving

735   highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. *Methods*

736   *in Ecology and Evolution* 5:1061–1069. DOI: 10.1111/2041-210X.12262.

737

738   Lindquist DG, Pietrafesa LJ. 1989. Current vortices and fish aggregations: the current field and

739   associated fishes around a tugboat wreck in Onslow Bay, North Carolina. *Bulletin of Marine*

740   *Science* 44:533–544.

741

742   Macieira RM, Simon T, Pimentel CR, Joyeux J-C. 2010. Protection in the giant: goliath grouper

743   (*Epinephelus itajara*) as a refuge for mackerel scad (*Decapterus macarellus*). *Marine*

744   *Biodiversity Records* 3:e45. DOI: 10.1017/S1755267209991011.

745   Mallet D, Pelletier D. 2014. Underwater video techniques for observing coastal marine

746   biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research* 154:44–62.

747   DOI: 10.1016/j.fishres.2014.01.019.

748

749   Manooch III CS, Haimovici M. 1983. Foods of greater amberjack, *Seriola dumerili*, and almaco

750   jack, *Seriola rivoliana* (Pisces: Carangidae), from the South Atlantic Bight. *Journal of the Elisha*

751   *Mitchell Scientific Society* 99:1–9.

752

753   Manooch III CS, Mason DL, Nelson RS. 1985. Foods of little tunny *Euthynnus alletteratus*
754   collected along the southeastern and Gulf coasts of the United States. *Nippon Suisan Gakkaishi*
755   51:1207–1218. DOI: 10.2331/suisan.51.1207.

756

757   del Mar Palacios M, Warren DT, McCormick MI. 2016. Sensory cues of a top-predator
758   indirectly control a reef fish mesopredator. *Oikos* 125:201–209. DOI: 10.1111/oik.02116.

759

760   Matheson RH, Huntsman GR, Manooch CS. 1986. Age, growth, mortality, food and
761   reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South
762   Carolina. *Bulletin of Marine Science* 38:300–312.

763

764   McCauley DJ, McLean KA, Bauer J, Young HS, Micheli F. 2012. Evaluating the performance of
765   methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological*
766   *Applications* 22:385–392. DOI: 10.1890/11-1059.1.

767

768   McFarland WN, Kotchian NM. 1982. Interaction between schools of fish and mysids.
769   *Behavioral Ecology and Sociobiology* 11:71–76. DOI: 10.1007/BF00300094.

770

771   Miller GC, Richards WJ. 1980. Reef fish habitat, faunal assemblages, and factors determining
772   distributions in the South Atlantic Bight. *Proceedings of the Gulf and Caribbean Fisheries*
773   *Institute* 32:114–130.
774   Moursund RA, Carlson TJ, Peters RD. 2003. A fisheries application of a dual-frequency
775   identification sonar acoustic camera. *ICES Journal of Marine Science* 60:678–683. DOI:
776   10.1016/S1054-3139(03)00036-5.

777

778   Naughton SP, Saloman CH, Vaught RN. 1986. *Species profile of round scad* Decapterus
779   punctatus *(Cuvier 1829)*. U.S. Department of Commerce, National Oceanic and Atmospheric
780   Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama
781   City Laboratory, Panama City, FL, NOAA Technical Memorandum NMFS-SEFC-181.

782

783   NC Division of Marine Fisheries. 2020.Location of Hard Bottom Habitat. *Available at*

784   *http://portal.ncdenr.org/web/mf/habitat/hard-bottom* (accessed February 5, 2020).

785

786   Niizato T, Gunji Y-P. 2011. Metric–topological interaction model of collective behavior.

787   *Ecological Modelling* 222:3041–3049. DOI: 10.1016/j.ecolmodel.2011.06.008.

788

789   Paine RT. 1984. Ecological determinism in the competition for space: The Robert H. MacArthur

790   Award Lecture. *Ecology* 65:1339–1348. DOI: 10.2307/1939114.

791

792   Parker RO, Chester AJ, Nelson RS. 1994. A video transect method for estimating reef fish

793   abundance, composition, and habitat utilization at Gray's Reef National Marine Sanctuary,

794   Georgia. *Fishery Bulletin* 92:787–99.

795

796   Parker RO, Colby DR, Willis TD. 1983. Estimated amount of reef habitat on a portion of the

797   U.S. South Atlantic and Gulf of Mexico continental shelf. *Bulletin of Marine Science* 33:935–

798   940.

799

800   Parrish JK, Viscido SV, Grunbaum D. 2002. Self-organized fish schools: an examination of

801   emergent properties. *Biological Bulletin* 202:296–305.

802

803   Paxton AB, Blair E, Blawas C, Fatzinger MH, Marens M, Holmberg J, Kingen C, Houppermans

804   T, Keusenkothen M, McCord J, Silliman BR, Penfold LM. 2019. Citizen science reveals female

805   sand tiger sharks (*Carcharias taurus*) exhibit signs of site fidelity on shipwrecks. *Ecology*

806   100:e02687. DOI: 10.1002/ecy.2687.

807

808   Peckol P, Searles RB. 1984. Temporal and spatial patterns of growth and survival of invertebrate

809   and algal populations of a North Carolina continental shelf community. *Estuarine, Coastal and*

810   *Shelf Science* 18:133–143. DOI: 10.1016/0272-7714(84)90101-X.

811

812 Pollard D, Smith A. 2009. *Carcharias taurus*. The IUCN Red List of Threatened Species.

813 *Available at http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T3854A10132481.en* (accessed

814 December 18, 2019).

815

816 Posey MH, Ambrose WG. 1994. Effects of proximity to an offshore hard-bottom reef on

817 infaunal abundances. *Marine Biology* 118:745–753. DOI: 10.1007/BF00347524.

818

819 Preisser EL, Bolnick DI, Benard MF. 2005. Scared to death? The effects of intimidation and

820 consumption in predator-prey interactions. *Ecology* 86:501–509. DOI: 10.1890/04-0719.

821

822 Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS. 2009. The

823 rise of the mesopredator. *BioScience* 59:779–791. DOI: 10.1525/bio.2009.59.9.9.

824

825 Rieucau G, Fernö A, Ioannou CC, Handegard NO. 2015. Towards of a firmer explanation of

826 large shoal formation, maintenance and collective reactions in marine fish. *Reviews in Fish*

827 *Biology and Fisheries* 25:21–37. DOI: 10.1007/s11160-014-9367-5.

828

829 Rieucau G, Holmin AJ, Castillo JC, Couzin ID, Handegard NO. 2016. School level structural

830 and dynamic adjustments to risk promote information transfer and collective evasion in herring.

831 *Animal Behaviour* 117:69–78. DOI: 10.1016/j.anbehav.2016.05.002.

832

833 Riggs SR, Snyder SW, Hine AC, Mearns DL. 1996. Hardbottom morphology and relationship to

834 the geologic framework; Mid-Atlantic continental shelf. *Journal of Sedimentary Research*

835 66:830–846. DOI: 10.1306/D4268419-2B26-11D7-8648000102C1865D.

836 Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity

837 conservation. *Ecology Letters* 12:982–998. DOI: 10.1111/j.1461-0248.2009.01347.x.

838

839 Rountree RA. 1989. Association of fishes with Fish Aggregation Devices: Effects of structure

840 size on fish abundance. *Bulletin of Marine Science* 44:960–972.

841

842   Rountree RA. 1990. Community structure of fishes attracted to shallow water fish aggregation
843   devices off South Carolina, U.S.A. *Environmental Biology of Fishes* 29:241–262. DOI:
844   10.1007/BF00001183.
845

846   Rountree R, Sedberry G. 1991. In-situ observations of the schooling behavior of planktivorous
847   fishes. *Unpublished* draft manuscript:DOI: 10.13140/RG.2.1.2371.5289. DOI:
848   10.13140/RG.2.1.2371.5289.
849

850   SAFMC. 1998. *Final Habitat Plan for the South Atlantic Region: Essential fish habitat*
851   *requirements for fishery management plans of the South Atlantic Fishery Management Council*.
852   North Charleston, SC. 457 p.+appendices: South Atlantic Fishery Management Council.
853

854   Saloman CH, Naughton SP. 1984. *Food of crevalle jack (*Caranx hippos*) from Florida,*
855   *Louisiana, and Texas*. NOAA Technical Memorandum NMFS-SEFC-134: U.S. Department of
856   Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries
857   Service, Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL.
858

859   Schmitz OJ, Krivan V, Ovadia O. 2004. Trophic cascades: the primacy of trait-mediated indirect
860   interactions. *Ecology Letters* 7:153–163. DOI: 10.1111/j.1461-0248.2003.00560.x.
861

862   Schneider CW. 1976. Spatial and temporal distributions of benthic marine algae on the
863   continental shelf of the Carolinas. *Bulletin of Marine Science* 26:133–151.
864

865   Schneider CW, Searles RB. 1973. North Carolina marine algae. II. New records and observations
866   of the benthic offshore flora. *Phycologia* 12:201–211. DOI: 10.2216/i0031-8884-12-3-201.1.
867   Schneider CW, Searles RB. 1991. *Seaweeds of the southeastern United States: Cape Hatteras to*
868   *Cape Canaveral*. Durham, NC: Duke University Press.
869

870   Sedberry G, Van Dolah R. 1984. Demersal fish assemblages associated with hard bottom habitat
871   in the South Atlantic Bight of the U.S.A. *Environmental Biology of Fishes* 11:241–258. DOI:
872   10.1007/BF00001372.

873

874   Seghers BH. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary

875   response to predation. *Evolution* 28:486–489. DOI: 10.1111/j.1558-5646.1974.tb00774.x.

876

877   Shaw E, Tucker A. 1965. The optomotor reaction of schooling carangid fishes. *Animal*

878   *Behaviour* 13:330-IN7. DOI: 10.1016/0003-3472(65)90052-7.

879

880   Sih A, Englund G, Wooster D. 1998. Emergent impacts of multiple predators on prey. *Trends in*

881   *Ecology & Evolution* 13:350–355. DOI: 10.1016/S0169-5347(98)01437-2.

882

883   Sley A, Jarboui O, Ghorbel M, Bouain A. 2009. Food and feeding habits of *Caranx crysos* from

884   the Gulf of Gabès (Tunisia). *Journal of the Marine Biological Association of the United*

885   *Kingdom* 89:1375–1380. DOI: 10.1017/S0025315409000265.

886

887   Smale MJ, Booth AJ, Farquhar MR, Meÿer MR, Rochat L. 2012. Migration and habitat use of

888   formerly captive and wild raggedtooth sharks (*Carcharias taurus*) on the southeast coast of

889   South Africa. *Marine Biology Research* 8:115–128. DOI: 10.1080/17451000.2011.617756.

890

891   Smith K, Scarr M, Scarpaci C. 2010. Grey nurse shark (*Carcharias taurus*) diving tourism:

892   Tourist compliance and shark behaviour at Fish Rock, Australia. *Environmental Management*

893   46:699–710. DOI: 10.1007/s00267-010-9561-8.

894

895   Struhsaker P. 1969. Demersal fish resources: Composition, distribution, and commercial

896   potential of the continental shelf stocks off the southeastern United States. *Fisheries Independent*

897   *Research* 4:261–300.

898   Terborgh JW. 2015. Toward a trophic theory of species diversity. *Proceedings of the National*

899   *Academy of Sciences* 112:11415. DOI: 10.1073/pnas.1501070112.

900

901   Teter S, Wetherbee B, Fox D, Lam C, Kiefer D, Shivji M. 2015. Migratory patterns and habitat

902   use of the sand tiger shark (*Carcharias taurus*) in the western North Atlantic. *Marine and*

903   *Freshwater Research* 66:158–169. DOI: 10.1071/MF14129.

904

905 Toonen RJ, Bowen BW, Iacchei M, Briggs JC. 2016. Biogeography, Marine. In: Kliman RM ed.

906 *Encyclopedia of Evolutionary Biology*. Oxford: Academic Press, 166–178. DOI: 10.1016/B978-

907 0-12-800049-6.00120-7.

908

909 Wenner EL, Knott DM, Van Dolah RF, Burrell VG. 1983. Invertebrate communities associated

910 with hard bottom habitats in the South Atlantic Bight. *Estuarine, Coastal and Shelf Science*

911 17:143–158. DOI: 10.1016/0272-7714(83)90059-8.

912

913 Wickham DA, Jr JWW, Ogren LH. 1973. The efficacy of midwater artificial structures for

914 attracting pelagic sport fish. *Transactions of the American Fisheries Society* 102:563–572. DOI:

915 10.1577/1548-8659(1973)102<563:TEOMAS>2.0.CO;2.

916

917 Wootton JT. 1993. Indirect effects and habitat use in an intertidal community: Interaction chains

918 and interaction modifications. *The American Naturalist* 141:71–89. DOI: 10.1086/285461.

919

Occurrence of sand tiger sharks, round scad, and six mesopredator species in SharkCam videos.

Videos analyzed (n=1024, 20-min clips) were collected November 2014-January 2019. Frequency of occurrence data are for all videos, and those known to contain STs (n=216, 20-min clips). The frequency of STs + RS in all clips was 0.138.

Common Name	*Species*	Acronym	Videos containing	Frequency of occurrence	
				In STs clips (n=216)	In all clips (n=1024)
Sand Tiger Shark	*Carcharias taurus*	STs	216	1.000	0.213
Round Scad	*Decapterus punctatus*	RS	186	0.861	0.648
Greater Amberjack	*Seriola dumerili*	GA	106	0.491	0.580
Almaco Jack	*Seriola rivoliana*	AJ	89	0.412	0.351
Blue Runner	*Caranx crysos*	BR	61	0.282	0.210
Crevalle Jack	*Caranx hippos*	CJ	25	0.116	0.164
Little Tunny	*Euthynnus alletteratus*	LT	34	0.157	0.078
Atlantic Bonito	*Sarda sarda*	AB	9	0.042	0.015
			Frequency containing STs + RS + ≥1 MPs =	0.837	0.163

MPs

Figure 1

Sand tiger sharks and round scad in association behaviors.

(A) No visible interaction (NVI). Image from 18 April 2017, 12:43 EDT, (B) Loosely associated (LA). Image from 11 November 2019, 16:05 EST, (C) Tightly associated (TA). Image from 13 March 2018, 14:14 EDT. Image credits: Erin Burge/Explore.org.

Figure 2

Frequency of occurrence of sand tiger sharks and round scad indicate the seasonality of their presence at Frying Pan Tower.

Seasonality of sand tiger sharks (STs) and round scad (RS) are represented by frequency of occurrence data (solid line, STs; dashed line, RS) from SharkCam videos (n=1024, 20 min clips) from November 2014–January 2019. Sea surface temperatures (SST) are plotted as 2016 mean daily water temperature (°C) ± SD (open circles), 2003–2008 long term mean monthly SST (black circles on gray line), and 2003–2008 minimum and maximum monthly SST (gray stippled lines) at Frying Pan Tower (data from NOAA NBDC Station 41013 (LLNR 815)–Frying Pan Shoals, NC).
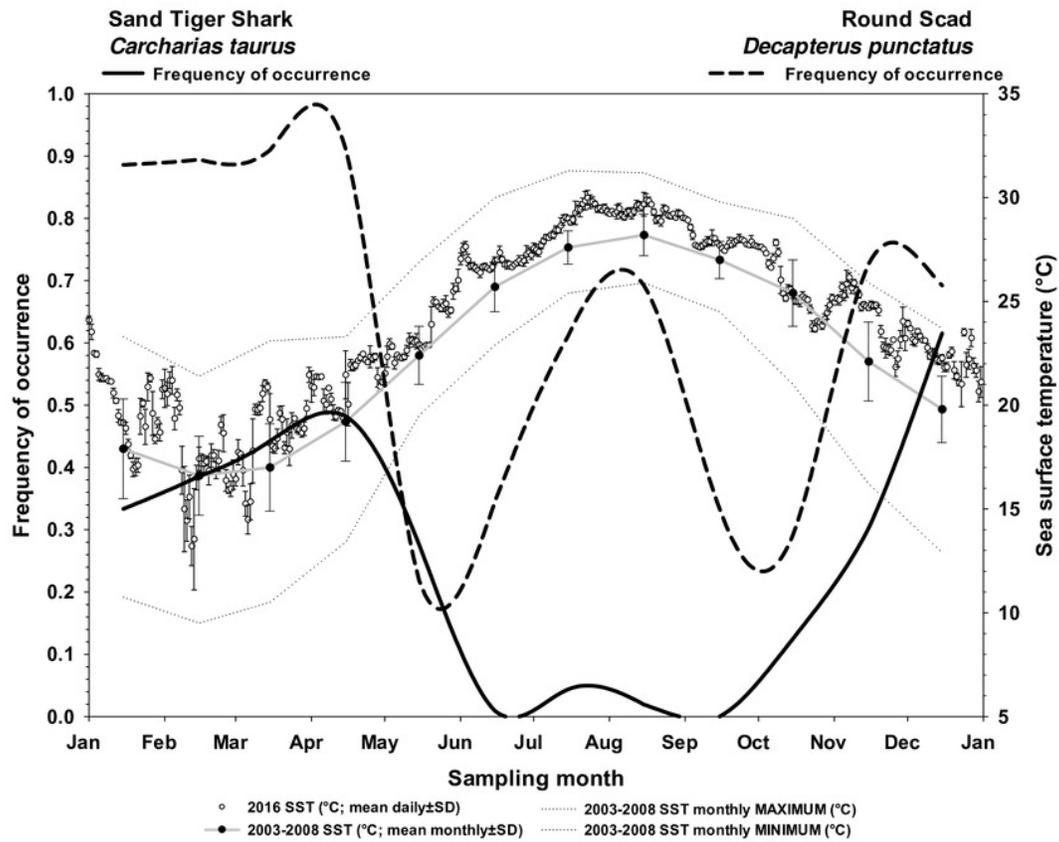
Figure 3

Cluster analysis of Bray-Curtis similarity to illustrate associations between sand tiger sharks (STs), round scad (RS), and individual mesopredator species (MPs).

See Table 1 for mesopredator species acronyms. STs and RS cluster strongly (92.5% similarity), while MPs have lower similarities. Clusters containing red-dashed branches are significant (Simprof, α= 0.05).
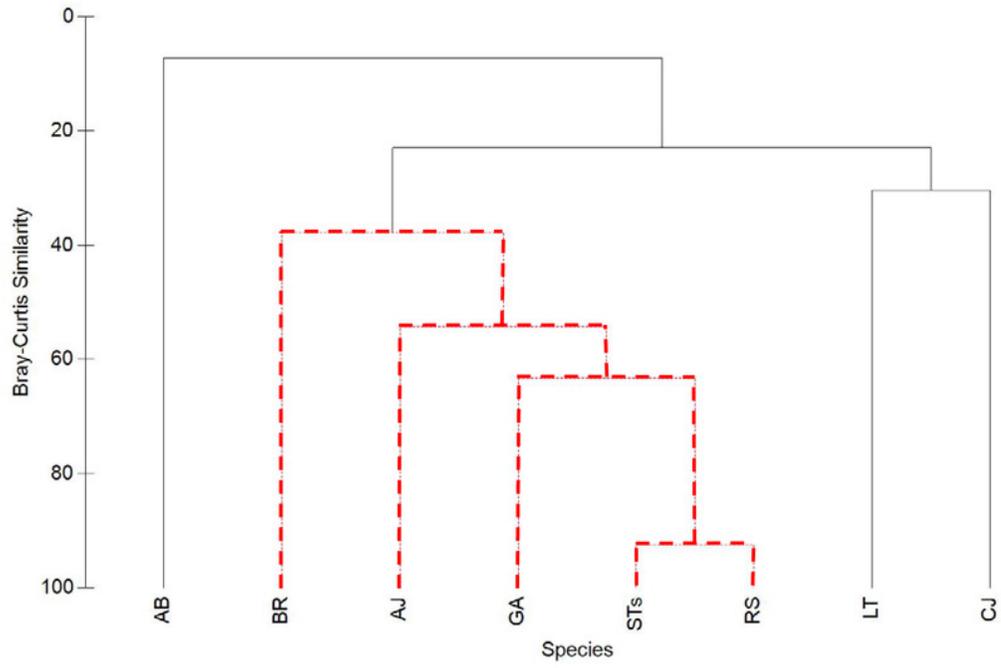
Figure 4

Association behavior counts between sand tiger sharks (STs) and round scad (RS).

(A) without and with the presence of mesopredators (MPs), and observed and expected frequencies (B) of association behaviors in video clips collected from SharkCam (n=186, 20-min clips). Tightly associated behavior between STs and RS occurred significantly more often than expected (Pearson's χ^2 = 20.981 (df 2), p < 0.000) in the presence of MPs.