

Virtual Reality Camera Technology Facilitates Sampling of Interactions Between Reef Piscivores and Prey

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Introduction

Predation by piscivorous fishes is an important ecological process that structures fish communities across a diversity of ecological settings (Bond et al., 2019; Estes et al., 2011; Jackson et al., 2001). Indeed, understanding the suite of predatory interactions within marine communities can greatly increase our ability to conserve, manage, and restore ocean ecosystems (Travis et al., 2014). Traditionally, assessing prey consumed by predators via stomach content analysis has been used for evaluating the strength and direction of trophic interactions. However, information about the complexities of the behaviors within and between species leading to capture of prey, as well as nonconsumptive effects such as shifts in habitat use to reduce predation risk, have important implications for understanding the variability of species interactions in sustaining community processes (e.g., Ritchie & Johnson, 2009). While quantifying the behavioral web that exists within and between

ABSTRACT

Predation is an important process influencing the structure of fish communities. There are multiple approaches used to quantify predatory interactions, and all approaches are beneficial but have their limitations. For example, food habit studies only represent results of successful predation events, direct observations by divers are time limited by both depth and temperature as well as observer effects, acoustic approaches cannot directly identify species, and video has field-of-view constraints when using standard cameras. While no approach is without constraints, the recent availability of small off-the-shelf virtual reality (VR) video cameras that can be used in marine environments offers a more spatially comprehensive field-of-view for conducting studies of community composition and species interactions both on the seafloor and in the overlying water column. Here, we demonstrate an approach for collection and analysis of data from stationary VR video to quantify predator-prey interactions at subtropical reefs in Gray's Reef National Marine Sanctuary (NW Atlantic). This approach does not substitute for other widely used census and behavioral research approaches but augments those with unique analytical products and interpretation.

Keywords: behavior, fish, predation, forage, video

species is critical for understanding variability in the dynamics of fish species and communities, our knowledge of these types of interactions remains limited (e.g., Auster et al., 2019; Gil et al., 2018; Haak et al., 2020; Stallings & Dingeldein, 2012).

At the subtropical “live-bottom” reefs of Gray's Reef National Marine Sanctuary (GRNMS; northwest Atlantic, Carolina biogeographic province), composed of outcropped sandstone ledge with dense structure-forming invertebrates, there is a complex web of behavioral interactions among fishes. These interactions are associated with predation within single and mixed-species groups of piscivores hunting for forage fish (Auster et al., 2013b;

Campanella et al., 2019). Given the complexity of these interactions, we infer that such behaviors benefit predators by increasing the success rate of predatory attacks and reducing energy required to locate and hunt for prey. To ultimately predict how these behaviors contribute to survivorship, growth, and reproduction of predator species, we need to better understand attack and capture rates in relation to the diversity of species interactions in multiple ecological settings. Given that most piscivorous fishes at GRNMS are also the target of commercial and recreational fisheries, understanding their ecological role in the community of fishes is critical for the success of their conservation and management

in a multi-species and ecosystem-based management context (Dill et al., 2003).

Combining multiple observation methods can be powerful in elucidating the interactions of predators and prey on reefs, more so than one method alone. For example, Campanella et al. (2019) applied both split-beam sonar and diver transects and direct behavioral observations to address the day-night variability of interactions between reef piscivores and forage fish prey at GRNMS. The authors found that the co-location of predators and prey in the Gray's Reef area changed considerably over the diel cycle. Prey modified their patterns of habitat use and distribution throughout the day, presumably in response to interactions with predators and associated predation risk. Crepuscular periods were confirmed to be the most active phases for predator-prey interactions and consequently the most variable. Midwater piscivores corralled and attacked forage fish, driving them down toward reefs, with demersal piscivores aggregating in those areas and attacking prey from below. This combination of behaviors supports the inferences of predation risk-driven habitat selection not previously revealed by either method alone. Furthermore, these results have important implications for planning and interpreting fish surveys based on survey time and location. We have also used other approaches to describe and quantify species interactions at GRNMS. Besides direct underwater observation to address the topology of species interactions, variation in group size, and attack rates (Auster et al., 2013b), we have used dual-frequency identification sonar to assess rates of attack by piscivores in the absence of divers (Price et al., 2013), split-beam

hydro-acoustics to assess spatial and temporal variation in prey resources and predator distributions at landscape scale around reefs (Campanella et al., 2019; Gabriel et al., 2020), and time-lapse video with standard point-of-view cameras at select sites within reefs (data analysis in process). Each of these approaches has both benefits and limitations. Diver-based surveys benefit from the mobility of divers and direct viewing of animals and behavior over a wide field of view in multiple directions but have severe bottom time limits and potential, but systematic, observer effects. Sonar approaches can cover larger areas and are not limited by visibility in the water but suffer from lack of taxonomic resolution in acoustic records. Finally, time-lapse video, using standard underwater video cameras, can record over long periods of time (e.g., multiple days) but have limited field of view from a single location and in a single direction, unless using multiple cameras.

Studies that require, or would be improved by, a more spatially inclusive field of view of the surrounding environment have used multiple point-of-view video cameras (e.g., up to six cameras in underwater housings mounted in a rigid frame designed to confirm edge overlap to account for the 360° sphere around the camera). Using the video products for research has involved either separate review of video from each camera to account for sightings of single fish in multiple cameras, selection of a single camera to efficiently review video from multiple sites (e.g., maximum species counts for relative abundance and diversity), or use of sophisticated software to stitch video from multiple synchronized cameras for review by flatscreen or virtual reality (VR) view-

ing systems (e.g., Kilfoil et al., 2017; Sheehan et al., 2019).

Commercial off-the-shelf VR video cameras have recently become available. These cameras are sold for under \$1,000 USD and record over a 360° sphere (or nearly so) around the camera with two hemispheric lenses (i.e., some models require underwater lens ports and, due to refraction, narrow the field of view and produce a narrow nadir in the image where the two hemispheric fields of view meet but do not join). Such cameras are small, low profile, light weight (<250 g in air), self-contained, and waterproof (depth limits vary by model but 10- to 30-m cameras are available) and record high-resolution (4K) video. Battery power (mediated by water temperature) and digital memory are limiting factors, but the cameras can be deployed for continuous recording for up to 2-h periods (longer than normal air scuba dives) and, for point sampling, without the potential effects of diver disturbance. Deploying multiple cameras across reefs and over different time periods can facilitate sampling designs to assess variation of species interactions.

Here, we report on an evaluation of the use of high-resolution VR video cameras as a sampling tool to study the interactions of mixed-species groups of piscivores and prey on live-bottom reefs in GRNMS. The study focused on six previously identified undercut live-bottom reefs (ledges) that serve as primary study sites in ongoing piscivore ecology studies. These sites, like other undercut sedimentary reefs, are areas of intense species interactions of fishes due to enhanced shelter and shade in crevices under the outcropped ledge, structure-forming epifauna, and enhanced flows that aggregate prey fishes via advection of zooplankton (Auster et al., 2013b; Campanella

et al., 2019; Kendall et al., 2009). The resultant video records were analyzed as a proof of concept for approaches to assess space and time variation in behavioral interactions of predatory fishes.

Methods

We used Nikon KeyMission 360 VR video cameras to collect video samples. The camera has dual 1.6-mm (8.2-mm as 35-mm format equivalent) $f/2.0$ fixed focal length lenses for spherical coverage and uses 23.9-megapixel CMOS image sensors. Light sensitivity ranges from ISO 100 to 1600. The camera records video up to 4K resolution (3840 × 2160 lines, 24p frame rate as .MOV files in MPEG-4 AVC/H. 264 format

for either NTSC or PAL; we used NTSC). Additional lens ports were required to extend the working depth of the camera (30-m maximum depth), and these produce a narrow nadir around the field of view of each hemispheric lens when images are joined during post-processing. Recording times with a completely charged battery (Li-ion Battery EN-EL1) were typically 70–90 min at our study sites with approximately 27°C bottom-water temperature at 18- to 20-m depth.

Cameras were deployed by divers on the upper edge of undercut live-bottom reefs during daylight hours (1000–1600 EDT) from August 2 to 7, 2018 (Figure 1; see reef description in Campanella et al., 2019). Cameras were mounted on short tri-

pods, so the stationary camera (as in a point count survey) was stable in currents and was approximately 10–15 cm off bottom (Figure 2). Each camera was numbered to facilitate tracking of deployment and recovery times and locations. Eight cameras were prepared prior to each field day to allow two cameras per reef at two reefs during morning and two in the afternoon, without the need to open the cameras while at sea and expose internal elements to humidity and potential condensation effects. The plan for deployments was limited in this case by the number of divers and vessel logistics.

Reefs were selected based on previous studies (e.g., Auster et al., 2013b; Campanella et al., 2019; PJA, unpublished data), which indicated expected areas of dense forage fish and associated predators. Two cameras were deployed at each reef to maximize the potential of capturing interactions among predators and forage fish given movement based on light and tidal variation (Gabriel et al., 2020). Cameras were enabled, and divers left the seafloor immediately. Most cameras recorded continuously until battery power was expended (0.73–1.4 h).

Recordings were copied from memory cards onto an external USB hard drive and parsed into folders labeled by date, station, time period (morning or afternoon), and camera identification number. Individual video files within a folder were approximately 7.5-min long and labeled sequentially in the camera throughout each deployment (i.e., 9–11 video files were recorded for each deployment).

Analysis of video records was conducted using Nikon KeyMission 360/170 Utility Software (v. 1.1.0, Nikon Corporation). Each video file was

FIGURE 1

Map of the study sites (black circles) in GRNMS with VR video deployments. Multibeam sonar image of the seafloor visualizes landscape variation from shallow (light, ~14.5 m) to deep (dark, ~21.8 m). A designated research area is located below the horizontal line, where all fishing is prohibited. Station numbers designate inside or outside the research area with “alt” locations indicating *a priori* shifts in location to include undercut reefs. Inset shows the location of GRNMS off the coast of Georgia, USA.

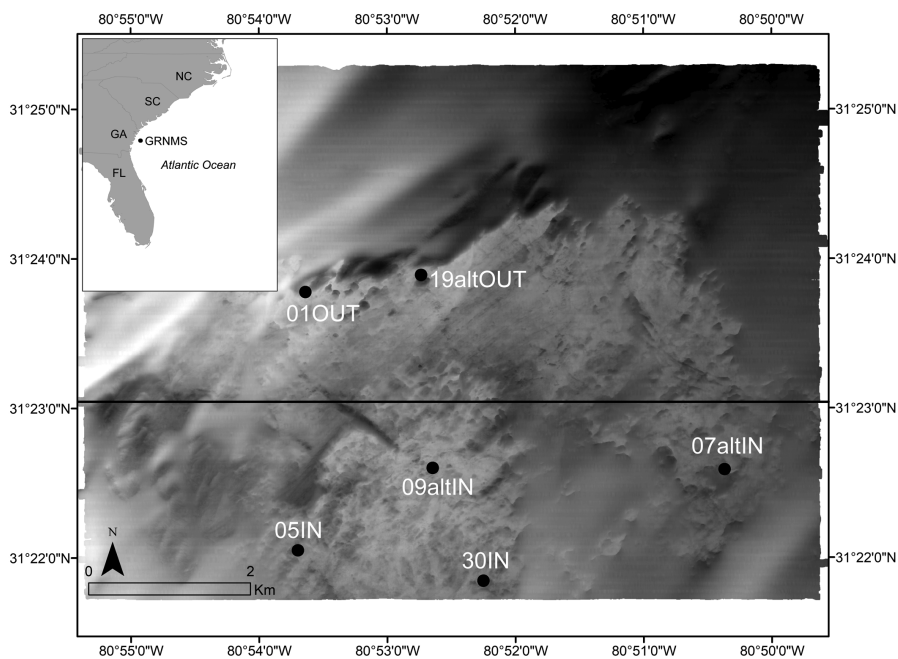
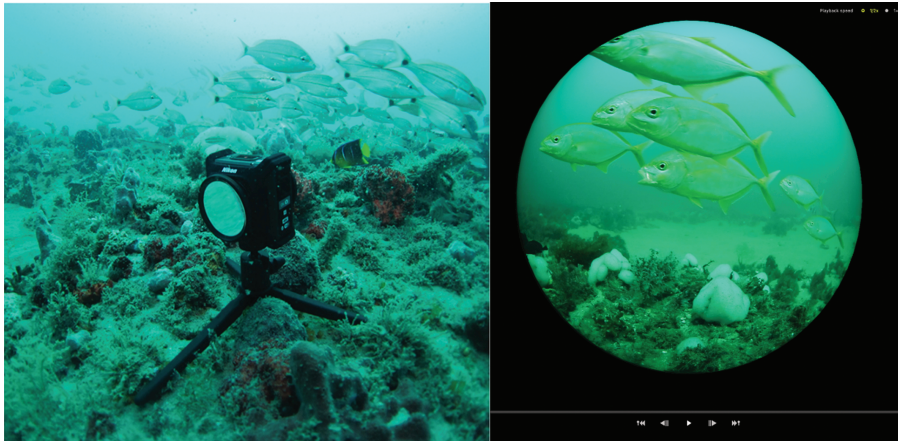


FIGURE 2

(Left) VR video camera deployed on tripod at reef edge. (Right) Screen capture of software interface with hemispheric view to facilitate analysis.



played at 0.5× magnification and set to view a full single hemisphere using the image pan-tilt controls and played in real time (i.e., 1×). Zoom, slow motion, and pause functions were used to clarify species identifications and interactions when necessary. Sample period was set *a priori* at 1-min (60-s) intervals from the beginning of the first file of a deployment and proceeded throughout the video record (i.e., through sequential files). For each 1-min interval, the predator species and maximum abundance (MaxN) were recorded. Schooling prey species were identified, and abundance estimates of 100, 1,000, and 10,000s (+) were recorded. Behaviors of predators were categorized as station-keeping (maintaining a stationary position), slow transit (swimming ca. < 1 body length per second), stalking-approach (to potential prey), or attack (burst speed directed at potential prey). Prey behavior was characterized as feeding (distributed above reef feeding on advected prey), vigilant feeding (slow descent towards reef while continuing to feed), rapid flight (scatter), or vacuole (localized flight forming a gap among

aggregation of prey fish in response to predator movement). The opposite hemisphere for each video file was reviewed in the same manner.

Visualization and characterization of hunting patterns and species interactions was facilitated by plotting species abundance versus time. Attacks by predators that elicited response from prey aggregations were plotted for each sample interval when this occurred (regardless of a single attack or multiple attacks within each 1-min time period). Data sets from each hemisphere were joined such that the MaxN for each species in each 1-min sample period was used as an estimate of total abundance (to avoid double counting). Attacks, regardless of hemisphere, were aggregated in the final data set such that each sample interval indicated presence of an attack or not as “1” or “0,” respectively. Presence or absence of forage fish aggregations within the field of view was similarly assessed. Cross-correlation function (CCF) analyses were used to identify the significance of relationships between time series counts of species pairs as well as the lag in the number of time periods

maximizing correlation (i.e., in this case, time between maximal species co-occurrences). Significance was determined when the absolute maximum CCF value was greater than $2/\sqrt{(n-k)}$, where n is the number of observations and k is the absolute value of the lag time. Runs tests were implemented for pairwise comparisons of time-series species data. This procedure detects nonrandom patterns such as cluster, mixture, trends, and oscillation of the data and determines statistical significance. Both CCF and runs test analyses were implemented using Minitab statistical software (ver. 18.1).

Results from a select set of deployments that were representative of the range of predator-prey aggregations observed serve as examples for the analytical approaches described above ($n = 11$ at six stations; four sites were replicated on different days).

Results

In total, we collected and analyzed 789 min (i.e., 1-min sample periods) of VR video with a mean of 71.7 continuous minutes per deployment (range: 44–82 min per deployment). Aggregating prey occurred in 488-min periods with a mean of 44.3 min with aggregating prey per deployment (range: 0–74 per deployment; mean: 62% of samples). Based on all prey behavior categories indicative of prey escape response to predators (attacks or perceived threat of attack), 154 samples included prey escape behaviors with a mean of 14 per deployment (range: 0–47 per deployment; mean: 20% of samples). Repeat deployments at four sites (i.e., 05 In, 09 alt In, and 19 alt Out on two different days each, 07 alt In on three different days) revealed

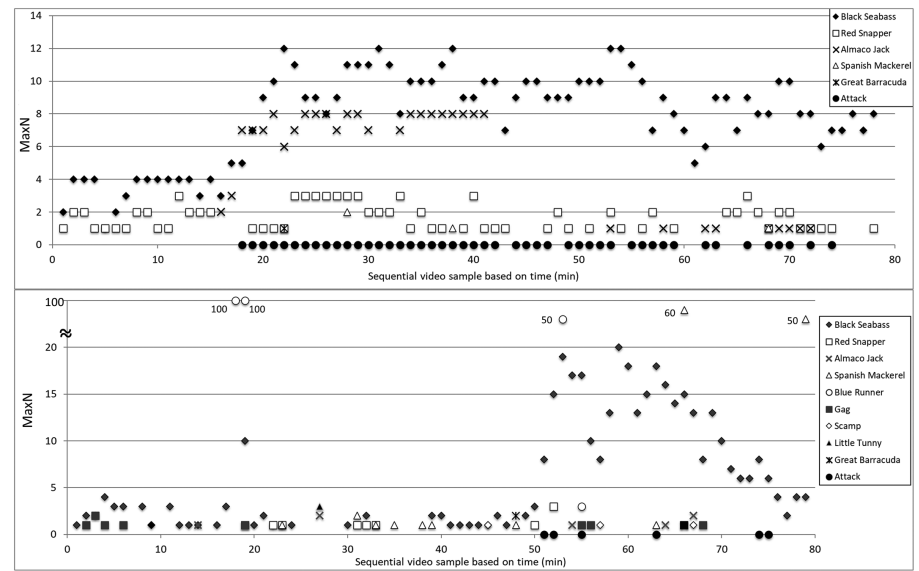
differences in local occurrence of prey and rates of predator-prey interactions.

Species observed and enumerated in VR video records were midwater piscivores almaco jack (*Seriola rivoliana*), Spanish mackerel (*Scomberomorus maculatus*), great barracuda (*Sphyræna barracuda*), yellow jack (*Carangoides bartholomæi*), blue runner (*Caranx crysos*), and little tunny (*Euthynnus alletteratus*); demersal piscivores black sea bass and bank sea bass (*Centropristis striata* and *C. ocyurus*; referred hereafter as black sea bass due to numerical dominance of this species and difficulty differentiating the two species due to orientation to the camera and distance), red snapper (*Lutjanus campechanus*), gag grouper (*Mycteroperca microlepis*), and scamp grouper (*Mycteroperca phenax*); and aggregating-schooling prey species tomtate (*Haemulon aurolineatum*), and round and mackerel scad (*Decapterus punctatus* and *D. macarellus*; referred hereafter as scad species due to identification difficulties as noted above). Spottail pinfish (*Diplodus holbrookii*), belted sandfish (*Serranus subligarius*), leopard toadfish (*Opsanus pardus*), gulf flounder (*Paralichthys albiguttata*), white-spotted soapfish (*Rypticus maculatus*), Atlantic guitarfish (*Pseudobatos lentiginosus*), and nurse shark (*Ginglymostoma cirratum*) were also observed in videos, generally in low numbers, and not addressed in subsequent analyses presented here. Common names are used in subsequent text.

MaxN versus time plots at 1-min intervals for each video sample aided in visualization of patterns in the data and demonstrated the dynamics of species co-occurrences and behaviors at point locations of reefs (Figure 3). Figure 3 is an example of multi-species variation within a reef site with

FIGURE 3

Examples of MaxN versus time plots from representative camera deployments to visualize variation in species presence and predator co-occurrences. Abundance (number of individuals) is based on MaxN for each species per sample period from either right or left hemispheric fields of view. Attacks are plotted along the x-axis to indicate when prey exhibited escape behaviors consistent with predator attacks, regardless of whether a predator was observed in the field of view. (Top graph) Station 05 In on 20180802. Prey schools were continuously present from 8 to 78 min. (Bottom) Station 07 alt In on 20180803. Schooling prey were present in only ten sample periods and were coincident with the six periods of attacks. See Table 1 for pairwise comparisons of species interactions.



both resident and transient predators, at least during the period of observation. Noteworthy is the large variability in abundance of black sea bass (i.e., presence-absence, numerical abundance). Species that were linked to such variability were almaco jack, Spanish mackerel, blue runner, and scamp grouper. Patterns of increasing black sea bass MaxN were coincident with the arrival of midwater predators with concurrent predatory attacks. This was a common pattern across samples where forage fish were present over consecutive time periods and predatory attacks were frequent (Table 1). Forage fish that occurred in dense aggregations over reefs and were targeted as prey of piscivores were scad species and young-of-year tomtate. Adult tomtates were not associated

behaviorally with large schooling aggregations of scad and tomtate at reef edges.

Results of CCF analyses revealed an overall relationship between the co-occurrence of black sea bass and multiple midwater piscivores (Table 1). In general, the significance of relationships was stronger where forage fish were present and attacks were frequent. However, there is an example at station 30 In where black sea bass and midwater predators exhibited a significant correlation in MaxN with no forage fish or attacks to act as a behavioral cue. Lag times for patterns in co-occurrences of black sea bass and multiple midwater piscivores were generally close to zero but sometimes as high as 17 min (such lag periods could indicate predation activities at other locations along the reef

TABLE 1

Date, station, and results of video analyses.

Date	Station	Sample Periods	Species Pairs	CCF	Lag Period	Significance Threshold	Sig.	Number of Attacks	Number of Forage Present	Runs About Median	Expected Runs	Longest Run, Median	ρ -Value Clustering	ρ -Value Mixtures	Runs Up or Down	Expected Runs	Longest Run, Up-Down	ρ -Value Trends	ρ -Value Oscillation
20180802	05 In	78	Bsb-Alim	0.4665	-1	0.2279	Sig	47	71	13	40.0	25	<0.001	1.000	33	51.7	7	<0.001	1.000
20180803	07 alt In	79	Bsb-Blu	0.0971	0	0.2250	NS	6	5	12	40.3	30	<0.001	1.000	36	52.3	8	<0.001	1.000
20180803	07 alt In	79	Bsb-Spa	0.3341	13	0.2462	Sig	6	5	16	40.3	27	<0.001	1.000	37	52.3	6	<0.001	1.000
20180803	09 alt In	73	Bsb-Alim	0.2239	8	0.2480	NS	0	3	29	36.0	8	0.043	0.957	32	48.3	8	<0.001	1.000
20180804	05 In	76	Bsb-Alim	0.4116	-1	0.2309	Sig	15	63	23	39.0	8	<0.001	1.000	46	50.3	6	0.116	0.884
20180804	07 alt In	74	Bsb-Alim	0.4687	-14	0.2582	Sig	12	64	15	37.3	25	<0.001	1.000	40	49.0	7	0.006	0.994
20180804	07 alt In	74	Bsb-Spa	0.4959	-15	0.2604	Sig	12	64	21	37.9	12	<0.001	1.000	38	49.0	7	0.001	0.999
20180804	07 alt In	74	Bsb-Blu	0.3808	0	0.2325	Sig	12	64	16	38.0	21	<0.001	1.000	34	49.0	10	<0.001	1.000
20180804	30 In	44	Bsb-Blu	0.4986	15	0.3714	Sig	0	0	7	21.4	21	<0.001	1.000	13	29.0	22	<0.001	1.000
20180804	30 In	44	Bsb-Sca	0.3750	5	0.3203	Sig	0	0	9	22.6	9	<0.001	1.000	15	29.0	9	<0.001	1.000
20180805	07 alt In	54	Bsb-Alim	0.3745	0	0.2722	Sig	39	54	19	28.0	8	0.007	0.993	36	35.7	3	0.544	0.456
20180805	07 alt In	54	Bsb-Spa	0.4059	0	0.2722	Sig	39	54	13	28.0	17	<0.001	1.000	32	35.7	4	0.114	0.886
20180805	07 alt In	54	Bsb-Blu	0.2946	0	0.2722	Sig	39	54	17	27.9	8	0.001	0.999	30	35.7	5	0.031	0.969
20180805	09 alt In	76	Bsb-Alim	0.1382	0	0.2294	NS	13	74	22	38.3	15	<0.001	1.000	34	50.3	8	<0.001	1.000
20180805	19 alt Out	79	Bsb-Spa	0.1885	17	0.2540	NS	4	41	33	37.2	9	0.152	0.848	48	52.3	6	0.121	0.879
20180806	01 Out	74	Bsb-Alim	0.2851	-7	0.2443	Sig	16	74	22	37.6	14	<0.001	1.000	45	49.0	4	0.132	0.868
20180806	19 alt Out	74	Bsb-Spa	0.2852	3	0.2374	Sig	2	38	30	37.6	11	0.036	0.964	43	49.0	4	0.047	0.953

Solid horizontal lines in the table separate results for different species pairs from distinct camera deployments. Sample periods = number of 1-min sample units. Species pairs: Bsb = black sea bass, Alm = Almaco jack, Spa = Spanish mackerel, and Blu = blue runner. Lag = time lag for peak CCF value, Significance Threshold = calculated significance threshold per methods; Sig. = significant or NS; Number of Attacks = sample intervals with attacks based on flight response of forage fish; Number of Forage Present = sample intervals with aggregations of forage fish species. Runs test metrics addressing nonrandom behavior with runs through the median line = observed runs about the median, expected runs through median if random, ρ -value to indicate clustering on one side of the median, and ρ -value of mixtures with clusters of multiple runs through median. Runs test metrics addressing number of runs up and down = observed number of runs up or down, expected number of runs, longest number of observations as a continuous run, ρ -value for nonrandom fluctuations up and down.

FIGURE 4

Example of runs chart comparing black sea bass and almaco jack MaxN counts in sequential time periods from station 05 In on 20180802. Small gray points represent counts from both species. Large dark points connected by lines are the mean value of each pair of points at each time period. The horizontal line is the median value of all points. The oval at top center is an example of clustering on one side of the median. Note $p < 0.001$ for this test (Table 1) is highly significant. The oval at the left is the longest run of seven points crossing the median. Multiple runs of multiple points up and down result in a significant trend pattern.

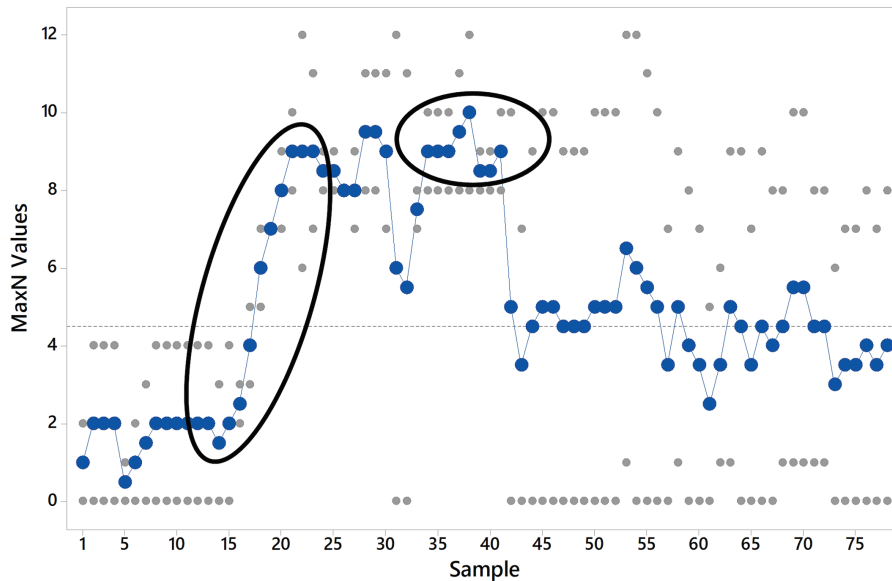
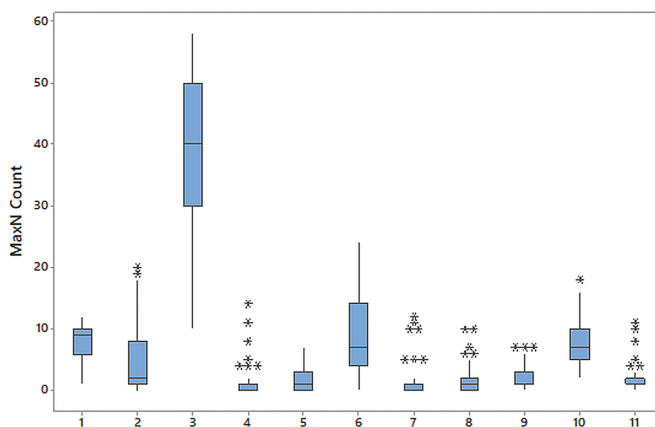


FIGURE 5

Boxplots to compare variation in MaxN of black sea bass within sample periods and across sample sites. The center line through each box indicates the median value. Top and bottom of each box mark the bottom of the third and the top of the first quartile of the data, respectively. The top whisker extends to the highest value in the top quartile, and the bottom whisker extends to the lowest value in the first quartile. Stars indicate statistical outliers. The order of samples corresponds to the order of sites in Table 1 (sample site on x-axis: 1–05 In, 2–07 alt In, 3–09 alt In, 4–05 In, 5–07 alt In, 6–30 In, 7–07 alt In, 8–09 alt In, 9–19 alt Out, 10–01 Out, and 11–19 alt Out; note repeated stations sampled on different dates).



or a fear response based on the presence of other predators).

Runs tests (Table 1) results are remarkably consistent across stations and days, with significant clustering of black sea bass and multiple mid-water piscivores, indicating nonrandom co-occurrences on time scales of minutes (Figure 4). Noteworthy is the lack of significant mixture patterns in the data suggesting that species movements are linked by some behavioral mechanism. Similarly, tests for trends are significant in most samples, while oscillations were not observed.

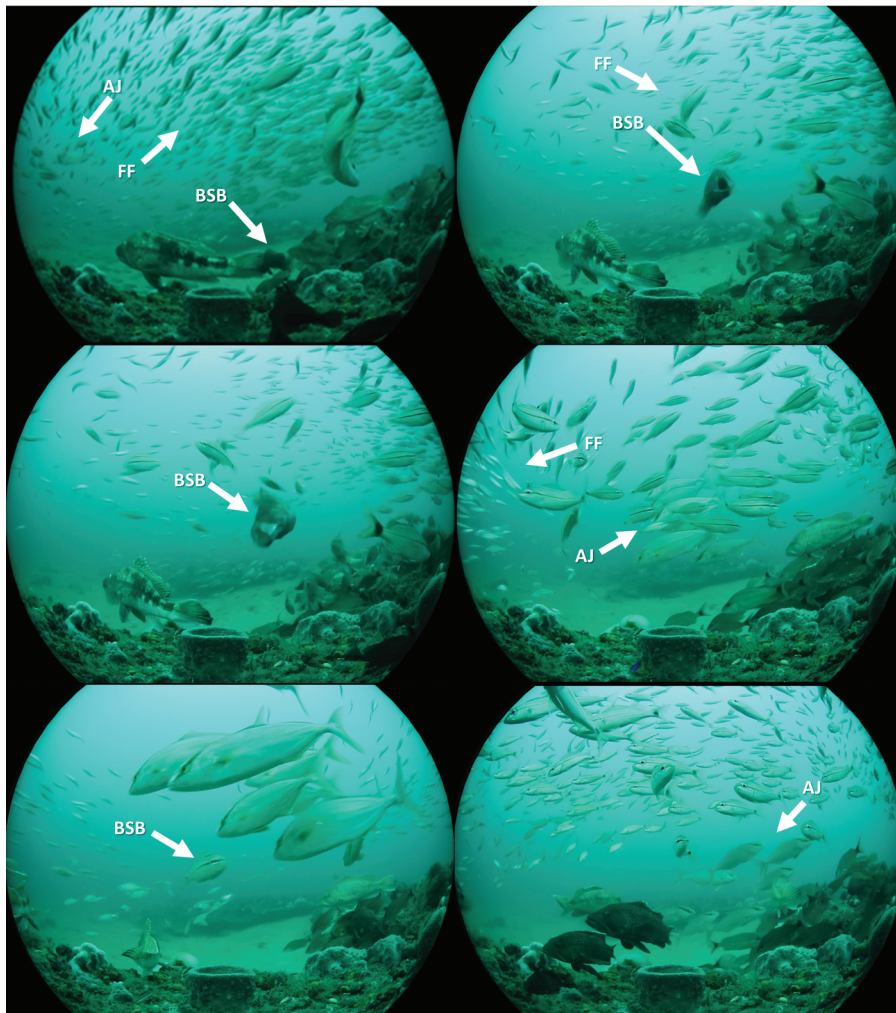
Variation of black sea bass MaxN counts (Figure 5) within relatively short sample periods and across sites, indicating rapid behavioral responses to availability of prey based on facilitation by mixed-species groups of predators, is also noteworthy. Figure 6 is an example of the interactions of almaco jack, black sea bass, and tomtate and scad as prey at a reef site, with attacks from the midwater predator eliciting escape responses of prey and facilitating attacks by black sea bass.

Discussion

We identified statistically significant paired-species interactions on reefs and consistent patterns of species co-occurrences using a stationary VR video sampling approach that enhances our ability to resolve these behaviors. This technology also provided further evidence of the importance of mixed-species predation as a process in structuring trophic webs in reef communities. While our results are based on limited sampling for a technology demonstration project, we have demonstrated the benefits of using VR video for sampling transient predators (or other

FIGURE 6

Exemplars of species interactions observed with VR video samples. Sequence of almaco jack (AJ) attacking and eliciting escape response of forage fish (FF), with subsequent attack by black sea bass (BSB) and associated behavioral cues on AJ movements.



species) and assessing uncertainty in metrics developed from census data using point sampling (Bohnsack & Bannerot, 1986; Koenig & Stallings, 2015).

VR video cameras allow continuous video recording in nearly spherical space of behavior and species interactions that are rarely captured using “standard” point-of-view cameras with a single lens of normal (mid-range) focal length. While standard cameras and sampling approaches are useful for determining ecological metrics, such as index of

abundance, they do not capture the full spatial element in which multiple species interact. Like all imaging and visual approaches for data collection, VR cameras have their limitations: visibility limits the ability to detect and follow individuals. Observations of midwater predators are sometimes problematic due to downwelling light during daytime. The response of automatic exposure functions with wide angle optics can also reduce the distance fishes in silhouette can be identified (e.g., Spanish mackerel). That said, while some predatory inter-

actions were not observed directly in the VR camera’s field of view due to distance, the fear responses of prey served as proxies for attacks from midwater predators, with assumed information sharing within the aggregations of the attacked forage species (i.e., given consistent responses of prey to attacks by almaco jack, Spanish mackerel, blue runner, and scamp).

Variation in MaxN over short time periods suggests the need to ensure that surveys operate within the range of movements of animals over the course of their daily ambit. The techniques we have described herein do not replace standard survey methodology for evaluating species composition and density, but they augment surveys and time series by addressing issues related to species interactions, spatial and temporal variation, and the behavioral processes behind such variation.

The results presented here demonstrate the analytical approaches that are facilitated by VR sampling. Other applications of VR video for evaluating abundance, MaxN, rare encounters, and size (using objects of known size for scale) are also possible (Kilfoil et al., 2017). This imaging approach, with an enhanced capability to address the spatial and temporal extent of species interactions, improves our ability to reveal elements of the invisible fabric of nature and allows us to better understand fish community function and interactions that are critical for conservation and management of natural resources (Auster et al., 2013a; Travis et al., 2014).

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