



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

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ABSTRACT

In marine systems, behaviorally-mediated indirect interactions between prey, mesopredators, and higher trophic-level, large predators are less commonly investigated than other ecologic interactions, likely because of inherent difficulties associated with making observations. Underwater videos ($n = 216$) from SharkCam, a camera installation sited beneath Frying Pan Tower, a decommissioned light house and platform, on a natural, hard bottom site approximately 50 km off Cape Fear, North Carolina, were used to investigate association behavior of round scad *Decapterus punctatus* around sand tiger sharks *Carcharias taurus*. Videos containing sand tiger sharks were analyzed for the simultaneous presence of round scad, and six species of scad mesopredators, with scad-shark interactions assigned to one of three categories of association: no visible interaction, loosely associated, or tightly associated. The likelihood of scad being loosely or tightly associated with sharks was significantly higher in the presence of scad mesopredators, suggesting that sharks provide a predation refuge for scad. This behaviorally-mediated indirect interaction has important implications for trophic energy transfer and mesopredator control on hard bottoms, as scad are one of the most abundant planktivorous fish on hard bottoms in the western Atlantic Ocean. Although we were not able to provide statistical evidence that sand tiger sharks also benefit from this association behavior, we have clear video evidence that round scad association conceals and attracts mesopredators, enhancing predation opportunities for sand tiger sharks. These interactions potentially yield additional trophic consequences to this unique association and highlight the value of exploring behaviorally-mediated interactions in marine communities.

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INTRODUCTION

Multispecies interactions highlight the underlying interdependency between organisms that exist in all communities (*Hutchinson, 1959; Paine, 1984; Beard & Dess, 1988*). These interactions are often categorized as direct, between two species, or indirect, where the interaction between two species ultimately affects a third species (*Wootton, 1993*).

Behaviorally-mediated indirect interactions (BMIs) are a further classification of trait-mediated indirect interactions (TMIs) that are regulated by changes in a species' behavior (*Dill, Heithaus & Walters, 2003*). Both direct and indirect interactions produce changes in a species' density or behavior and are useful in understanding food webs and trophic exchanges. Indeed, indirect effects alter the risk landscapes of prey, including mesopredators which are prey species for larger carnivores (*Ritchie & Johnson, 2009*), especially in aquatic ecosystems (*Preisser, Bolnick & Benard, 2005; Heupel et al., 2014*), and can initiate trophic cascades (*Schmitz, Krivan & Ovidia, 2004; Creel & Christianson, 2008*). Competitor facilitation has been used in the context of BMIs when the presence of one species of predator causes a change in the behavior of a prey species that makes that prey species more accessible for a second species of predator (*Dill, Heithaus & Walters, 2003*). For example, some marine, demersal mesopredatory fishes access pelagic prey that are driven towards the seafloor by pelagic mesopredators, enhancing feeding opportunities (*Auster et al., 2009; Auster et al., 2013; Campanella et al., 2019*). Despite their importance, BMIs are less commonly investigated than other ecologic interactions because of the difficulty attributed to quantifying changes in behavior, especially within marine habitats.

Underwater observations

Underwater videography using stationary cameras is an efficacious method to conduct in-situ marine observations, including surveying marine fish assemblages for species richness and abundance, and behavioral observations (reviewed in *Mallet & Pelletier, 2014*). For example, video has revealed that hard bottom habitat near Frying Pan Tower, 50 km offshore of Cape Fear, North Carolina, supports a diverse assemblage of both temperate and tropical reef fish species that fluctuates seasonally (*Burge et al., 2012; Burge & O'Brien, 2020*). With few exceptions, the use of underwater video to assess multispecies behavior that includes large and highly mobile predators, is much more limited (but see *Davis et al., 1999; Dunbrack & Zielinski, 2003; Barker, Peddemors & Williamson, 2011; Bond et al., 2012; Kanno et al., 2019; Brown et al., 2020*), despite evidence that video may be an advantageous survey method (*McCauley et al., 2012*).

Once recorded, videos can be reviewed multiple times to optimize the amount of data collected from a single event, and can potentially increase recognition of behaviors that would otherwise be difficult to assess during SCUBA diving observations, which are depth and time limited, especially in multispecies interactions where participants may have different reactions to the presence of observers. Potential bias associated with SCUBA surveys can be introduced as fish react to the presence of divers, sometimes for long periods post-survey (*Emslie et al., 2018*), and this effect has been observed to be species specific (*Cole, 1994; Kulbicki, 1998; Burge et al., 2012; Lindfield et al., 2014*). For example, sand tiger sharks display increased respiration and movement in the presence of SCUBA divers (*Barker, Peddemors & Williamson, 2011*), providing evidence that underwater stationary videography may be a better alternative to observe the behavior of this species.

Sand tiger sharks (STs)

Sand tiger sharks, *Carcharias taurus* Rafinesque, 1810, are large (to >4 m), heavy-bodied lamniforms found in coastal and continental shelf waters of warm-temperate and tropical

seas worldwide. The diet of *C. taurus* is diverse and dominated by bony fishes and other elasmobranchs (Gelsleichter, Musick & Nichols, 1999). Individuals and aggregations occur especially in coastal areas of Australia (where they are known locally as grey nurse sharks), the east coast of South Africa (raggedtooth sharks), and the east coast of the United States (sand tiger sharks). Sand tiger shark aggregations are associated with migratory behavior, feeding, and reproduction (Compagno, 2001), and complex social networks and behaviors are described in this species (Haulsee et al., 2016a). Year-to-year site fidelity on shipwrecks and other artificial structures has been reported in North Carolina (Paxton et al., 2019) and individuals tagged in Delaware Bay undergo long-distance migrations to overwinter in continental shelf waters of North Carolina (Teter et al., 2015) and return to Delaware Bay predictably (Haulsee et al., 2016b). Additionally, sand tiger sharks are one of the few large-bodied sharks commonly housed in captivity (Govender, Kistnasamy & Van Der Elst, 1991; Gordon, 1993; Smale et al., 2012).

The conservation status of *C. taurus* is listed as globally Vulnerable (Pollard & Smith, 2009) with some regional populations considered endangered or critically endangered (Cavanagh et al., 2003; Chiaramonte, Domingo & Soto, 2007). Assessment of *C. taurus* in the northwestern Atlantic has suggested this population declined precipitously since the 1970s from overfishing in the 1980s to the mid-1990s (Musick, Branstetter & Colvocoresses, 1993; Musick et al., 2000), but analyses of multiple datasets now suggest only low to moderate declines in abundance (0.2–6.2%) (Carlson et al., 2009), in conflict with previous reports. More recent data suggest that the northwestern Atlantic population may be stabilized (Frazier, Paramore & Rootes-Murdy, 2019; Latour & Gartland, 2020). Regardless, conservative management is recommended due to the very low productivity for this species (Goldman, Branstetter & Musick, 2006; Carlson et al., 2009). Harvest of sand tigers is currently prohibited in the United States under Highly Migratory Species regulations and Habitat Area of Particular Concern designations are under further consideration (NOAA Fisheries, 2019).

Round scad (RS)

Round scad, *Decapterus punctatus* (Cuvier, 1829), are small-bodied (<300 mm) carangids found in the western Atlantic Ocean southward from Nova Scotia, at Bermuda, and in the Gulf of Mexico, Caribbean Sea, and along continental shores of South America to Rio de Janeiro (Naughton, Saloman & Vaught, 1986). In the South Atlantic Bight (SAB), round scad (typically 60–170 mm) are abundant in continental shelf waters in summer and fall, and move to hard bottoms in deeper, warmer areas of the mid- and outer shelf in winter (Hales Jr, 1987). Throughout their range, adult round scad are diurnal zooplankton specialists with the diet dominated by pelagic species and life stages (for meroplankton), as opposed to demersal plankton (Hales Jr, 1987; Donaldson & Clavijo, 1994).

Round scad are very frequently reported as stomach contents of pelagic and demersal piscivores (Matheson, Huntsman & Manooch, 1986; Naughton, Saloman & Vaught, 1986), and are often the most abundant species on FADs (Rountree, 1990), wrecks (Lindquist & Pietrafesa, 1989), and natural live bottoms (Parker, Chester & Nelson, 1994; Kendall, Bauer & Jeffrey, 2009; Burge et al., 2012) in portions of the SAB. Round scad schooling behaviors

around artificial structures (*Rountree, 1989; Rountree, 1990; Lindquist & Pietrafesa, 1989; Rountree & Sedberry, 1991*), while feeding (*Rountree & Sedberry, 1991*), and in response to their predators (*Auster et al., 2009; Auster et al., 2013; Campanella et al., 2019*) suggest an affinity for physical objects which can include larger fishes and elasmobranchs (*Fuller & Parsons, 2019*).

Mesopredators (MPs)

A diverse assemblage of pelagic and demersal piscivorous mesopredatory fishes inhabit hard bottom habitats of the SAB (*Chester et al., 1984; Sedberry & Van Dolah, 1984; Kendall, Bauer & Jeffrey, 2009; Burge et al., 2012; Burge & O'Brien, 2020*). Pelagic mesopredators include medium to large-sized jacks (e.g.: greater amberjack *Seriola dumerili* (Risso, 1810), almaco jack *Seriola rivoliana* Valenciennes in Cuvier and Valenciennes, 1833, blue runner *Caranx crysos* (Mitchill, 1815), crevalle jack *Caranx hippos* (Linnaeus, 1766)) and scombrids (e.g.: little tunny *Euthynnus alletteratus* (Rafinesque, 1810), and Atlantic bonito *Sarda sarda* (Bloch, 1793)). All are reported to prey on round scad or similar small fishes (*Manooch III & Haimovici, 1983; Saloman & Naughton, 1984; Manooch, Mason & Nelson, 1985; Campo et al., 2006; Sley et al., 2009; Fletcher, Batjakas & Pierce, 2013*).

Hard bottom habitat

Hard bottoms, or “live bottoms”, are rocky habitats and conspicuous geological features on the mainly soft sediment-dominated continental shelf within the SAB. In the Carolina Capes region of the SAB (offshore of North and South Carolina) (*Riggs et al., 1996*) estimates of hard bottom areal coverage vary on both latitudinal and longitudinal bases, with the greatest proportions on the shelf to the south of Cape Lookout, North Carolina (*Parker, Colby & Willis, 1983; SAFMC, 1998*). Extensive areas of hard bottom have been mapped and detailed geological descriptions have been published for the arcuate coastal embayments of Onslow Bay (southeastern North Carolina; Cape Lookout to the north and Cape Fear, North Carolina, to the south), and Long Bay (southeastern NC and northeastern South Carolina; Cape Fear to Cape Romaine, South Carolina) (*Milliman, 1972; Parker, Colby & Willis, 1983; Riggs, Cleary & Snyder, 1995; Cleary et al., 1996; Riggs et al., 1996; Ojeda et al., 2004; Denny et al., 2007; Taylor et al., 2016; Wheaton, 2018; NC Division of Marine Fisheries, 2020*). These bays are separated at Cape Fear by the Frying Pan Shoals, an area of shallow, shifting sediments that extend offshore approximately 50 km.

In general, hard bottoms within the Carolina Capes region are emergent areas of sedimentary and biogenic rock (fossiliferous limestones) formed from earlier Pleistocene and Tertiary deposits. They are typically surrounded by much more extensive areas of unconsolidated sediments (mainly sands) deposited during the Holocene. Hard bottoms vary in emergent relief from flat pavements with shallow veneers of sediment (*Riggs et al., 1996*), and typically depauperate epifauna and a near absence of infauna (*Renaud et al., 1996; Renaud et al., 1997; Renaud, Syster & Ambrose Jr, 1999*), to high-relief scarped hard bottoms (often called ledges) that may be meters above the surrounding sands with vertical or sloped cliffs and combinations of undercuts and overhangs (*Riggs et al., 1996*). Ledges in particular have rich communities of epifauna and rock-boring infauna (*Wenner et al., 1983*).

Hard bottoms provide structural habitat for the settlement of benthic sessile foundation species, including rich assemblages of sponges, scleractinian and octocorallian corals, ascidians, and macroalgae (*Struhsaker, 1969; Miller & Richards, 1980; Wenner et al., 1983*). The growth of these sessile organisms contributes to hard bottom reef structural complexity. Compared to adjacent soft-sediment dominated areas of the sea floor, hard bottoms create a striking contrast in habitat that supports high richness and abundance of fishes (*Sedberry & Van Dolah, 1984; Hopkinson, Jansson & Schubauer-Berigan, 1991*), invertebrates (*Wenner et al., 1983; Peckol & Searles, 1984*), and macroalgae (*Schneider & Searles, 1973; Schneider & Searles, 1991; Schneider, 1976; Freshwater & Idol, 2013*). Specifically, hard bottom reefs are home to often large aggregations of small schooling fishes, such as scads (*Decapterus* spp.) and young tomtate (*Haemulon aurolineatum* Cuvier in Cuvier and Valenciennes, 1830), that serve as important prey resources for many pelagic and demersal piscivorous fishes (*Kracker, Kendall & McFall, 2008; Auster et al., 2013*).

On hard bottoms off the coast of Georgia, competitive facilitation, an example of a BMII, was observed as schools of round scad and tomtate retreated from multispecies associations of pelagic piscivorous fish towards the seafloor, increasing predation opportunities for demersal piscivorous fishes (*Auster et al., 2009; Auster et al., 2013*). Furthermore, *Auster et al. (2009)* observed round scad and tomtate responding to the presence of pelagic predators by reducing nearest neighbor distance and forming more polarized aggregations.

Polarity in fish schools describes the likelihood of alignment and synchronization of movement among individuals (*Shaw, 1978; Soria, Freon & Chabanet, 2007*). Increased polarization is a common response to predators for many prey species that form aggregations and has been found to reduce the vulnerability of prey aggregations (reviewed in *Lima & Dill, 1990*). In addition to increasing polarization, prey fishes use several other strategies to reduce vulnerability to predators. Alternative strategies include temporal and spatial changes in forage fish distribution (*Campanella et al., 2019*) and forming aggregations around physical objects, which is hypothesized to be advantageous to prey by serving as a “schooling companion” (*Klima & Wickham, 1971*).

The abundance and taxonomic richness of species on hard bottom reefs and ledges facilitate unique interspecies interactions that are often driven by enhanced feeding opportunities or decreased vulnerability to predators (*McFarland & Kotchian 1982; Diamant & Shpigel, 1985; Baird, 1993*). For example, associations between blue runner, greater amberjack, and other large piscivorous fishes have been observed during coordinated predatory foraging on hard bottoms (*Auster et al., 2009*). Additionally, facilitative changes in predator behavior and prey reaction are linked to population processes (*Auster et al., 2013*) and patterns of temporal and spatial use of habitat by both predators and prey (*Campanella et al., 2019*). Effects of such associations containing multiple predators on prey mortality has been heavily debated and several studies have reported both additive and reduced predation effects (reviewed in *Sih, Englund & Wooster, 1998*).

Objectives

In this study, we examined association behavior between sand tiger sharks (STs), round scad (RS), and scad mesopredators (MPs) using video records from a unique, long-term underwater video installation sited on a hard bottom system off the coast of Cape Fear, North Carolina. Based on video observations collected to assess the fish species assemblage (E. Burge, 2020, unpublished data) and video and in situ observations by Burge and others, we repeatedly noticed the unusual association between STs and RS. Consequently, we hypothesized that association behaviors between round scad and sand tigers were more frequent in the presence of pelagic mesopredators than in their absence because the presence of mesopredators represents a potential predation threat for round scad. Strength of the association behavior was believed to be a response to mesopredators that reflects round scad vulnerability. We also suspect that aggregations of round scad may be mutually beneficial to sand tiger sharks by providing camouflage (*Auster et al., 2013*) and increasing predation opportunities on mesopredators. Direct, visual observations of wild behavior of sand tiger sharks are very limited (but see *Smith, Scarr & Scarpaci, 2010*; *Barker, Peddemors & Williamson, 2011*), and this species is currently IUCN Red listed globally as Vulnerable, making research and conservation efforts necessary for protection of this species. Investigating this association behavior may be insightful for a deeper understanding of predation strategies of sand tiger sharks, protective behaviors of a common prey species, and contribute knowledge of trophic dynamics on hard bottom reefs in the South Atlantic Bight.

MATERIALS & METHODS

Study site and infrastructure

Video collected in this project are from SharkCam, an underwater, live-streaming camera, publicly-viewable from <https://explore.org/livecams/oceans/shark-cam> (Explore.org, Los Angeles, CA). The camera is sited beneath Frying Pan Tower (33°29'N, 77°35'W) which is located at the seaward edge of Frying Pan Shoals, approximately 50 km off the coast of Cape Fear, North Carolina. Frying Pan Shoals is within the biogeographic Carolina Province (Cape Hatteras to Cape Canaveral, Florida), a warm-temperate to subtropical zone of the Western Atlantic Region (*Floeter et al., 2008*; *Briggs & Bowen, 2012*; *Briggs & Bowen, 2013*; *Toonen et al., 2016*). The camera is attached to a horizontal support at the base of Frying Pan Tower in about 15 m of water and is surrounded by an expansive area of natural hard bottom (*Riggs et al., 1996*; *NC Division of Marine Fisheries, 2020*) and steel debris, such as large pipes, beams, and gratings, from the exterior of the tower (*Collins Engineers Inc, 2010*) (https://www.youtube.com/playlist?list=PLK1g13VpyT6oYUJL7U3hRPlt2U5L_mcKL). To date, videos from SharkCam have been used to identify 116 temperate and tropical marine fish species (November 2014–February 2020) (*Burge & O'Brien, 2020*).

View Into The Blue® (Boulder, CO) cameras with CleanSweep™ hardware were used for all footage captured (<https://www.viewintothelblue.com/>). The cameras used (six during the span of this project) featured HD 720p (November 2014–July 2016 footage) or HD 1080p (after October 2016) video resolution, 360° pan-tilt-zoom that rotated on

a pre-determined schedule, or with manual remote control, and a field of view of $62^\circ \times 37^\circ$ (horizontal \times vertical). Automatic white balance (color control) was enabled in April 2017 to more closely approximate surface light for color correction. Power is provided by a solar installation atop Frying Pan Tower and data transmission used a line-of-sight radio to shore (Burge & O'Brien, 2020).

Video selection and analysis

SharkCam video files containing sand tiger shark *Carcharias taurus* (STs) records were extracted from a larger video database of all fish species occurrences gathered from non-consecutive, 20-min clips ($n = 1024$) analyzed as part of a larger community analysis project (E. Burge 2020, unpublished data). Video files were recorded during local daylight hours between November 2014 and January 2019.

All 20-min clips containing STs were re-analyzed to confirm shark identification, presence or absence of round scad (RS) *Decapterus punctatus* or a visually indistinguishable species, such as mackerel scad *D. macarellus* (Cuvier in Cuvier and Valenciennes, 1833) or redbtail scad *D. tabl* Berry, 1968, and the identification of mesopredators (MPs). Duration of the STs on screen (seconds) was recorded to obtain average observation time.

This more detailed analysis of clips from the larger video database resulted in the rejection of some data records ($n = 26$) because the initial shark identification was not confirmed ($n = 11$ clips), only a fleeting glimpse of STs was available and/or visibility was poor ($n = 12$), or the original video could not be located ($n = 3$). Poor visibility compromised identification of RS or MPs. To these confirmed STs records from the larger database we were able to add 24 clips that contained STs from other video files not previously included in the larger video database by using more recently analyzed clips, personal observations, or reports from citizen scientists recorded with the live video stream on-line (<https://explore.org/livecams/oceans/shark-cam>). In these added clips, the shark was located and a 20-min clip of video was analyzed as described with the shark centered in the middle. In total, 216 clips with the confirmed presence of STs were analyzed.

Clips with STs were reviewed for the simultaneous co-occurrence of RS and assigned a descriptive category of the association behavior between them using the following categories: no visible interaction (NVI), loosely associated (LA), and tightly associated (TA) (Fig. 1). No visible association was defined as both species moving independently of each other or in opposing directions and with their heads oriented in different directions. Loosely associated aggregations were defined as both species moving in a similar direction, their heads oriented in a similar direction, and RS maintaining an estimated five scad body lengths or more from STs and other school members. Tightly associated aggregations were defined as both species moving as one entity, their heads oriented in the same direction, and RS maintaining less than five estimated body lengths from STs and other school members. These behaviors represent a spectrum of association that we hypothesize correlates with the vulnerability of RS to predation in response to the presence of pelagic mesopredators (MPs); NVI representing the least vulnerable and TA representing the most vulnerable. Video files with multiple sightings of STs were treated as independent occurrences if shark observations were separated by 10-min or greater. Multiple association observations

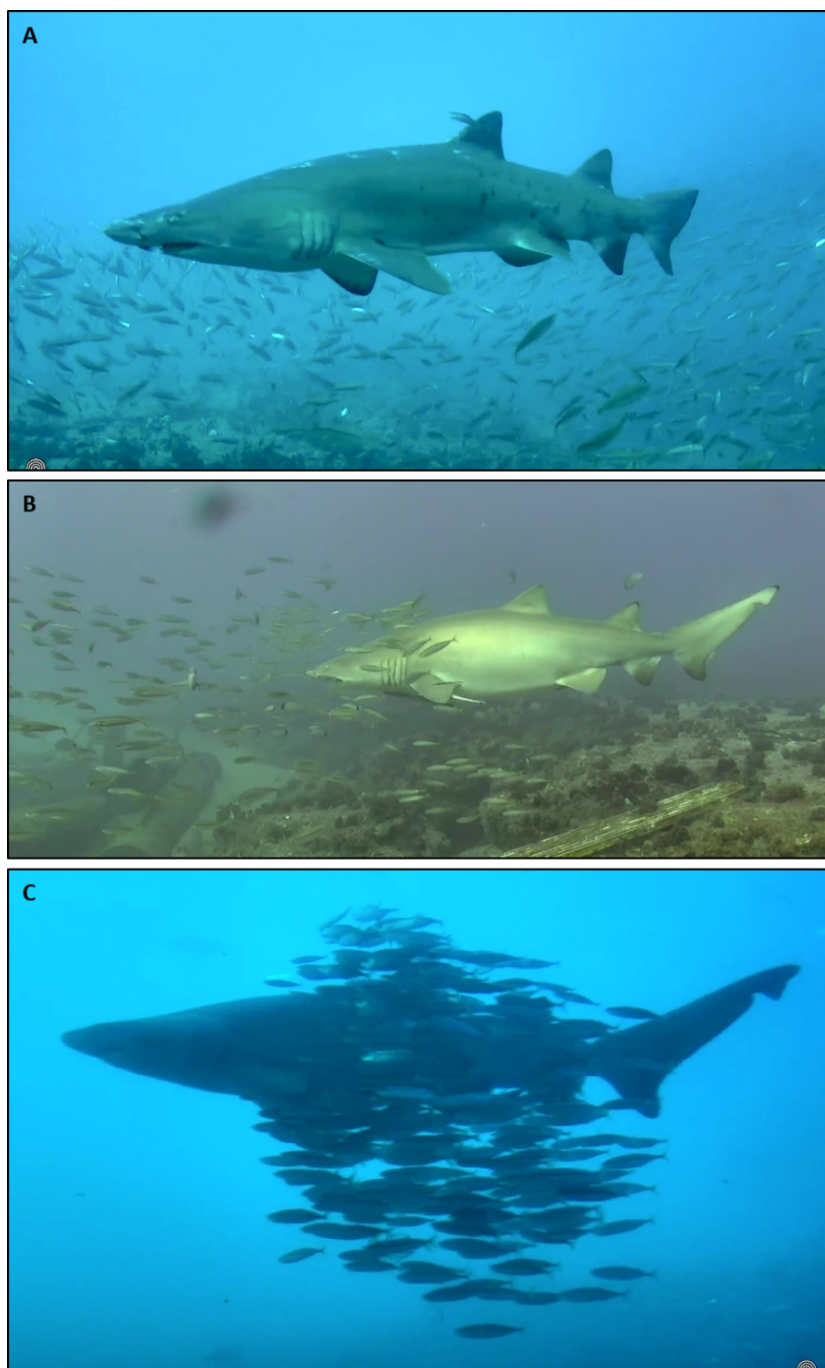


Figure 1 Sand tiger sharks and round scad in association behaviors. (A) No visible interaction (NVI). Image from 18 April 2017, 12:43 EDT, (B) Loosely associated (LA). Image from 11 November 2019, 16:05 EST, (C) Tightly associated (TA). Image from 13 March 2018, 14:14 EDT. Image credits: Erin Burge/Explore.org.

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within a 10-min interval were assigned a descriptive category that best described the general association behavior of the recurring individuals. We were not able to individually identify observed STs, however, we have no reason to believe that this association behavior was limited to individual sharks given the multi-year duration over which videos were collected.

Mesopredators (MPs) were hypothesized to be mediators of RS and STs association behavior, and so in order to assess this behaviorally-mediated response, we documented the presence, identity, and occurrence of six pelagic MPs selected a priori within all 20-min video clips that also contained STs. These were almaco jack (*Seriola rivoliana*, AJ), Atlantic bonito (*Sarda sarda*, AB), blue runner (*Caranx crysos*, BR), crevalle jack (*Caranx hippos*, CJ), greater amberjack (*Seriola dumerili*, GA), and little tunny (*Euthynnus alletteratus*, LT). Mesopredators were selected based on preliminary observations of co-occurrence and predation attempts on RS recorded in the larger video database (E. Burge, 2020 unpublished data), published reports that suggest facilitated, or even cooperative, hunting ([Auster et al., 2013](#); [Auster et al., 2019](#)), and shared characteristics of size (individual body size approximately 0.5 m–1.5 m), highly active feeding behavior, and diet overlap ([Manooch III & Haimovici, 1983](#); [Saloman & Naughton, 1984](#); [Manooch, Mason & Nelson, 1985](#); [Campo et al., 2006](#); [Sley et al., 2009](#); [Fletcher, Batjakas & Pierce, 2013](#)).

Data analysis

Hierarchical cluster analysis using Bray-Curtis similarity on presence or absence data was used to illustrate the strength of co-occurrences between STs, RS, and each species of mesopredator in all recorded instances of sharks ($n = 216$). Statistical significance was tested with 1,000 simulation permutations by Simprof ($\alpha = 0.05$) in PRIMER-e 6 (Plymouth Marine Laboratory UK).

Pearson's chi-squared test (χ^2) was used to further investigate whether the frequency of association behaviors between STs and RS were more commonly observed than expected if each category of association had an equal chance of occurring (33%). Equal likelihoods of each association category occurring were assumed to represent a condition in which RS did not benefit from a close physical association with STs. Pearson's χ^2 was also used to test the frequency of association behaviors in the presence of one or more species of mesopredator. The behavior categories were used to represent a continuum of association that reflected the relative vulnerability of RS to pelagic MPs.

Multinomial logistic regression ('multinom', R version 3.5.1) was used to calculate the log-odds of association behavior (i.e., LA and TA behaviors) in the presence or absence of one or more species of mesopredator. This analysis expanded on the results from the χ^2 analysis, which only compared the frequency of association behavior in the presence of MPs, by making predictions of the frequency of association behavior in the presence and absence of MPs. Odds ratios were exponentially transformed to obtain percentage values. We hypothesized that MPs facilitated association behavior between STs and RS, therefore presence or absence data of MPs was used as the independent variable and the association behavior was the dependent variable for this analysis. We expected to see the log-odds of association behavior increase in the presence of mesopredators, therefore the association

Table 1 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	<i>Carcharias taurus</i>	STs	216	1.000	0.213
Round Scad	<i>Decapterus punctatus</i>	RS	186	0.861	0.648
Greater Amberjack	<i>Seriola dumerili</i>	GA	106	0.491	0.580
Almaco Jack	<i>Seriola rivoliana</i>	AJ	89	0.412	0.351
Blue Runner	<i>Caranx crysos</i>	BR	MPs 61	0.282	0.210
Crevalle Jack	<i>Caranx hippos</i>	CJ	25	0.116	0.164
Little Tunny	<i>Euthynnus alletteratus</i>	LT	34	0.157	0.078
Atlantic Bonito	<i>Sarda sarda</i>	AB	9	0.042	0.015
Frequency containing STs + RS + ≥ 1 MPs =				0.837	0.163

Note.
MPs are in bold.

category that represented the least degree of round scad vulnerability, NVI, was used as the baseline in the analysis.

RESULTS

All clips ($n = 216$) that contained one or more sand tigers sharks (STs) were used for hierarchical cluster analysis with Bray-Curtis similarity. Among all clips, 186 (86%) included simultaneous observations of RS and STs and were used in multinomial logistic regression. Of the videos that contained STs and RS, 159 (85%) contained one or more species of MPs and were used in the Pearson's χ^2 (Table 1). Average observation time of STs and RS association behavior within clips was 36 ± 37.5 s (mean \pm SD), range 3–254 s, median 26 s.

Visual observations

In the absence of MPs and STs, RS were commonly observed swimming in unpolarized, distributed schools as they foraged for plankton. Foraging and plankton feeding were inferred from a commonly seen behavior where individuals flex their bodies slightly upward while simultaneously opening the mouth (head-tipping), often with slight lateral adjustments, presumably to ingest individual plankters (https://youtu.be/7_i8hoQXeAU; Table S1).

When STs were not observed and MPs were actively foraging on RS, RS responded by forming denser schools (i.e., reducing nearest neighbor distance), and often retreated to the sea floor or associated with the structure of Frying Pan Tower (<https://youtu.be/IesLMb9OStw>, <https://youtu.be/CTwih5UYaqw>, <https://youtu.be/CIFLIu2FVfA>; Table S1).

During LA behavior with STs, RS exhibited unpolarized schooling behaviors, but maintained proximity and speed with the STs (https://youtu.be/_CIqWVUprmU). During

TA aggregation behavior, RS decreased distance to nearest neighbor and STs, and moved with the STs as a highly coordinated group (<https://youtu.be/P37lg7iiDJo>; Table S1).

Distinct transitions between behavioral categories were rarely observed, and the few observed transitions captured the movement from LA aggregations to TA aggregations (Fig. 2). During these observations, RS displayed an immediate response (less than one second) to MPs. In some of these occurrences, RS can be described as “pulsating” around the shark, as they transitioned constantly between a LA and TA state (https://youtu.be/9WuEyByf_Pw, <https://youtu.be/1Ss-AvAMkVg>, Table S1).

Predation attempts

Regardless of the species involved, apparently successful piscivorous predation seen on SharkCam is exceedingly rare (E. Burge, 2020, unpublished data). During data collection from 1024, 20-min intervals of video (>340 h), we recorded all likely successful fish-on-fish predation events and noted the species involved. Only a small number of observations of STs predation attempts on MPs or other species were made ($n = 5$, Table 2) and these were always on prey species much larger than round scad. Attempted predation was documented on two MPs species, little tunny and blue runner, with two additional attempts on gag *Mycteroperca microlepis* (Goode and Bean, 1879) and red drum *Sciaenops ocellatus* (Linnaeus, 1766). Additionally, STs were only observed making predation attempts on other fishes when tightly associated with RS, with no observations of attempted predation during NVI and LA behaviors. The timing of these events did not suggest a bias towards crepuscular feeding although a very small sample size currently exists (Table 2).

During these rare phenomena, sand tiger sharks made quick lunges toward approaching fishes that appeared oblivious to the presence of the STs, presumably due to shrouds of RS tightly associated with the shark (Fig. 3). Although STs were never observed capturing prey during these attempts, it appeared that schools of RS concealed the presence of STs and attracted scad predators to the STs (see videos in Table 2).

Descriptive frequencies

Sand tiger sharks are fall-winter-spring visitors seen most frequently during cool months (21.3% overall frequency of occurrence among all months, $n = 1024$; Fig. 4). Round scad are ubiquitous during cool months and appear to depart in May–June and September–October (64.8% overall frequency of occurrence among all months, $n = 1024$; Fig. 4), but are most frequently seen during periods of STs residency. The combinatorial frequency of occurrence for these two species (co-occurrence) was 13.8% within the 1024 videos. Additionally, the frequency of videos (of 1024) that contained STs, RS, and one or more species of up to six different MPs was 16.3% (combinatorial frequency of occurrence for 3+ species) (Table 1).

However, in videos selected because they contained STs (100% frequency of occurrence, $n = 216$), RS were much more likely to be seen (86.1% frequency of occurrence), and the likelihood of this co-occurrence was strongly clustered with the presence of one or more MPs species (Fig. 5) (83.7%, combinatorial frequency of occurrence for 3+ species). Of the six species of MPs selected for this study, four species (almaco jack, blue runner, little

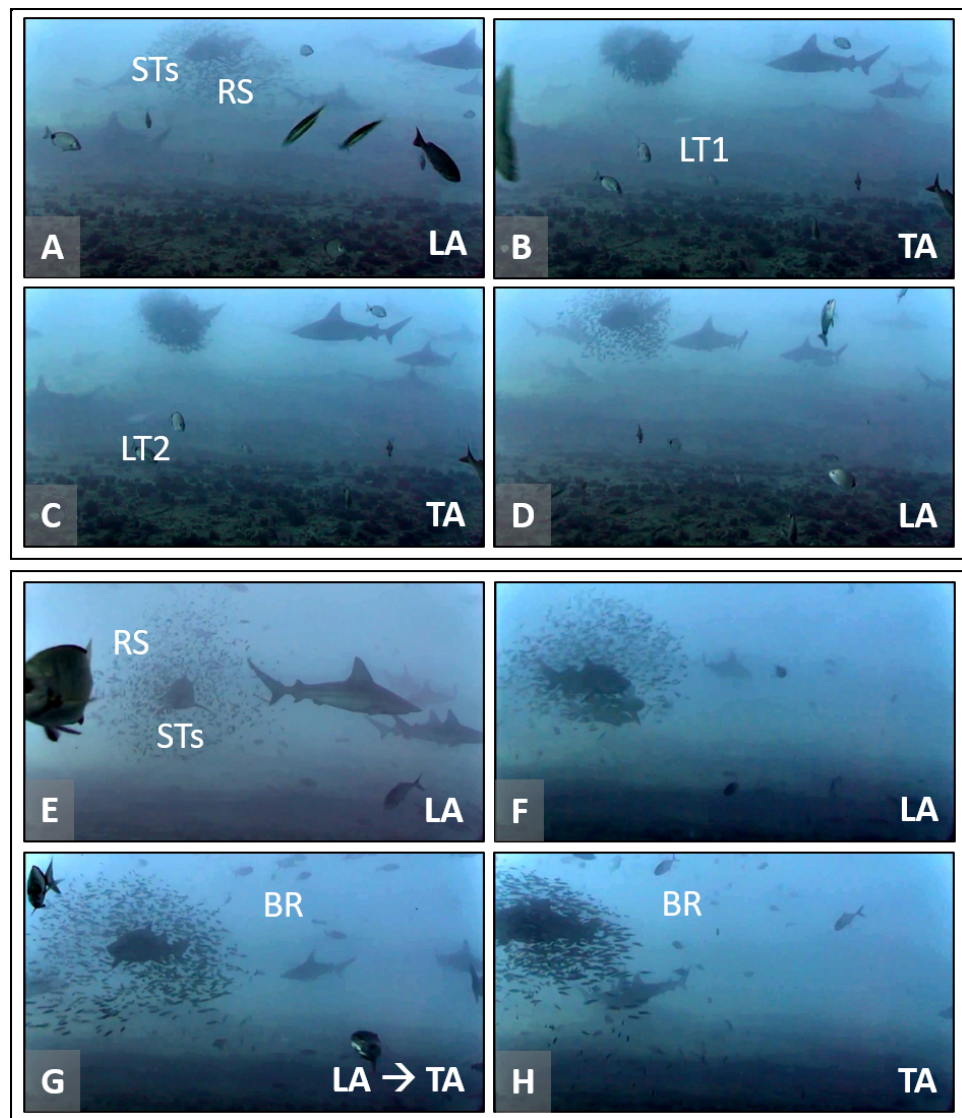


Figure 2 Association behavior between round scad (RS) and sand tiger sharks (STs) as a response to mesopredators (MPs). Two sets of screen captures (A–D and E–H, lower left of each image) are representative of transitions between loose association (LA) and tight association (TA) that occur between RS and STs in the presence of MPs, little tunny (LT) and blue runner (BR). (A–D) RS are in LA with a STs. Two LT successively cause a rapid transition to TA. Once attacking mesopredators depart, RS transition to LA rapidly. View video at <https://youtu.be/1Ss-AvAMkVg?t=180> (0:03:00). (E–H) RS are in LA with STs. A school of BR approaches and RS rapidly transition to TA behavior. View video at <https://youtu.be/1Ss-AvAMkVg?t=925> (0:15:25). Video files are deposited in a public online repository on Zenodo (doi:10.5281/zenodo.4477423). Note that sandbar sharks (*Carcharhinus plumbeus*) are also present in some images. Image credits: Erin Burge/Explore.org.

Full-size DOI: 10.7717/peerj.11164/fig-2

tunny, and Atlantic bonito) were more frequently observed within the data set of only STs videos ($n = 216$) than the SharkCam occurrence data set ($n = 1024$) (Table 1).

Table 2 Attempted predation events by sand tiger sharks (STs) on mesopredators (MPs in bold) while in association with round scad (RS + STs). All association behaviors were tightly associated (TA). Date (DD Mmm YYYY) and time (U.S. Eastern Standard Time, UTC/GMT -5) are local to the camera. Video time refers to the time within the video clip of the attempt (H:MM:SS). Video files are deposited in a public online repository on Zenodo (doi: <https://doi.org/10.5281/zenodo.4477423>).

Prey species	RS+STs	Date of occurrence	Clock time of occurrence	Video time	Video reference
Little Tunny <i>Euthynnus alletteratus</i>	TA	19 Dec 2015	1121 EST	0:00:08	https://youtu.be/P37lg7iiDJo
	TA	06 Jan 2019	1040 EST	0:00:09	https://youtu.be/PlIHZr-ioeo
Red Drum <i>Sciaenops ocellatus</i>	TA	12 Jan 2019	1148 EST	0:19:45	https://youtu.be/i5wO7ILbbd8
Blue Runner <i>Caranx crysos</i>	TA	12 Jan 2019	1150 EST	0:20:52	https://youtu.be/i5wO7ILbbd8
Gag <i>Mycteroperca microlepis</i>	TA	15 Jan 2019	0740 EST	0:00:07	https://youtu.be/cfGFAq1cQtl

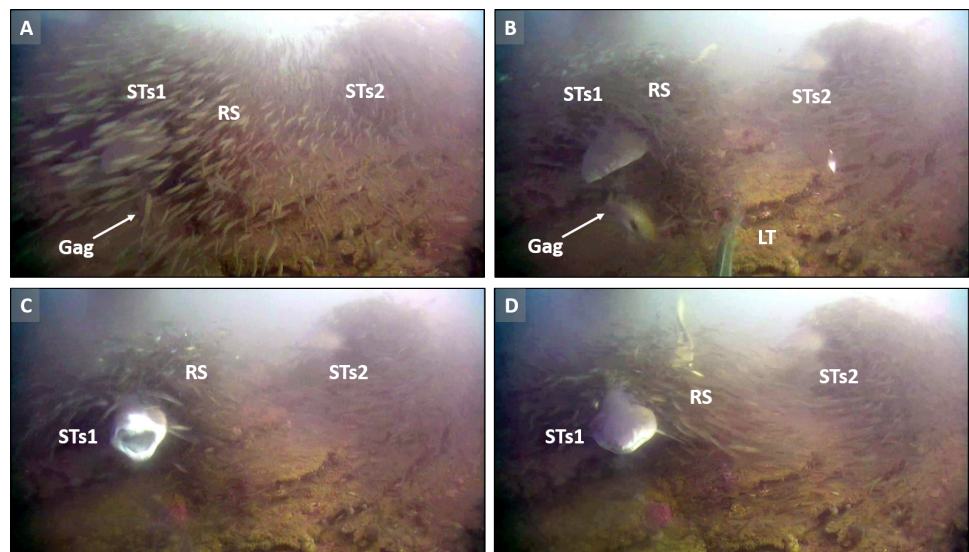


Figure 3 Association behavior and sand tiger shark predation. Screen captures (A–D) are representative of tight association (TA) behavior between sand tiger sharks (STs1 and STs2) and round scad (RS). (A) Gag *Mycteroperca microlepis*, approaches, apparently not recognizing the presence of STs1. (B) Simultaneously, a little tunny (LT), approaches shrouded STs1 in what appears to be predation behavior on RS, disrupting the shroud. (C) The STs attempts to prey upon the gag, but (D) is unsuccessful. See the example video for additional information (<https://youtu.be/cfGFAq1cQtl>). Video files are deposited in a public online repository on Zenodo (doi:10.5281/zenodo.4477423). Image credits: Erin Burge/Explore.org.

Full-size DOI: [10.7717/peerj.11164/fig-3](https://doi.org/10.7717/peerj.11164/fig-3)

Association behavior

Sand tiger sharks and RS clustered together the strongest (92.5%), while MPs had lower similarities (Fig. 5). Among MPs, GA was significantly clustered with RS and STs and had the highest similarity value of all MPs (63.4%). Almaco jack (AJ; 54.2% similarity) and BR (37.9% similarity) were also significantly clustered with STs, RS, and GA, while LT, CJ, and AB were not significantly clustered within the group.

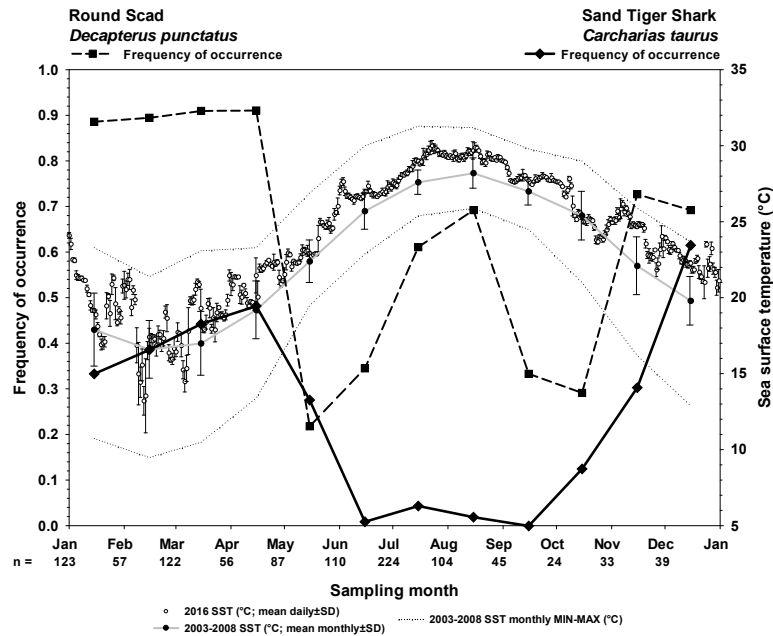


Figure 4 Frequency of occurrence of sand tiger sharks and round scad indicate the seasonality of their presence at Frying Pan Tower. Seasonality of sand tiger sharks (STs) and round scad (RS) are represented by frequency of occurrence data (solid line, STs; dashed line, RS) from SharkCam videos ($n = 1024$, 20 min clips) from November 2014–January 2019. Video clips analyzed by month are indicated as ($n =$). Sea surface temperatures (SST) are plotted as 2016 mean daily water temperature ($^{\circ}\text{C}$) \pm 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).

Full-size DOI: 10.7717/peerj.11164/fig-4

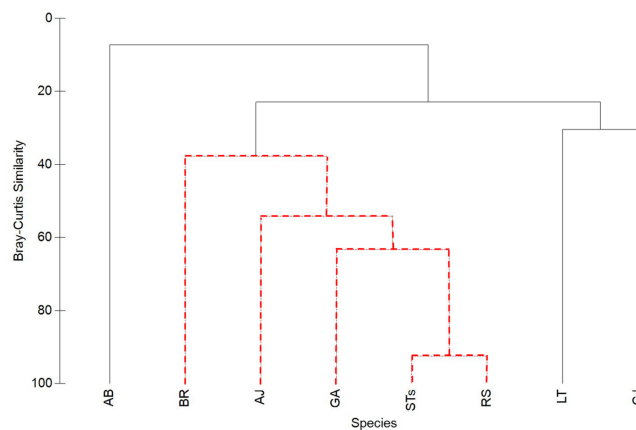


Figure 5 Cluster analysis of Bray-Curtis similarity to illustrate associations between sand tiger sharks (STs), round scad (RS), and individual mesopredator species (MPs). See Table 1 for species acronyms. STs and RS cluster strongly (92.5% similarity), while MPs have lower similarities. Clusters containing red-dashed branches are significant (Simprof, $\alpha = 0.05$).

Full-size DOI: 10.7717/peerj.11164/fig-5

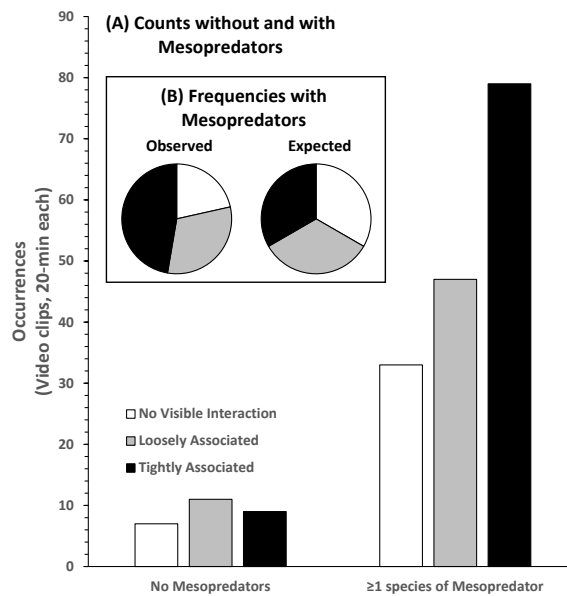


Figure 6 Association behavior counts between sand tiger sharks (STs) and round scad (RS). (A) Without and with the presence of mesopredators (MPs), and observed and expected frequencies (B) of association behaviors in video clips collected from SharkCam ($n = 186$, 20-min clips). Tightly associated behavior between STs and RS occurred significantly more often than expected (Pearson's $\chi^2 = 20.981$ (df 2), $p < 0.000$) in the presence of MPs.

Full-size DOI: 10.7717/peerj.11164/fig-6

Analysis of the 186 videos containing co-occurrence of STs and RS resulted in 40 observations of NVI, 58 observations of LA behavior, and 88 observations of TA behavior without regard to the presence or absence of MPs (Fig. 6). In the presence of MPs the frequency of LA and TA behaviors increased. NVI was least frequently observed ($n = 33$), and TA behavior was most frequently observed ($n = 79$). There was a significant difference in the observed occurrences of behavioral categories compared to their expected frequencies, assuming equal likelihoods of occurrence in the presence of MPs (Pearson's $\chi^2 = 20.981$; df 2; $p < 0.000$). Compared to no visible association, the log-odds of round scad being loosely associated with STs was 82.9% greater, and tightly associated behavior was 196% greater in the presence of mesopredators, but these results were not statistically significant (LA, $p = 0.727$; TA, $p = 0.218$), likely due to the number of NVI behaviors seen even when MPs were present.

DISCUSSION

Based on SharkCam underwater video observations conducted over more than 5 years and representing over 340 h of underwater footage, we demonstrate that round scad (RS) are significantly more likely to be associated with sand tiger sharks (STs) in the presence of potential scad mesopredators (MPs), than in their absence. This example of a behaviorally-mediated indirect interaction (BMII) has important implications for trophic energy transfer on hard bottoms in the SAB.

Round scad are one of the most abundant pelagic, planktivorous fish species observed on hard bottom habitats (Lindquist & Pietrafesa, 1989; Rountree, 1990; Burge et al., 2012), and high densities of RS are especially apparent on mid-shelf live bottoms of the SAB in winter (Hales Jr, 1987). Under these circumstances, MPs are likely dependent on RS and similar species such as mackerel scad *D. macarellus* and redbait scad *D. tabl* as primary prey resources, especially in cooler months. Given this, it was important to investigate round scad association behavior with sand tiger sharks and be aware that this interaction may relate to trophic transfer and mesopredator control. We have no reason to believe this STs and RS association behavior is unique to the hard bottom habitat off Cape Fear, North Carolina, therefore describing this behavior and its stimulus aids in understanding trophic interactions and prey strategies that influence predation success for pelagic predators.

While the possibility of benefit to STs as increased predation opportunities remains an open question, available observations (see videos in Table 2) provide evidence that STs use this association to perform an undocumented predation strategy. The concealment provided to STs by RS and the attraction of MPs to the shark suggest that this association behavior facilitates the feeding and foraging behavior of sand tiger sharks (Table 2). Feeding behaviors and bite kinematics in captive *C. taurus* have been described (Ferrara et al., 2011; Moyer, Shannon & Irschick, 2019), but foraging behavior in wild STs remains unclear, although several lines of evidence suggest that crepuscular and night foraging are probable in this species, with a need for substantial additional research (Hammerschlag et al., 2017). For example, Kneebone et al. (2018) report that juvenile sand tigers are more active at night in a nursery area of Plymouth, Kingston, Duxbury (PKD) Bay, Massachusetts. Using acoustic detections, accelerometer data, geospatial modelling, and field observations Kneebone et al. (2018) inferred that foraging behavior may be an important aspect of increased activity.

Admittedly, the limited field of view of SharkCam served as a constraint to fully observe behavior between STs, RS, and MPs because interactions occurred rapidly and in three-dimensional space (see videos in Table S1). In this study, occurrences of MPs outside the perspective of SharkCam undoubtedly influenced events captured on camera, and this is likely responsible for many of the observations of loosely associated (LA) and tightly associated (TA) behaviors that occurred in the absence of MPs (STs+RS-MPs, $n = 27$). One or more species of selected MPs occurred in approximately 84% of videos containing STs and RS (Table 1). Additionally, many other species of potential scad mesopredators are also present at Frying Pan Tower, including a diverse assemblage of demersal piscivores, and other pelagic species not designated as MPs in analyses (Table S2). Recent work by Brown et al. (2020), also on sand tiger sharks in North Carolina, has revealed that the presence of the sharks alters short-term reef fish community richness on shipwrecks, with the prevalence of pelagic mesopredators elevated, and those of demersal mesopredators depressed. They suggest that these differences in richness may be behaviorally-mediated responses attributed to mesopredator optimization of foraging strategy, with sharks as short-term drivers of spatial and temporal community composition for mesopredators. Given this, it is likely that there are few circumstances when aggregations of round scad are not exposed to potential predators. The inclusion of STs+RS-MPs videos in the multinomial logistic regression

likely resulted in the lack of statistical significance ($p = 0.727$ for LA and $p = 0.218$ for TA), despite the relatively large increases in the odds of association behavior as association strength increased (82.9% for LA and 196% for TA). This pattern is supported by the results of the chi-square analysis that show the frequency of occurrence of association behavior increased with association strength ($p < 0.000$, Fig. 6).

In research analyzing predator influence on prey behavior, *Seghers (1974)* hypothesized that guppies formed schools because they were always exposed to predation threats. Constant exposure to predators provides a strong explanation for why round scad are observed forming associations with sand tiger sharks when designated MPs are not seen on SharkCam. While observations of round scad association with sand tiger sharks in the absence of MPs observations may be a result of sampling bias (i.e., MPs were present but not observed on camera), it suggests that aggregation behavior is driven by perceived predation risk assessed by the scad, and further suggests near constant exposure to mesopredators. Experimental manipulation of mesopredators, their prey, and higher trophic-level predator presence have tested perceived predation risk to prey and mesopredators in marine (*Del Mar Palacios, Warren & McCormick, 2016*) and terrestrial (*Gordon et al., 2015*) settings—one commonality that emerges is that the presence of a high trophic-level predator alleviates perceived risk to prey by providing a “refuge effect” associated with behavioral changes in prey.

For example, the mackerel scad *Decapterus macarellus*, an ecologically similar and sympatric relative of round scad *D. punctatus*, associated with goliath grouper *Epinephelus itajara* (Lichtenstein, 1822) presumably to reduce their vulnerability to predation by the horse-eye jack *Caranx latus* Agassiz in Spix and Agassiz, 1831. Mackerel scad were described as forming a dense aggregation around the grouper while under threat by jacks, and the school of scad moved with the grouper as one unit. The authors concluded that this behavior was likely advantageous for mackerel scad by reducing their risk of predation by a mesopredator (jack) that was itself potential prey for the grouper (*Macieira et al., 2010*).

Behavioral descriptions of RS and STs association were created to classify three distinct levels of association based on preliminary observations. Inclusion of a continuous, quantitative variable to measure aggregation strength may have increased the accuracy of identifying round scad responses to mesopredators but was not necessary given how distinct existing behavioral categories were. Nearest neighbor distance is a structural measurement of fish aggregations and it is used to calculate the positional preference of individual fish within an aggregation based on the positions and movements of adjacent fish (*Parrish, Viscido & Grunbaum, 2002*). Evidence supports that synchronization and group coordination are mediated by an individual’s interactions with nearest group members (*Soria, Freon & Chabanet, 2007; Ballerini et al., 2008; Niizato & Gunji, 2011*). We visually estimated nearest neighbor distance of round scad to other aggregation members and to sand tiger sharks to incorporate a measure of aggregation structure into our behavioral descriptions in order to reduce observer bias. Conventionally, model simulations have been effectively used to understand the mechanisms that influence strength, response to stimulus, and coordination of fish schools (*Huth & Wissel, 1992; Parrish, Viscido & Grunbaum, 2002*). Observations of RS becoming more aggregated in response to perceived

predation threats are consistent with prior literature (*Rountree & Sedberry, 1991; Auster et al., 2009; Auster et al., 2013*). Reduction in nearest neighbor distance and increased polarity likely facilitates more efficient communication between school members which enhances group synchrony and coordination (*Rieucau, Fernö & Ioannou, 2015*).

In-situ marine field experiments analyzing fish aggregation dynamics are uncommon, likely given the difficulty to track individual fish in an open setting. Dual frequency identification sonar (DIDSON) has recently become a reliable method to conduct in-situ analysis of fish schooling behavior and has the capability of monitoring the movement of individual fish (*Moursund, Carlson & Peters, 2003; Boswell, Wilson & Cowan, 2008; Price, Auster & Kracker, 2013; Rieucau et al., 2016*). *Auster et al. (2013)* used DIDSON techniques to effectively analyze prey distribution during predator-prey interactions similar to those observed in this study on hard bottoms in the SAB. DIDSON analysis would support more quantitative data on the structure of associations between RS and STs, but was not necessary to understand interactions between RS and MPs and would introduce additional cost for support and maintenance.

Sharks were always the nucleus of association for round scad in our study. We hypothesized that proximity to sharks by round scad, in addition to changes in scad polarization and reduced nearest neighbor distance, served as an additional predation defense for round scad against mesopredators. Although we focused on association as protective for round scad with sharks, it is important to consider other potential explanations for this behavior.

Fuller & Parsons (2019) reported observations of association between RS and several species of sharks. In the Gulf of Mexico, aggregations of round scad and another carangid, Atlantic bumper (*Chloroscombrus chrysurus* (Linnaeus, 1766)), associated with blacktip sharks (*Carcharhinus limbatus* (Müller and Henle, 1839)), spinner sharks (*Carcharhinus brevipinna* (Müller and Henle, 1839)), and blacknose sharks (*Carcharhinus acronotus* (Poey, 1860)). In situ observations of association between RS and STs had not been previously described prior to the current study, but photographs available online document associations between round scad and sand tiger sharks on North Carolina reefs and wrecks (<https://ncaquariums.wildbook.org/gallery.jsp>), and these are mentioned by *Fuller & Parsons (2019)*. Their potential explanations for association behavior include protection from mesopredator predation, optomotor responses (*Shaw & Tucker, 1965*), and scatophagy on shark fecal clouds. We did not document the frequency of round scad feeding during associations or observe foraging on fecal clouds, but round scad foraging for plankton was common during observations (*Table S1*). As fish forage, especially pelagic planktivores like round scad, they become more vulnerable to predation; therefore, future studies should consider foraging benefits and how associations with sharks reduced vulnerability during foraging. It is also important to continue to explore the possible benefit of this association to sand tiger sharks to fully understand how this association influences trophic interactions.

CONCLUSIONS

Based on underwater video observations from SharkCam, we hypothesized that association behaviors between round scad and sand tiger sharks were more frequent in the presence of pelagic mesopredators than in their absence because the presence of mesopredators represents a potential predation threat for round scad. Scad were shown to be significantly more likely to be tightly associated with sand tiger sharks in the presence of mesopredators, compared to in their absence. This example of a behaviorally-mediated indirect interaction suggests that the presence of a large predator alleviates perceived risk to prey from mesopredators. These results illuminate a previously undescribed behaviorally-mediated indirect interaction with important consequences for trophic transfer and mesopredator control on hard bottom habitats, and supports the usage of long-term underwater camera installations for addressing questions in marine ecology.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Nicholas C. Coleman conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Erin J. Burge conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, supported ongoing maintenance at SharkCam, and managed video harvesting and database management, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data are available in Supplementary File 1. They consist of all sand tiger shark, scad, and mesopredator observations (n=216), indexed to unique video clips, with dates and times of observation.

Video clip files referred to in the Results, [Table 1](#), [Figs. 2](#) and [3](#) are deposited on Zenodo (DOI: [10.5281/zenodo.4477423](https://doi.org/10.5281/zenodo.4477423))

[Table S2](#) lists a description of each video (Descriptions), date (Date of occurrence) and time (Clock time of occurrence) of footage, a timing reference to the description within the video (video time), and a link to Youtube (Video reference) of the same footage.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.11164#supplemental-information>.

REFERENCES

- Auster PJ, Cortés J, Alvarado JJ, Beita-Jiménez A, Auster PJ, Cortés J, Alvarado JJ, Beita-Jiménez A. 2019.** Coordinated hunting behaviors of mixed-species groups of piscivores and associated species at Isla del Coco National Park (Eastern Tropical Pacific). *Neotropical Ichthyology* **17**:e180165
DOI [10.1590/1982-0224-20180165](https://doi.org/10.1590/1982-0224-20180165).
- Auster PJ, Godfrey J, Watson A, Paquette A, McFall G. 2009.** Behavior of prey links midwater and demersal piscivorous reef fishes. *Neotropical Ichthyology* **7**:109–112.
- Auster PJ, Kracker L, Price V, Heupel E, McFall G, Grenda D. 2013.** Behavior webs of piscivores at subtropical live-bottom reefs. *Bulletin of Marine Science* **89**:377–396
DOI [10.5343/bms.2011.1123](https://doi.org/10.5343/bms.2011.1123).
- Baird T. 1993.** A new heterospecific foraging association between the pudding-wife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: Evaluation of the foraging consequences. *Environmental Biology of Fishes* **38**:393–397
DOI [10.1007/BF00007535](https://doi.org/10.1007/BF00007535).
- Ballerini M, Cabibbo N, Candelier R, Cavagna A, Cisbani E, Giardina I, Lecomte V, Orlandi A, Parisi G, Procaccini A, Viale M, Zdravkovic V. 2008.** Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proceedings of the National Academy of Sciences* **105**:1232–1237
DOI [10.1073/pnas.0711437105](https://doi.org/10.1073/pnas.0711437105).
- Barker SM, Peddemors VM, Williamson JE. 2011.** A video and photographic study of aggregation, swimming and respiratory behaviour changes in the grey nurse shark (*Carcharias taurus*) in response to the presence of SCUBA divers. *Marine and Freshwater Behaviour and Physiology* **44**:75–92
DOI [10.1080/10236244.2011.569991](https://doi.org/10.1080/10236244.2011.569991).
- Beard DW, Dess GG. 1988.** Modeling organizational species' interdependence in an ecological community: an input–output approach. *Academy of Management Review* **13**:362–373
DOI [10.5465/amr.1988.4306941](https://doi.org/10.5465/amr.1988.4306941).
- Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD. 2012.** Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. *PLOS ONE* **7**:e32983
DOI [10.1371/journal.pone.0032983](https://doi.org/10.1371/journal.pone.0032983).
- Boswell KM, Wilson MP, Cowan JH. 2008.** A semiautomated approach to estimating fish size, abundance, and behavior from Dual-Frequency Identification Sonar (DIDSON) data. *North American Journal of Fisheries Management* **28**:799–807
DOI [10.1577/M07-116.1](https://doi.org/10.1577/M07-116.1).

- Briggs JC, Bowen BW. 2012.** A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography* **39**:12–30 DOI [10.1111/j.1365-2699.2011.02613.x](https://doi.org/10.1111/j.1365-2699.2011.02613.x).
- Briggs JC, Bowen BW. 2013.** Marine shelf habitat: biogeography and evolution. *Journal of Biogeography* **40**:1023–1035 DOI [10.1111/jbi.12082](https://doi.org/10.1111/jbi.12082).
- Brown CM, Paxton AB, Taylor JC, Van Hoeck RV, Fatzinger MH, Silliman BR. 2020.** Short-term changes in reef fish community metrics correlate with variability in large shark occurrence. *Food Webs* **24**:e00147 DOI [10.1016/j.fooweb.2020.e00147](https://doi.org/10.1016/j.fooweb.2020.e00147).
- Burge EJ, Atack JD, Andrews C, Binder BM, Hart ZD, Wood AC, Bohrer LE, Jagannathan K. 2012.** Underwater video monitoring of groupers and the associated hard-bottom reef fish assemblage of North Carolina. *Bulletin of Marine Science* **88**:15–38 DOI [10.5343/bms.2010.1079](https://doi.org/10.5343/bms.2010.1079).
- Burge EJ, O'Brien CE, jon-newbie. 2020.** *SharkCam fishes: A guide to nekton at Frying Pan Tower*. Los Angeles: Explore.org Ocean Frontiers Available at <https://explore.org/livecams/oceans/shark-cam>.
- Campanella F, Auster PJ, Taylor JC, Muñoz RC. 2019.** Dynamics of predator–prey habitat use and behavioral interactions over diel periods at sub-tropical reefs. *PLOS ONE* **14**:e0211886 DOI [10.1371/journal.pone.0211886](https://doi.org/10.1371/journal.pone.0211886).
- Campo D, Mostarda E, Castriota L, Scarabello MP, Andaloro F. 2006.** Feeding habits of the Atlantic bonito, *Sarda sarda* (Bloch, 1793) in the southern Tyrrhenian sea. *Fisheries Research* **81**:169–175 DOI [10.1016/j.fishres.2006.07.006](https://doi.org/10.1016/j.fishres.2006.07.006).
- Carlson JK, McCandless CT, Cortés E, Grubbs RD, Andrews KI, Musick JA. 2009.** An update on the status of the sand tiger shark, *Carcharias taurus*, in the northwest Atlantic Ocean. NOAA Technical Memorandum NMFS-SEFSC-585: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL.
- Cavanagh RD, Kyne PM, Fowler SL, Musick JA, Bennett MB. 2003.** The conservation status of Australian chondrichthyans: report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop. The University of Queensland, School of Biomedical Sciences, Brisbane, Australia.
- Chester AJ, Huntsman GR, Tester PA, Manooch CS. 1984.** South Atlantic Bight reef fish communities as represented in hook-and-line catches. *Bulletin of Marine Science* **34**:267–279.
- Chiaromonte G, Domingo A, Soto J. 2007.** *Carcharias taurus* (Southwest Atlantic subpopulation). The IUCN Red List of Threatened Species. Available at <http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T3854A10132481.en> (accessed on 09 December 2020).
- Cleary WJ, Riggs SR, Marcy DC, Snyder SW. 1996.** The influence of inherited geological framework upon a hardbottom-dominated shoreface on a high-energy shelf: Onslow Bay, North Carolina, USA. *Geological Society* **117**:249–266 DOI [10.1144/GSL.SP.1996.117.01.15](https://doi.org/10.1144/GSL.SP.1996.117.01.15).

- Cole RG. 1994.** Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in Northeastern New Zealand. *Biological Conservation* **70**:93–99 DOI [10.1016/0006-3207\(94\)90276-3](https://doi.org/10.1016/0006-3207(94)90276-3).
- Collins Engineers Inc. 2010.** Structural inspection and assessment of the U.S. Coast Guard Frying Pan Shoals Light Station. USCG Contract No. HSCG83-07-D-3WF172, USCG Task Order No. HSCG83-10-J-PCU005, Collins Job 6277-40, U.S. Coast Guard, Civil Engineering Unit Cleveland, Cleveland, Ohio.
- Compagno LJ. 2001.** An annotated and illustrated catalogue of shark species known to date. In: *Sharks of the world. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. Volume 2. Rome: Food & Agriculture Organization of the United Nations, 55–62.
- Creel S, Christianson D. 2008.** Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* **23**:194–201 DOI [10.1016/j.tree.2007.12.004](https://doi.org/10.1016/j.tree.2007.12.004).
- Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M. 1999.** Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**:993–996 DOI [10.1126/science.283.5404.993](https://doi.org/10.1126/science.283.5404.993).
- Del Mar Palacios M, Warren DT, McCormick MI. 2016.** Sensory cues of a top-predator indirectly control a reef fish mesopredator. *Oikos* **125**:201–209 DOI [10.1111/oik.02116](https://doi.org/10.1111/oik.02116).
- Denny J, Baldwin W, Schwab W, Gayes P, Morton R, Driscoll N. 2007.** Morphology and texture of modern sediments on the inner shelf of South Carolina's Long Bay from Little River Inlet to Winyah Bay. U.S. Geological Survey Woods Hole Science Center, Woods Hole, Massachusetts: U.S. Department of the Interior, U.S. Geological Survey.
- Diamant A, Shpigel M. 1985.** Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Agaba). *Environmental Biology of Fishes* **13**:153–159 DOI [10.1007/BF00002584](https://doi.org/10.1007/BF00002584).
- Dill LM, Heithaus MR, Walters CJ. 2003.** Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* **84**:1151–1157 DOI [10.1890/0012-9658\(2003\)084\[1151:BMHIM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1151:BMHIM]2.0.CO;2).
- Donaldson PL, Clavijo IE. 1994.** Diet of round scad (*Decapterus punctatus*) on a natural and an artificial reef in Onslow Bay, North Carolina. *Bulletin of Marine Science* **55**:501–509.
- Dunbrack R, Zielinski R. 2003.** Seasonal and diurnal activity of sixgill sharks (*Hexanchus griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology* **81**:1107–1111 DOI [10.1139/z03-087](https://doi.org/10.1139/z03-087).
- Emslie MJ, Cheal AJ, MacNeil MA, Miller IR, Sweatman HPA. 2018.** Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ* **6**:e4886 DOI [10.7717/peerj.4886](https://doi.org/10.7717/peerj.4886).
- Ferrara TL, Clausen P, Huber DR, McHenry CR, Peddemors V, Wroe S. 2011.** Mechanics of biting in great white and sandtiger sharks. *Journal of Biomechanics* **44**:430–435 DOI [10.1016/j.jbiomech.2010.09.028](https://doi.org/10.1016/j.jbiomech.2010.09.028).

- Fletcher N, Batjakas IE, Pierce GJ. 2013.** Diet of the Atlantic bonito *Sarda sarda* (Bloch, 1793) in the Northeast Aegean Sea. *Journal of Applied Ichthyology* **29**:1030–1035 DOI [10.1111/jai.12164](https://doi.org/10.1111/jai.12164).
- Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G. 2008.** Atlantic reef fish biogeography and evolution. *Journal of Biogeography* **35**:22–47.
- Frazier B, Paramore L, Rootes-Murdy K. 2019.** 2018 review of the Atlantic States Marine Fisheries Commission Fishery Management Plan for Coastal Sharks, 2017 Fishing Year. Atlantic States Marine Fisheries Commission. Available at http://www.asmf.org/uploads/file/5d00081cCoastalSharksFMPReview_2018.pdf.
- Freshwater DW, Idol JN. 2013.** Studies of North Carolina marine algae XIII. First reports of the genus *Cottoniella* (Rhodophyta, Sarcomeniaceae). *Marine Biodiversity Records* **6**:e88 DOI [10.1017/S1755267213000651](https://doi.org/10.1017/S1755267213000651).
- Fuller LN, Parsons GR. 2019.** A note on associations observed between sharks and teleosts. *Southeastern Naturalist* **18**:489–498 DOI [10.1656/058.018.0314](https://doi.org/10.1656/058.018.0314).
- Gelsleichter J, Musick JA, Nichols S. 1999.** Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. *Environmental Biology of Fishes* **54**:205–217 DOI [10.1023/A:1007527111292](https://doi.org/10.1023/A:1007527111292).
- Goldman KJ, Branstetter S, Musick JA. 2006.** A re-examination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. *Environmental Biology of Fishes* **77**:241–252 DOI [10.1007/s10641-006-9128-y](https://doi.org/10.1007/s10641-006-9128-y).
- Gordon CE, Feit A, Grüber J, Letnic M. 2015.** Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences* **282**:20142870 DOI [10.1098/rspb.2014.2870](https://doi.org/10.1098/rspb.2014.2870).
- Gordon I. 1993.** Pre-copulatory behaviour of captive sandtiger sharks, *Carcharias taurus*. *Environmental Biology of Fishes* **38**:159–164 DOI [10.1007/BF00842912](https://doi.org/10.1007/BF00842912).
- Govender A, Kistnasamy N, Van Der Elst RP. 1991.** Growth of spotted ragged-tooth sharks *Carcharias taurus* (Rafinesque) in captivity. *South African Journal of Marine Science* **11**:15–19 DOI [10.2989/025776191784287718](https://doi.org/10.2989/025776191784287718).
- Hales Jr SL. 1987.** Distribution, abundance, reproduction, food habits, age and growth of round scad, *Decapterus punctatus*, in the South Atlantic Bight. *Fishery Bulletin* **85**:251–268.
- Hammerschlag N, Skubel R, Calich H, Nelson E, Shiffman D, Wester J, Macdonald C, Cain S, Jennings L, Enchelmaier A, Gallagher A. 2017.** Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark. *Bulletin of Marine Science* **93**:355–374 DOI [10.5343/bms.2016.1046](https://doi.org/10.5343/bms.2016.1046).

- Haulsee DE, Fox DA, Breece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ. 2016a.** Social network analysis reveals potential fission–fusion behavior in a shark. *Scientific Reports* **6**:1–9 DOI [10.1038/srep34087](https://doi.org/10.1038/srep34087).
- Haulsee DE, Fox DA, Breece MW, Clauss TM, Oliver MJ. 2016b.** Implantation and recovery of long-term archival transceivers in a migratory shark with high site fidelity. *PLOS ONE* **11**:e0148617 DOI [10.1371/journal.pone.0148617](https://doi.org/10.1371/journal.pone.0148617).
- Heupel M, Knip D, Simpfendorfer C, Dulvy N. 2014.** Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series* **495**:291–298 DOI [10.3354/meps10597](https://doi.org/10.3354/meps10597).
- Hopkinson C, Jansson B-O, Schubauer-Berigan J. 1991.** Community metabolism and nutrient cycling at Gray’s Reef, a hard bottom habitat in the Georgia Bight. *Marine Ecology Progress Series* **73**:105–120 DOI [10.3354/meps073105](https://doi.org/10.3354/meps073105).
- Hutchinson GE. 1959.** Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**:145–159.
- Huth A, Wissel C. 1992.** The simulation of the movement of fish schools. *Journal of Theoretical Biology* **156**:365–385 DOI [10.1016/S0022-5193\(05\)80681-2](https://doi.org/10.1016/S0022-5193(05)80681-2).
- Kanno S, Schlaff AM, Heupel MR, Simpfendorfer CA. 2019.** Stationary video monitoring reveals habitat use of stingrays in mangroves. *Marine Ecology Progress Series* **621**:155–168 DOI [10.3354/meps12977](https://doi.org/10.3354/meps12977).
- Kendall MS, Bauer LJ, Jeffrey CFG. 2009.** Influence of hard bottom morphology on fish assemblages of the continental shelf off Georgia, southeastern USA. *Bulletin of Marine Science* **84**:265–286.
- Klima EF, Wickham DA. 1971.** Attraction of coastal pelagic fishes with artificial structures. *Transactions of the American Fisheries Society* **100**:86–99 DOI [10.1577/1548-8659\(1971\)100<86:AOCPFW>2.0.CO;2](https://doi.org/10.1577/1548-8659(1971)100<86:AOCPFW>2.0.CO;2).
- Kneebone J, Winton M, Danylchuk A, Chisholm J, Skomal GB. 2018.** An assessment of juvenile sand tiger (*Carcharias taurus*) activity patterns in a seasonal nursery using accelerometer transmitters. *Environmental Biology of Fishes* **101**:1739–1756 DOI [10.1007/s10641-018-0821-4](https://doi.org/10.1007/s10641-018-0821-4).
- Kracker L, Kendall M, McFall G. 2008.** Benthic features as a determinant for fish biomass in Gray’s Reef National Marine Sanctuary. *Marine Geodesy* **31**:267–280 DOI [10.1080/01490410802466611](https://doi.org/10.1080/01490410802466611).
- Kulbicki M. 1998.** How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology* **222**:11–30 DOI [10.1016/S0022-0981\(97\)00133-0](https://doi.org/10.1016/S0022-0981(97)00133-0).
- Latour RJ, Gartland J. 2020.** Dynamics of the shark community in the Mid-Atlantic Bight. *Marine Biology* **167**:100 DOI [10.1007/s00227-020-03720-y](https://doi.org/10.1007/s00227-020-03720-y).
- Lima SL, Dill LM. 1990.** Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640 DOI [10.1139/z90-092](https://doi.org/10.1139/z90-092).
- Lindfield SJ, Harvey ES, McIlwain JL, Halford AR. 2014.** Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished

areas. *Methods in Ecology and Evolution* 5:1061–1069

[DOI 10.1111/2041-210X.12262](https://doi.org/10.1111/2041-210X.12262).

- Lindquist DG, Pietrafesa LJ. 1989.** Current vortices and fish aggregations: the current field and associated fishes around a tugboat wreck in Onslow Bay, North Carolina. *Bulletin of Marine Science* 44:533–544.
- Macieira RM, Simon T, Pimentel CR, Joyeux J-C. 2010.** Protection in the giant: goliath grouper (*Epinephelus itajara*) as a refuge for mackerel scad (*Decapterus macarellus*). *Marine Biodiversity Records* 3:e45 [DOI 10.1017/S1755267209991011](https://doi.org/10.1017/S1755267209991011).
- Mallet D, Pelletier D. 2014.** Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research* 154:44–62 [DOI 10.1016/j.fishres.2014.01.019](https://doi.org/10.1016/j.fishres.2014.01.019).
- Manooch CS, Mason DL, Nelson RS. 1985.** Foods of little tunny *Euthynnus alletteratus* collected along the southeastern and Gulf coasts of the United States. *Nippon Suisan Gakkaishi* 51:1207–1218 [DOI 10.2331/suisan.51.1207](https://doi.org/10.2331/suisan.51.1207).
- Manooch III CS, Haimovici M. 1983.** Foods of greater amberjack, *Seriola dumerili*, and almaco jack, *Seriola rivoliana* (Pisces: Carangidae), from the South Atlantic Bight. *Journal of the Elisha Mitchell Scientific Society* 99:1–9.
- Matheson RH, Huntsman GR, Manooch CS. 1986.** Age, growth, mortality, food and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. *Bulletin of Marine Science* 38:300–312.
- McCauley DJ, McLean KA, Bauer J, Young HS, Micheli F. 2012.** Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications* 22:385–392 [DOI 10.1890/11-1059.1](https://doi.org/10.1890/11-1059.1).
- McFarland WN, Kotchian NM. 1982.** Interaction between schools of fish and mysids. *Behavioral Ecology and Sociobiology* 11:71–76 [DOI 10.1007/BF00300094](https://doi.org/10.1007/BF00300094).
- Miller GC, Richards WJ. 1980.** Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. *Proceedings of the Gulf and Caribbean Fisheries Institute* 32:114–130.
- Milliman JD. 1972.** Atlantic Continental Shelf and Slope of the United States—Petrology of the Sand Fraction of Sediments, Northern New Jersey to Southern Florida. United States Department of the Interior, Geological Survey.
- Moursund RA, Carlson TJ, Peters RD. 2003.** A fisheries application of a dual-frequency identification sonar acoustic camera. *ICES Journal of Marine Science* 60:678–683 [DOI 10.1016/S1054-3139\(03\)00036-5](https://doi.org/10.1016/S1054-3139(03)00036-5).
- Moyer JK, Shannon SF, Irschick DJ. 2019.** Bite performance and feeding behaviour of the sand tiger shark *Carcharias taurus*. *Journal of Fish Biology* 95:881–892 [DOI 10.1111/jfb.14086](https://doi.org/10.1111/jfb.14086).
- Musick JA, Branstetter S, Colvocoresses JA. 1993.** Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic Coast. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman GR, McGovern JC, Sedberry GR, Parker SJ,**

- Poss SG, Sala E, Schmidt TW, Weeks H, Wright SG. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6–30
DOI 10.1577/1548-8446(2000)025<0006:MEADFS>2.0.CO;2.
- Naughton SP, Saloman CH, Vaught RN. 1986. Species profile of round scad *Decapterus punctatus* (Cuvier 1829). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL, NOAA Technical Memorandum NMFS-SEFC-181.
- NC Division of Marine Fisheries. 2020. Location of hard bottom habitat. Available at <http://portal.ncdenr.org/web/mf/habitat/hard-bottom> (accessed on 05 February 2020).
- Niizato T, Gunji Y-P. 2011. Metric–topological interaction model of collective behavior. *Ecological Modelling* 222:3041–3049
DOI 10.1016/j.ecolmodel.2011.06.008.
- NOAA Fisheries. 2019. 2018 Stock Assessment and Fishery Evaluation (SAFE) Report for Atlantic Highly Migratory Species. Atlantic Highly Migratory Species Management Division, NOAA Fisheries, Silver Spring, Maryland.
- Ojeda GY, Gayes PT, Van Dolah RF, Schwab WC. 2004. Spatially quantitative seafloor habitat mapping: example from the northern South Carolina inner continental shelf. *Estuarine, Coastal and Shelf Science* 59:399–416
DOI 10.1016/j.ecss.2003.09.012.
- Paine RT. 1984. Ecological determinism in the competition for space: The Robert H. MacArthur Award Lecture. *Ecology* 65:1339–1348 DOI 10.2307/1939114.
- Parker RO, Chester AJ, Nelson RS. 1994. A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray’s Reef National Marine Sanctuary, Georgia. *Fishery Bulletin* 92:787–799.
- Parker RO, Colby DR, Willis TD. 1983. Estimated amount of reef habitat on a portion of the U.S. South Atlantic and Gulf of Mexico continental shelf. *Bulletin of Marine Science* 33:935–940.
- Parrish JK, Viscido SV, Grunbaum D. 2002. Self-organized fish schools: an examination of emergent properties. *Biological Bulletin* 202:296–305.
- Paxton AB, Blair E, Blawas C, Fatzinger MH, Marens M, Holmberg J, Kingen C, Houppermans T, Keusenkothen M, McCord J, Silliman BR, Penfold LM. 2019. Citizen science reveals female sand tiger sharks (*Carcharias taurus*) exhibit signs of site fidelity on shipwrecks. *Ecology* 100:e02687 DOI 10.1002/ecy.2687.
- Peckol P, Searles RB. 1984. Temporal and spatial patterns of growth and survival of invertebrate and algal populations of a North Carolina continental shelf community. *Estuarine, Coastal and Shelf Science* 18:133–143
DOI 10.1016/0272-7714(84)90101-X.
- Pollard D, Smith A. 2009. *Carcharias taurus*. The IUCN Red List of Threatened Species. Available at <http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T3854A10132481.en> (accessed on 18 December 2019).

- Preisser EL, Bolnick DI, Benard MF. 2005.** Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* **86**:501–509 DOI [10.1890/04-0719](https://doi.org/10.1890/04-0719).
- Price VE, Auster PJ, Kracker L. 2013.** Use of high-resolution DIDSON sonar to quantify attributes of predation at ecologically relevant space and time scales. *Marine Technology Society Journal* **47**:33–46 DOI [10.4031/MTSJ.47.1.6](https://doi.org/10.4031/MTSJ.47.1.6).
- Renaud PE, Ambrose Jr WG, Riggs SR, Syster DA. 1996.** Multi-level effects of severe storms on an offshore temperate reef system: Benthic sediments, macroalgae, and implications for fisheries. *Marine Ecology* **17**:383–398.
- Renaud PE, Riggs SR, Ambrose Jr WG, Schmid K, Snyder SW. 1997.** Biological-geological interactions: storm effects on macroalgal communities mediated by sediment characteristics and distribution. *Continental Shelf Research* **17**:37–56.
- Renaud PE, Syster DA, Ambrose Jr WG. 1999.** Recruitment patterns of continental shelf benthos off North Carolina, USA: effects of sediment enrichment and impact on community structure. *Journal of Experimental Marine Biology and Ecology* **237**:89–106.
- Rieucou G, Fernö A, Ioannou CC. 2015.** Towards of a firmer explanation of large shoal formation, maintenance and collective reactions in marine fish. *Reviews in Fish Biology and Fisheries* **25**:21–37 DOI [10.1007/s11160-014-9367-5](https://doi.org/10.1007/s11160-014-9367-5).
- Rieucou G, Holmin AJ, Castillo JC, Couzin ID. 2016.** School level structural and dynamic adjustments to risk promote information transfer and collective evasion in herring. *Animal Behaviour* **117**:69–78 DOI [10.1016/j.anbehav.2016.05.002](https://doi.org/10.1016/j.anbehav.2016.05.002).
- Riggs S, Cleary W, Snyder S. 1995.** Influence of inherited geologic framework on barrier shoreface morphology and dynamics. *Marine Geology* **126**:213–234 DOI [10.1016/0025-3227\(95\)00079-E](https://doi.org/10.1016/0025-3227(95)00079-E).
- Riggs SR, Snyder SW, Hine AC, Mearns DL. 1996.** Hardbottom morphology and relationship to the geologic framework; Mid-Atlantic continental shelf. *Journal of Sedimentary Research* **66**:830–846 DOI [10.1306/D4268419-2B26-11D7-8648000102C1865D](https://doi.org/10.1306/D4268419-2B26-11D7-8648000102C1865D).
- Ritchie EG, Johnson CN. 2009.** Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**:982–998 DOI [10.1111/j.1461-0248.2009.01347.x](https://doi.org/10.1111/j.1461-0248.2009.01347.x).
- Rountree RA. 1989.** Association of fishes with Fish Aggregation Devices: effects of structure size on fish abundance. *Bulletin of Marine Science* **44**:960–972.
- Rountree RA. 1990.** Community structure of fishes attracted to shallow water fish aggregation devices off South Carolina, U.S.A. *Environmental Biology of Fishes* **29**:241–262 DOI [10.1007/BF00001183](https://doi.org/10.1007/BF00001183).
- Rountree R, Sedberry G. 1991.** In-situ observations of the schooling behavior of planktivorous fishes. Unpublished draft manuscript DOI [10.13140/RG.2.1.2371.5289](https://doi.org/10.13140/RG.2.1.2371.5289).
- SAFMC. 1998.** Final habitat plan for the south atlantic region: essential fish habitat requirements for fishery management plans of the South Atlantic Fishery Management

- Council. North Charleston, SC: South Atlantic Fishery Management Council. 457 p.+appendices.
- Saloman CH, Naughton SP. 1984.** Food of crevalle jack (*Caranx hippos*) from Florida, Louisiana, and Texas. NOAA Technical Memorandum NMFS-SEFC-134: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL.
- Schmitz OJ, Krivan V, Ovadia O. 2004.** Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163
[DOI 10.1111/j.1461-0248.2003.00560.x](https://doi.org/10.1111/j.1461-0248.2003.00560.x).
- Schneider CW. 1976.** Spatial and temporal distributions of benthic marine algae on the continental shelf of the Carolinas. *Bulletin of Marine Science* 26:133–151.
- Schneider CW, Searles RB. 1973.** North Carolina marine algae. II. New records and observations of the benthic offshore flora. *Phycologia* 12:201–211
[DOI 10.2216/i0031-8884-12-3-201.1](https://doi.org/10.2216/i0031-8884-12-3-201.1).
- Schneider CW, Searles RB. 1991.** *Seaweeds of the southeastern United States: Cape Hatteras to Cape Canaveral*. Durham: Duke University Press.
- Sedberry G, Van Dolah R. 1984.** Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. *Environmental Biology of Fishes* 11:241–258 [DOI 10.1007/BF00001372](https://doi.org/10.1007/BF00001372).
- Seghers BH. 1974.** Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. *Evolution* 28:486–489
[DOI 10.1111/j.1558-5646.1974.tb00774.x](https://doi.org/10.1111/j.1558-5646.1974.tb00774.x).
- Shaw E. 1978.** Schooling fishes. *American Scientist* 66:166–175.
- Shaw E, Tucker A. 1965.** The optomotor reaction of schooling carangid fishes. *Animal Behaviour* 13:330–IN7 [DOI 10.1016/0003-3472\(65\)90052-7](https://doi.org/10.1016/0003-3472(65)90052-7).
- Sih A, Englund G, Wooster D. 1998.** Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* 13:350–355
[DOI 10.1016/S0169-5347\(98\)01437-2](https://doi.org/10.1016/S0169-5347(98)01437-2).
- Sley A, Jarboui O, Ghorbel M, Bouain A. 2009.** Food and feeding habits of *Caranx crysos* from the Gulf of Gabès (Tunisia). *Journal of the Marine Biological Association of the United Kingdom* 89:1375–1380 [DOI 10.1017/S0025315409000265](https://doi.org/10.1017/S0025315409000265).
- Smale MJ, Booth AJ, Farquhar MR, Meyer MR, Rochat L. 2012.** Migration and habitat use of formerly captive and wild raggedtooth sharks (*Carcharias taurus*) on the southeast coast of South Africa. *Marine Biology Research* 8:115–128
[DOI 10.1080/17451000.2011.617756](https://doi.org/10.1080/17451000.2011.617756).
- Smith K, Scarr M, Scarpaci C. 2010.** Grey nurse shark (*Carcharias taurus*) diving tourism: Tourist compliance and shark behaviour at Fish Rock, Australia. *Environmental Management* 46:699–710 [DOI 10.1007/s00267-010-9561-8](https://doi.org/10.1007/s00267-010-9561-8).
- Soria M, Freon P, Chabanet P. 2007.** Schooling properties of an obligate and a facultative fish species. *Journal of Fish Biology* 71:1257–1269
[DOI 10.1111/j.1095-8649.2007.01554.x](https://doi.org/10.1111/j.1095-8649.2007.01554.x).

- Struhsaker P. 1969.** Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off the southeastern United States. *Fisheries Independent Research* **4**:261–300.
- Taylor CJ, Paxton AB, Voss CM, Sumners BW, Buckel CA, Vander Pluym JL, Ebert EF, Viehman TS, Fegley SR, Pickering EA, Adler AM, Freeman C, Peterson CH. 2016.** Benthic habitat mapping and assessment in the Wilmington-East Wind Energy Call Area, final report. U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM). Atlantic OCS Region, Sterling, VA. OCS Study BOEM 2016-003 and NOAA Technical Memorandum 196: OCS Study BOEM 2016-003.
- Teter S, Wetherbee B, Fox D, Lam C, Kiefer D, Shivji M. 2015.** Migratory patterns and habitat use of the sand tiger shark (*Carcharias taurus*) in the western North Atlantic. *Marine and Freshwater Research* **66**:158–169 DOI [10.1071/MF14129](https://doi.org/10.1071/MF14129).
- Toonen RJ, Bowen BW, Iacchei M, Briggs JC. 2016.** Biogeography, Marine. In: Kliman RM, ed. *Encyclopedia of evolutionary biology*. Oxford: Academic Press, 166–178 DOI [10.1016/B978-0-12-800049-6.00120-7](https://doi.org/10.1016/B978-0-12-800049-6.00120-7).
- Wenner EL, Knott DM, van Dolah RF, Burrell VG. 1983.** Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. *Estuarine, Coastal and Shelf Science* **17**:143–158 DOI [10.1016/0272-7714\(83\)90059-8](https://doi.org/10.1016/0272-7714(83)90059-8).
- Wheaton C. 2018.** Hardbottom characterization and relationship to the geologic framework in Long Bay, South Carolina. Master of Science in Coastal Marine and Wetland Studies Thesis, Conway, South Carolina: Coastal Carolina University.
- Wootton JT. 1993.** Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *The American Naturalist* **141**:71–89 DOI [10.1086/285461](https://doi.org/10.1086/285461).