

Use of High-Resolution DIDSON Sonar to Quantify Attributes of Predation at Ecologically Relevant Space and Time Scales

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Introduction

Predation plays a critical role in the structure of reef fish communities (Tupper & Boutilier, 1997; Carr et al., 2002; Hixon & Beets, 2003). In addition to the direct effects on mortality of prey populations, predators also affect the distribution and behavior of co-occurring predators and prey species (Cosner et al., 1999). Predator-prey interactions are generally thought of most frequently in terms of direct mortality of prey and observed in the field using indirect methods such as stomach content sampling (e.g., Lindquist et al., 1994). Acoustic telemetry of muscle contraction rates (e.g., related to swimming speed) and stomach temperature have also been employed to infer patterns of feeding (Oswald, 1978; Sepulveda et al., 2004). Such indirect

ABSTRACT

Predator-prey interactions of large vagile fishes are difficult to study in the ocean due to limitations in the space and time requirements for observations. Small-scale direct underwater observations by divers (ca. <10 m radius) and large-scale hydroacoustic surveys (10 s m² to 100 s km²) are traditional approaches for surveying fish. However, large piscivorous predators identify and attack prey at the scale of meters to tens of meters. Dual-Frequency Identification Sonar (or DIDSON) is a high-resolution acoustic camera operating in the MHz range that provides detailed continuous video-like imaging of objects up to a range of 30 m. This technology can be used to observe predator-prey interactions at ecologically relevant space and time scales often missed by traditional methods. Here we establish an approach for quantifying predation-related behaviors from DIDSON records. Metrics related to predator and prey group size, prey responses to predation, predation rate, predator strategies, and the nonrandom use of landscape features by both predator and prey are described. In addition, relationships between patterns in these attributes are tested and issues regarding sampling strategies for future studies are discussed. We suggest that approaches combining direct visual observation and acoustic sampling at multiple scales are required to quantify variation in these relationships across underwater landscapes.

Keywords: predator, prey, behavior, reef, hydroacoustics

approaches are employed without regard to the more complex behavioral interactions between competing predators as well as between predators and prey, and their surrounding habitat that ultimately mediate predation success (but see Crowder et al., 1997). However, indirect methods cannot identify other important variables that influence predation dynamics and the impacts they have on population and community structure (Dill et al., 2003) such as predator group composition, effects of predator abundance, variation in the functional roles of species, interactions with landscape features, distribution and behavior of

prey, and indirect species interactions (between predators as well as between predator and prey). The nature of these interactions makes them difficult to observe in any direct fashion at ecologically relevant space and time scales.

Variation in prey density has been shown to modify the relationship between prey survival and refuge availability through density-dependent predation mortality (Lannin, 2011). There are several mechanisms that mediate this phenomenon. Predator abundance can affect species richness of prey fish communities by forcing competition for refuge as well as altering species distributions (Cosner et al.,

1999). Anderson (2001) found that increasing habitat complexity produced a pattern of density-dependent prey mortality that had a stabilizing effect on prey fish populations. However, these patterns have an implicit assumption of homogenous distribution of predators and prey. A shortage of prey refugia has also been shown to cause short-term density dependent mortality due to predation (Johnson, 2006). If prey use particular seafloor features for refuge, predators may then occur at a higher density around these features (Kracker et al., 2008; Auster et al., 2009, 2011, 2013). Cosner et al. (1999) suggests that predation rates are therefore density dependent for both predator and prey as competition between predators increases.

The importance of intra- and interspecific interactions that facilitate predation, such as herding and confusing prey for other group members to attack or ambush (e.g., Hobson, 1968; Strand, 1988; Parrish, 1993; Auster et al., 2013), is unknown in most ecological settings in the ocean. However, where studies have been conducted, the act of facilitation between predator species (*sensu* Dill, 2003) appears to be common. For example, pelagic predators drive schools of prey to the surface, which increases prey availability to sea birds and has important population level effects (Au & Pitman, 1986; Ribic et al., 1997; Safina, 1990; Clua & Grosvalet, 2001; Robinson & Tetley, 2007). Auster et al. (2013) observed predation by single and mixed-species groups of piscivores at subtropical reefs off the southeast United States and eastern Gulf of Mexico, where only 11% of 379 predation events involved only a single piscivore. All other events involved facilitation of predation by monospecific and mixed species groups

of midwater and demersal predators. Most complex were events where midwater predators forced prey species to retreat to the seafloor, resulting in ephemeral high density patches of prey, which were then attacked by single and mixed species groups of demersal piscivores (67% of 274 events off the southeast United States and 28% of 105 events in the northeast Gulf of Mexico). Other studies of the interactions of multiple predators on a single prey species demonstrated that prey risk either decreased due to interactions between the predators themselves or increased because of conflicting prey responses to multiple predators (Sih et al., 1998). Clearly greater understanding of the outcomes of such interactions is critical to the development of a mechanistic understanding behind variations in local predator and prey populations as well as community structure. Such data can provide the foundation for improving the effectiveness of conservation and management strategies for reef fish communities.

To observe predation events at suitable space and time scales, new observational techniques are needed. Data collected by direct underwater observations by divers provide high-resolution “snapshots” of species composition and predator-prey interactions in a specific area but are limited in space and time (e.g., ca. <10 m horizontal radius, <1 h observation time). Hydroacoustic approaches can be used to expand observations in both space and time; for example, to investigate schooling behavior in response to predation (Gerlatto et al., 2006; Brierly & Cox, 2010) and examine the spatial distribution of prey species (Mayer et al., 2002). Ship-mounted split beam sonar systems are commonly used to assess large-scale patterns of fish distribution and abundance (e.g., 10 s m²

to 100 s km²) but lack the spatio-temporal resolution necessary to capture individual predation events as they occur. The scale at which high-resolution sonar imaging operates falls between the spatiotemporal resolution of these two approaches by expanding the range of visible diver observations, especially in turbid waters, and by providing detailed imagery of predation events at single sites within the context of the marine landscape surveyed using hydroacoustics.

DIDSON (Dual-Frequency Identification Sonar, SoundMetrics Corp.) is a high-frequency (i.e., MHz range) sonar camera that produces video-like images at a rapid rate allowing the movement and behavior of individual animals to be observed and quantified. Recent applications of DIDSON sonar include fish counts (e.g., salmonids passing particular areas in a river) and size estimates (Boswell, 2007; Maxwell & Gove, 2007). Work has also been done using DIDSON to perform abundance estimates of fishes in turbid waters, such as mangrove channels, where diver observations are not practical or possible (Frias-Torres & Luo, 2009). Behavioral studies using DIDSON to investigate the spawning of chum salmon (Tiffan et al., 2010) and avoidance by fishes of trawl gear (Rakowitz et al., 2012) illustrate the potential to investigate behavior on a scale useful for predation studies.

The DIDSON sonar used in this study ensonifies a region ranging from 1 to 30 m from the transducer. This allows for the collection of data at ecologically relevant space and time scales, capturing the fine-grain characteristics of predation. Because the use of DIDSON for behavioral observations is still exploratory, there is a need to first develop metrics and approaches to quantify attributes of predator-prey

interactions from sonar records. Here we report on the development of a set of metrics and related analytical approaches for using DIDSON imagery to assess attributes of piscivory in reef fish communities. Our intent is to develop an approach for using this state-of-the-art tool to ultimately gain a more thorough understanding of the role of predation processes in reef fish communities.

Materials and Methods

DIDSON System Characteristics

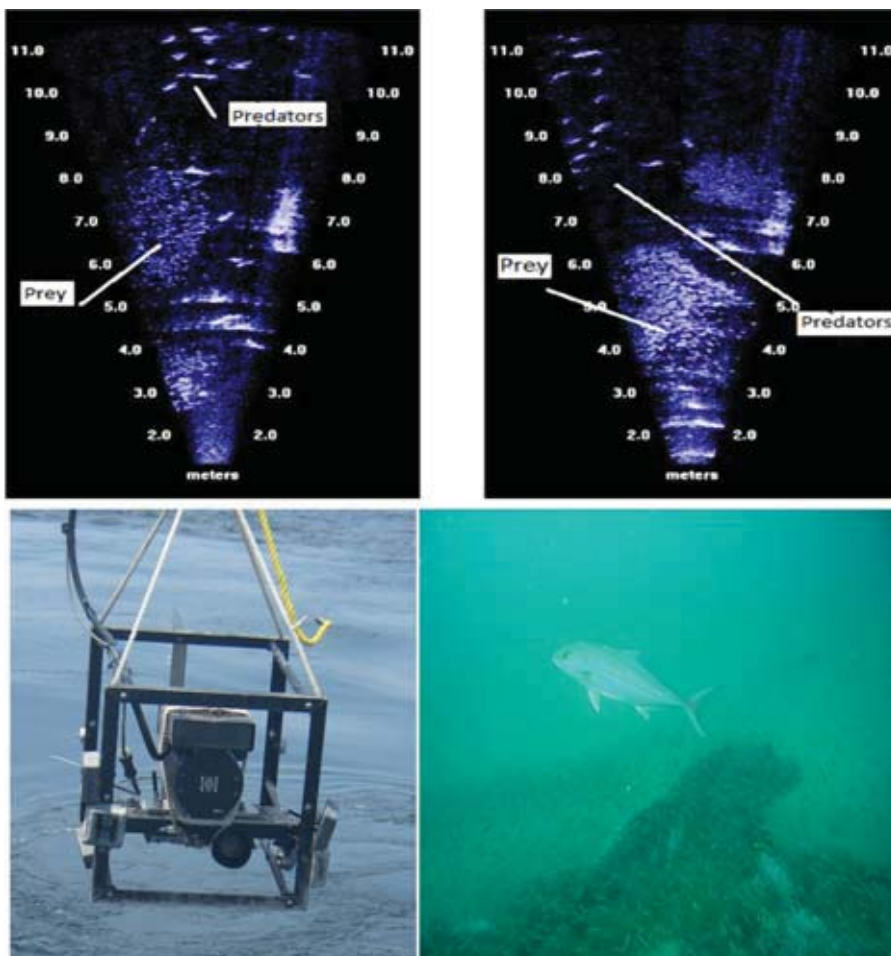
We used a DIDSON standard model 300M in this study. It is a high-resolution sonar unit that operates at a 1.1- or 1.8-MHz frequency, producing video-like images (Figures 1a and 1b). For this study the system was set to 1.8 MHz with a 2- to 11-m horizontal range. The sensor produces 96 beams with a $28.8^\circ \times 12^\circ$ field of view. Data were collected continuously at a rate of 8 frames s^{-1} with data files parsed into 12-min segments. The subsea sonar unit was mounted in a weighted frame affixed with a metal fin to orient into the current. The system was deployed shipside via power and data cable (the vessel was stationary using dynamic positioning) and rested on the sea floor facing along the edge of a reef (Figure 1c).

Study Site

Anchor Ledge ($31^\circ 37.7'N$, $80^\circ 34.6'W$; depth 25 m) is located approximately 20 miles off the coast of Georgia. It is part of a large network of subtropical sandstone reef habitat representing approximately 5% of the continental shelf off the southeast United States (Powles & Barans, 1980; Parker et al., 1983). Emergent ledges in this region are up to 3 m in height surrounded by sand plains and exposed

FIGURE 1

(a and b) Example still frames of DIDSON imagery from 17 June 2009 illustrating a group of predators interacting with aggregations of prey. Note herding of prey at center of image b. (c) Deployment of DIDSON shipside via power and data cable. (d) Example of typical ledge with greater amberjack and prey.



flat hard substratum. Hard substratum is dominated by suspension feeding organisms such as coral and sponge (Kendall et al., 2007). This structurally complex environment provides shelter and prey resources for a diversity of fishes, subsequently mediates their distribution, and affects spatial patterns of predator-prey interactions (Figure 1d; Sedberry & Van Dolah, 1984). Common midwater piscivores at these reefs include bar jack *Carangoides ruber*, blue runner *Caranx crysos*, greater amberjack *Seriola dumerili*, great barracuda *Sphyraena barracuda*, and Spanish mackerel

Scomberomorus maculatus. Demersal piscivores include black sea bass *Centropristis striata*, bank sea bass *Centropristis ocyurus*, scamp *Mycteroperca phenax* and gag grouper *Mycteroperca microlepis*. Both groups prey upon highly abundant round scad *Decapterus punctatus*, mackerel scad *Decapterus macarellus*, and juvenile tomtate *Haemulon aurolineatum* (Auster et al., 2009, 2013).

Attributes of Predation and Analysis

Initial review of DIDSON records from this study revealed discrete

predation events with quantifiable behavioral attributes. Earlier work based on direct observation by divers (Auster et al., 2009) used discrete predation events as sample units and this approach is continued here for analysis. Small and large fish were present and moving within and through the ensounded volume in most records; however, this by itself does not indicate predation related behaviors. Because it is impossible to verify if the actual consumption of prey occurred, criteria were established to determine if a predation-related event (PRE) occurred (Figure 2). Both predator and prey needed to be present in the field of view for a PRE to occur, and we assumed that predator reaction to prey was evident by a rapid change in predator trajectory. Likewise, response by prey was evident in a rapid change

in prey trajectory. It is important to recognize that these images are a two-dimensional representation of three-dimensional phenomena and that elements of each event may be occurring outside the ensounded region. However, we assumed that the individuals and interactions in the field of view are representative of each event and scaled appropriately in both space and time. If multiple attacks by two different groups of predators were observed, then they were considered separate events. Alternatively, two attacks by the same group were considered a single event.

Image files were initially reviewed using DIDSON Control and Display software (SoundMetrics Corp., V5.25.16). Records for each PRE were delineated based on the file time code and then individual frames

in jpeg format extracted at three points (Figure 3): when the largest number of individuals were present in the field of view (referred to as Image 1_max), just prior to the PRE (referred to as Image 2_pre), and at the moment predators reacted to prey (i.e., at the time of a rapid change in predator trajectory; referred to as Image 3_react).

Sixteen metrics (13 measures of continuous data and 3 categorical classifications) were developed *a priori* to describe each event (Table 1). However, one measure based on continuous data was eliminated from the present study and four were ultimately treated as categorical data. Measures of predator length were eliminated due to large numbers of small individuals with variation affected by image resolution and animal orientation. Rather than using predator length as a continuous measure, predators were binned into 20-cm size classes instead. Number of prey groups and number of predator groups varied little and were classified by abundance category.

For counts and areal measurements, image files were digitized using Image J software (version 1.45s; Abramoff et al., 2004), which converted the DIDSON screen captures to 8-bit jpeg format with the low and high contrast threshold set to 30 and 255, respectively, enhancing the contrast between fish and background. These values were determined through an iterative process to eliminate background reflectance and facilitate counts and measurements. Predator and prey group area measurements as well as areal extent of prey response measurements (using Image1_max) were made in Image J based on an intercalibration of a known length acquired from an image. That is, a 1-m measured distance normal to the transducer at a 6-m range was translated to 57.4 pixels using the Image J Set

FIGURE 2

Decision diagram to determine if a predation-related event occurred. Reaction to prey was determined by a rapid change in predator trajectory. Response by prey was determined by a rapid change in prey trajectory.

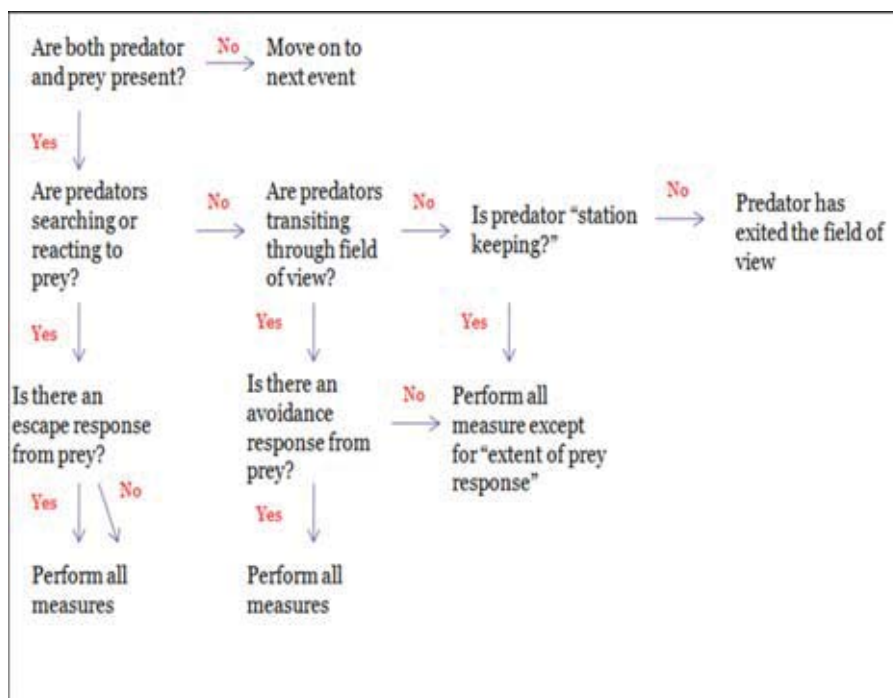
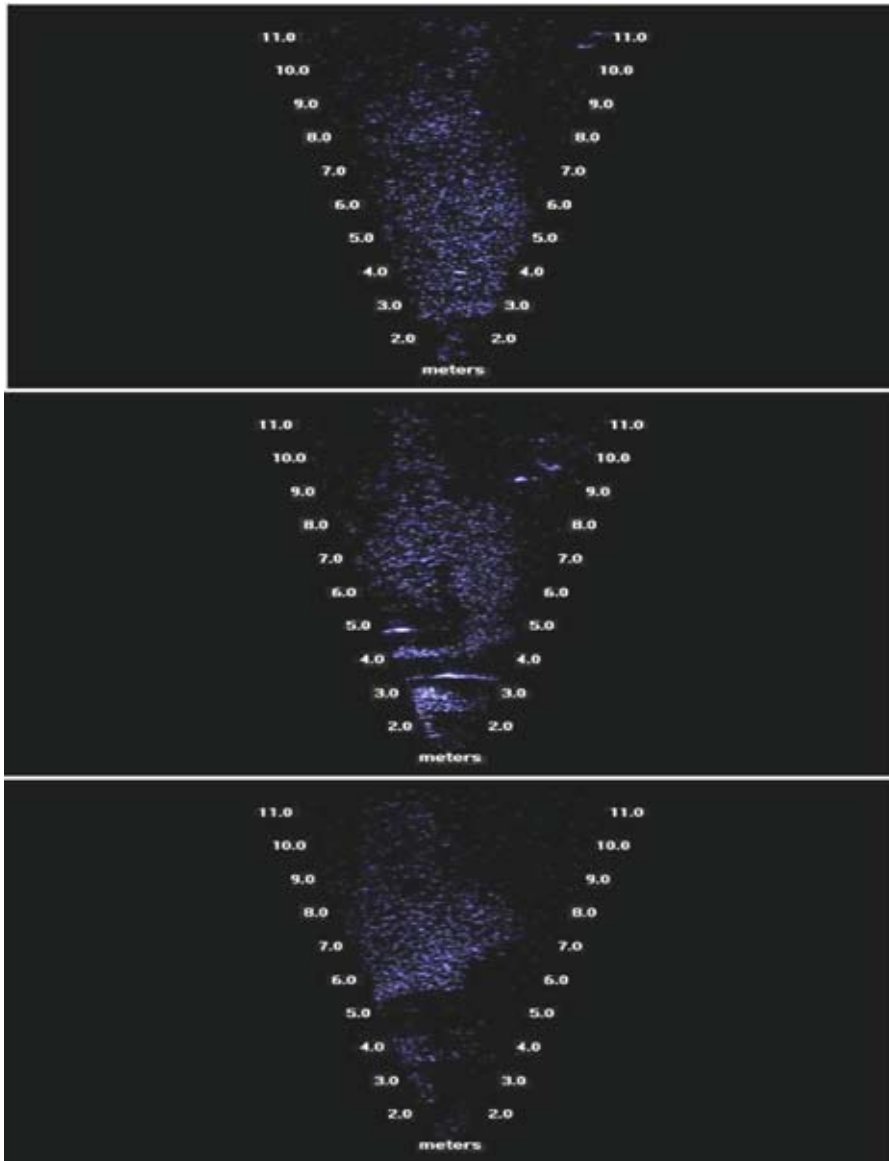


FIGURE 3

Example frame grabs from a single PRE used for analysis as described: just prior to the PRE (top), during the event (center), and just after the event (bottom).



Scale tool. While there is a decrease in resolution with increasing distance from the transducer, measurements taken at 6 m did not differ by more than 2 cm across the 1- to 12-m range.

Density of predator and prey schools were measured using the particle counting tool for objects over 5 cm in Image1_max. The areal extent of prey response was measured as the

difference in prey school area just prior to and during the PRE by comparing Image2_pre and Image3_react (Figure 4). The number of total attacks by all predator schools per event was measured, as well as the predation rate for each event (i.e. the number of attacks/duration of the PRE). The duration of events (in seconds) was also recorded, as well as by

the total PRE rate per file (i.e., the number of events per 12-min file—admittedly an arbitrary sample unit time based on software configuration).

Categorical data include sizes of predators in each PRE, which were binned by 20-cm size classes. Predator trajectory through the field of view was classified to assess predator orientation to the long axis of the reef. Classes are either along the reef axis (parallel to) or across (intersecting) the reef from an off reef position. Predator behavior was classified based on shape of aggregations and orientation within or outside of prey schools. The formation of predators relative to prey schools were classed as: single individuals, a distinctly linear formation of multiple individuals, or as a circular-like group (or polygon) with individuals three or more deep. Furthermore, predators initiated PREs either within or adjacent to aggregations of prey. Therefore, inclusive categories are circular/along (CA), circular/integrated (CI), linear/along (LA), linear/integrated (LI), singular/along (SA), and singular/integrated (SI) (Figures 5a and 5b). Behavior classifications based on movements in relation to prey and habitat elements were made by viewing original records using DIDSON software.

To assess the relationships between metrics, a correlation matrix based on the Pearson's R statistic was computed. The *a priori* threshold for significance was $p < 0.05$. To better visualize and contrast relationships between pairs of metrics and to assess the degree of linearity in these relationships, a regression matrix was produced with a scatterplot of data points and a linear regression forced through the origin. As each variable has an independent distribution, the right side of the matrix plots y on x and the left side plots x on y , hence each side of the matrix is not a mirror image.

TABLE 1

Description of continuous and categorical metrics.

Metric	Description
<i>Measures with continuous data</i>	
Predator length	Size of individual predators; changed to categorical
Number of prey groups	Number of schools of prey (presented as numerical classes)
Number of predator groups	Number of schools of predators (presented as numerical classes)
Predator group size	The number of individuals in a school of predators
Predator group density	Number of individuals/area of group
Prey group size	Number of individuals in a school of prey fish
Prey group area	Area of prey group
Prey group density	Number of individuals/area of group
Areal extent of prey response	Measurement of change in prey group area during predation-related event
Number of attacks event ⁻¹	The number of times all predator schools attacked a prey school
Predation rate	Number of attacks min ⁻¹ within each event
Duration of event	Time elapsed from first reaction to prey to end of reaction to prey
Global predation rate	Number of attacks per 12-min file
<i>Categorical data</i>	
Size class of predators	The average size of predators in the school; 20 cm increments
Formation of predators relative to prey school	Circular/along (CA), circular/integrated (CI), linear/along (LA), linear/integrated (LI), singular/along (SA), and singular/integrated (SI)
Trajectory of predators across field of view	Across or along field of view

To determine if patterns of predation are patchy (clumped) over time, a two-term local quadrat variance (TTLQV) analysis was performed. The TTLQV was originally developed to quantify patterns of spatial patchiness from quadrat data, but in this case we used temporal period in lieu of quadrats to assess patchiness in time. Here global predation rate based on each 12-min file was the sample unit. The two-term local

quadrat variance method blocks sample units at a consistent scale (here set at 10%). The mean square difference between neighboring blocks is then calculated to determine the variance across a range of distances (i.e., in this case time) between blocks (Rosenberg & Anderson, 2011).

Because this was an exploratory effort to assess approaches for future research, we also performed a *post hoc* power analysis to determine approxi-

mate sample sizes needed for future studies, assuming future data exhibit similar statistical distributions. Here we specified the range of numerical differences between sample means (i.e., 1–5) based on a power level of 0.8 and significance level of $p < 0.05$ for a two-sample t test. Sample size requirements were calculated based on the standard deviation for each metric.

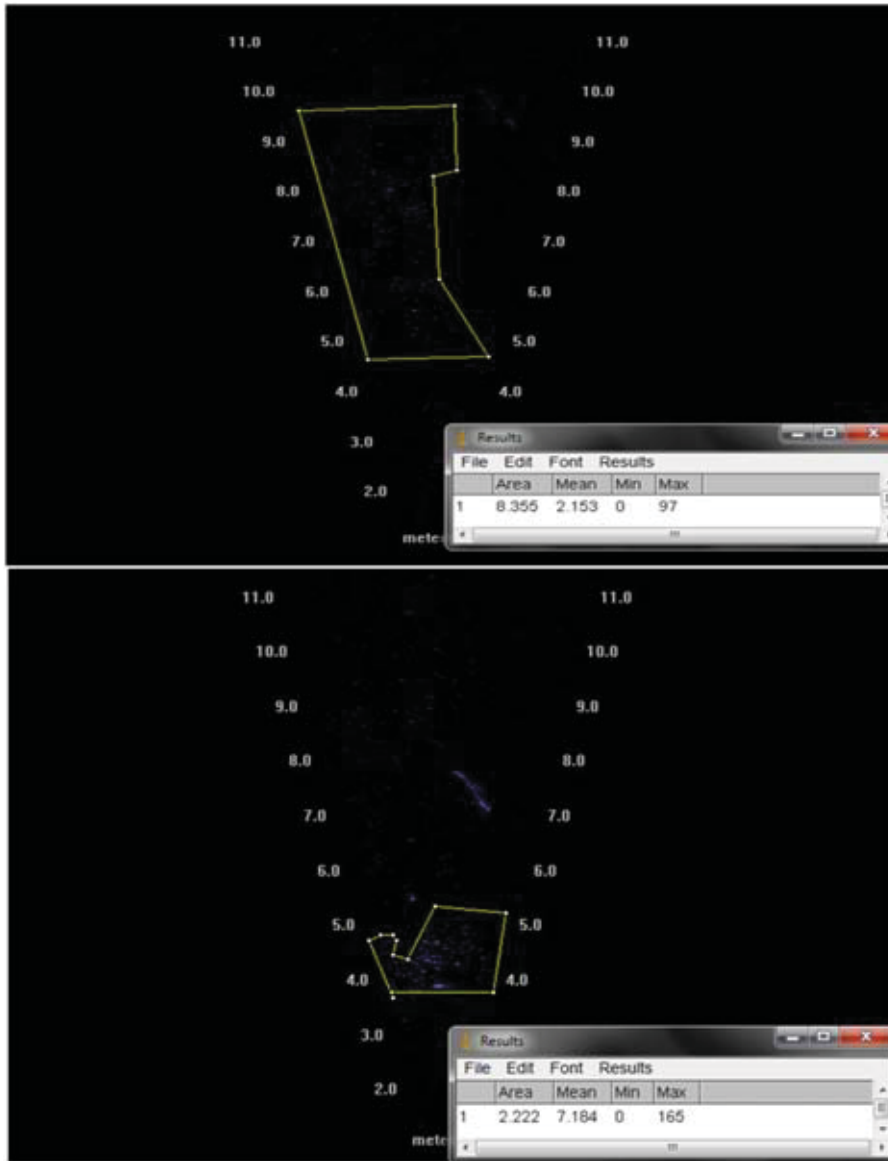
Results

A total of 192 min of sonar data (parsed in sixteen 12-min record files) were recorded at Anchor Ledge from 1051 to 1336 EST on 17 June 2009. Analyses of sonar imagery yielded a total of 111 PREs. Descriptive statistics for each metric based on continuous data are summarized in Table 2. Only one measure, global predation rate, had a normal distribution based on the Anderson-Darling test for normality ($p > 0.05$). All others were non-normal ($p < 0.05$). Note that normally distributed data have a skewness of 0 and a kurtosis of 3. All metrics here have high skewness (a measure of asymmetry) and a wide range of kurtosis (a measure of peaked versus flat distribution).

Typically, predator group size was small (<20 individuals; Figure 6), and groups had relatively low density (Figure 7). The majority of PREs (68%) consisted of a single predator group and a single prey group; however, there were 15 events with multiple predator groups and a single prey group. Seventy-three percent of predator groups moved through the field of view along the reef axis. Fifty percent of predators were between 20 and 39 cm in length and groups always contained similarly sized individuals. Five percent of predators were over 100 cm in length, and

FIGURE 4

Example of measurement of extent of prey response; comparison in area pre (top) and during (bottom) an event. Inset windows are from Image J software.



these individuals were always solitary (Figure 8). Ninety percent of events were under 1 min in duration (Figure 9). Table 3 contrasts the relationships in metrics based on continuous data with only 12 statistically significant paired contrasts. Interestingly, the relationship between predator group size (mean 10.4 individuals, $SD = 16.8$) and extent of prey response (mean 2.99 m^2 , $SD = 2.16$) was not significant ($p = 0.99$, $r^2 = 0.1197$).

A significant negative relationship was found between prey group area and predator group size ($p = 0.018$, $r^2 = 0.0514$) as well as predation rate and extent of prey response ($p = 0.04$, $r^2 = 0.070$). There was a positive relationship between the number of attacks per event and predator group size ($p < 0.001$, $r^2 = 0.1420$) as well as event duration and predator group size ($p < 0.001$, $r^2 = 0.2990$). As expected prey group area, density and the extent

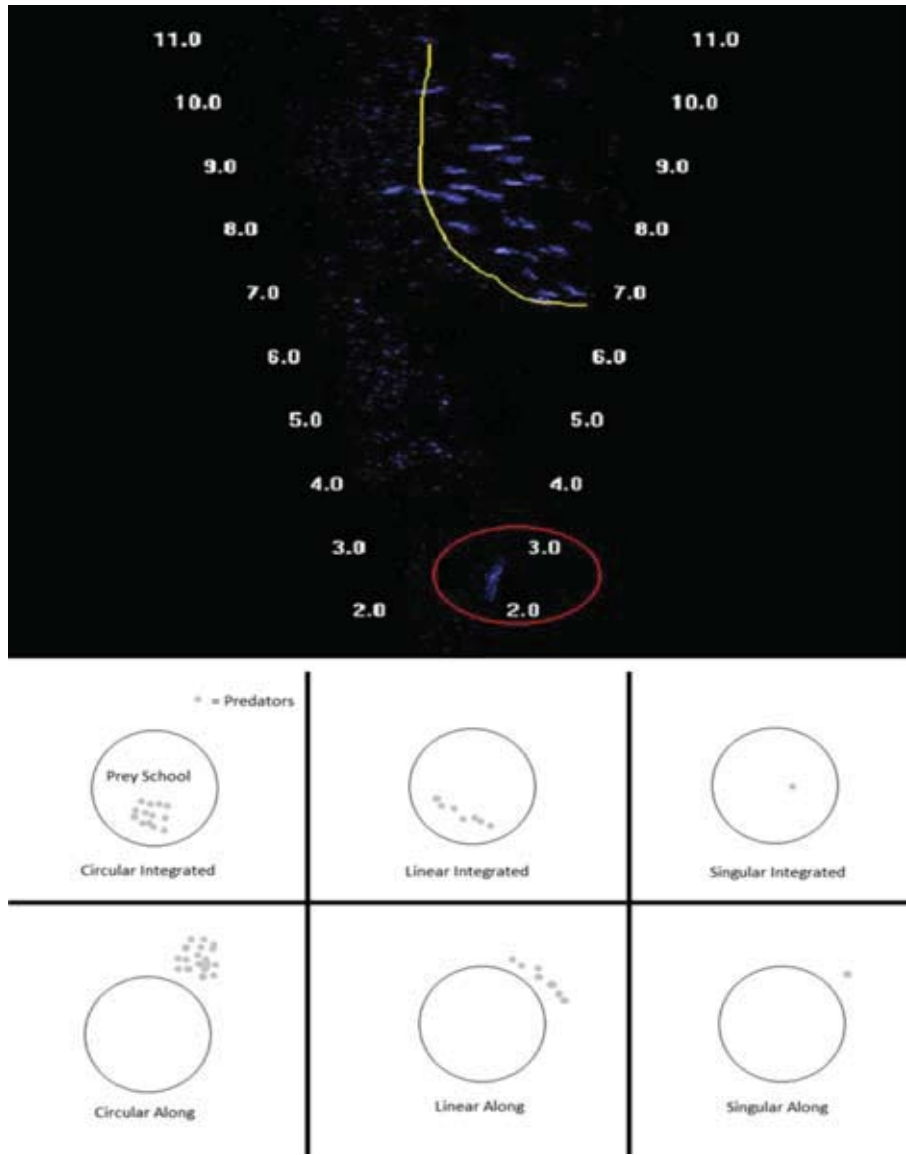
of prey response were strongly correlated ($p < 0.05$, $r^2 = 0.4060, 0.1341, 0.2460$, respectively), as well as the duration of event, number of attacks, and predation rate ($p < 0.01$, $r^2 = 0.4104, 0.0500, 0.0110$, respectively). The regression matrix (Figure 10) illustrates that even with significant r values few pairs exhibited a linear relationship, suggesting some form of polynomial relationship is required.

Predation rate and prey group size varied over time (Figure 11); with a pattern of higher activity in the morning and afternoon, and with a minimum at midday. The relationship between predation rate and prey group size was marginally significant ($p = -0.0713$, $r^2 = 0.0020$). The two-term local quadrat variance analysis of global predation rate revealed that variance was highest over time at a scale of three blocked sample units (30% of the total sample time or 57.6 min). As blocks represent a radius when used in a spatial context, the peak values are doubled to calculate the degree of patchiness. In a temporal context therefore time is doubled, indicating patchiness in predation events at roughly 120 min (Figure 12). Over the entire observation period, mean predation rate was $0.485 \text{ events min}^{-1}$, ranging from 0.0 to $1.25 \text{ events min}^{-1}$.

The *post hoc* power analysis revealed that sample size requirements varied widely in order to detect differences between samples at a 95% confidence level (power coefficient = 0.80). Detecting differences between sample means of three or more will require observation of a reasonable number of predation events for most metrics (i.e., less than 500 events per site; Table 4). Prey group size had such a large standard deviation (i.e., 89.09) that sample sizes in excess of 4,900 events would be required

FIGURE 5

(a) Example of a predator group classified as "circular/along" to prey group (outlined in yellow); a second predator group is present close to the transducer (outlined in red). (b) Illustration of categories for predator group orientation to prey. (Color versions of figures available online at: <http://www.ingentaconnect.com/content/mts/mts/2013/00000047/00000001>.)



to detect significant differences between mean values that, in the present case, are around 150 individuals.

Discussion

Here we demonstrated that analyses of DIDSON records can be used to produce quantitative measures to describe multiple attributes of predator-

prey interactions of large vagile fishes. This study was conducted explicitly to establish approaches for processing DIDSON records, and based on these results, we are now in a position to implement studies to answer important ecological questions. DIDSON records enable a powerful approach for collecting data over long periods within and between sites irrespective of bottom

time, depth and visibility, which typically impose severe limitations for direct visual data collection by divers or remote video cameras alone. Understanding variation in predator and prey abundance, behavior and rate of interactions within and between sites will allow tests of hypotheses related to facilitation and interference between predators, variation in prey response, and the role of variation in structural habitat and oceanographic settings. Based on the limited data sets produced from this work, it is clear that relatively large sample sizes (ca. $n = 500$) will be needed to test for differences across treatments. If 3 h of observation yields approximately 100 PREs, then a 15-h deployment per station could produce sufficient sample sizes for most metrics to conduct appropriate statistical contrasts. Such a time period, while long by traditional visual sampling approaches, covers normal day (or night) periods inclusive of crepuscular periods over much of the globe and can capture variability at particular sample sites. The metrics derived from DIDSON imaging support, in general, diver observations related to the range in numbers and sizes of predators, coordinated group behaviors, and patchy prey distribution localized to ledge features (Auster et al., 2009, 2013).

The lack of statistical significance in many of the relationships between paired metrics raises many questions for further investigation regarding whether this pattern is due to limitations based on the region ensounded with a single DIDSON or a true lack of a relationship. The metrics that one would expect to be strongly correlated (e.g. density and area, duration and number of attacks) were indeed so, suggesting that the sample region was not the limiting factor. While one

TABLE 2

Descriptive statistics of continuous metrics.

Variable	Mean	SD	Minimum	Q1	Median	Q3	Maximum	Skewness	Kurtosis
Predator group size (count)	10.47	16.89	1	1	3	12.5	81	2.48	5.81
Predator group density (m ⁻²)	4.579	5.617	0.043	2.211	3.887	5.398	55.556	7.17	63.69
Prey group size (count)	155.84	89.09	24	95.5	136	199.5	501	1.66	3.65
Prey group area (m ²)	7.1	4.46	0.897	4.353	5.833	9.325	24.29	1.36	2.08
Prey group density (m ⁻²)	28.72	21.94	2.27	14.43	22.52	34.58	134.75	2.52	8.94
Extent of prey response (m ²)	2.944	2.146	0.013	1.426	2.445	3.854	14.85	2.01	7.81
Attacks per event	1.5138	1.0239	1	1	1	2	7	2.68	8.78
Predation rate (events s ⁻¹)	0.1428	0.3209	0.0147	0.0436	0.0667	0.125	3	7.19	60.06
Duration of event (s)	25.94	20.62	2	9	19	39.5	90	1.08	0.56

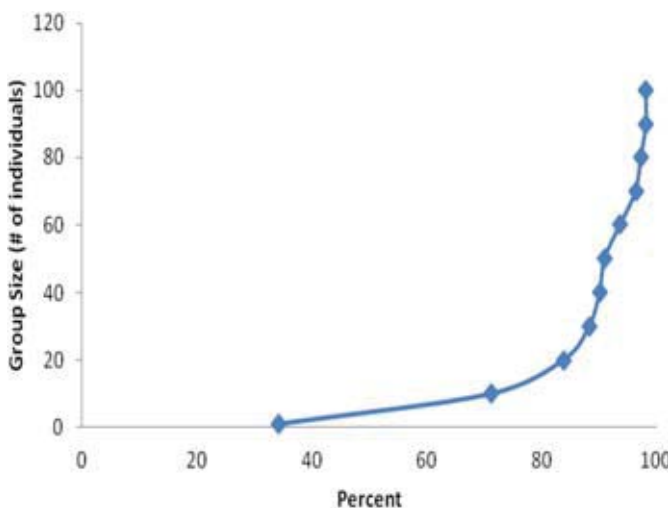
would assume that a greater abundance of predators would elicit a larger areal response of prey (i.e., extent of prey response), it may be that prey actively engage in risk assessment when foraging and do not always view predators as an immediate threat (Ferrari et al., 2010). That is, the area of prey reaction is the same for small and large groups. An alternative explanation is that activities of both predator and prey groups may be occurring outside

the ensounded region as well as in acoustic shadows cast by landscape features. It is important to emphasize that the DIDSON beam has a fairly narrow swath of about 28° horizontally and 12° vertically. While we assumed that behaviors observed in the ensounded region were representative of the sampling site and that variation in metrics addressed this problem, these space and time issues have yet to be fully resolved, especially when address-

ing limitations on accurately measuring absolute group size and dimensions. Development of sampling methods to address spatial variation in the ensounded region may produce a more refined picture of these dynamic interactions. For example, placing a single DIDSON on a pan-tilt unit and conducting either timed samples over a range of pre-set positions or periodic sweeps of a larger volume can increase overall sample volume both horizontally and

FIGURE 6

Distribution of predator group size. Predator schools were predominantly under 20 individuals in size, although groups ranged from 1 to 100+ individuals.

**FIGURE 7**

Distribution of predator group density. Schools were generally loosely packed.

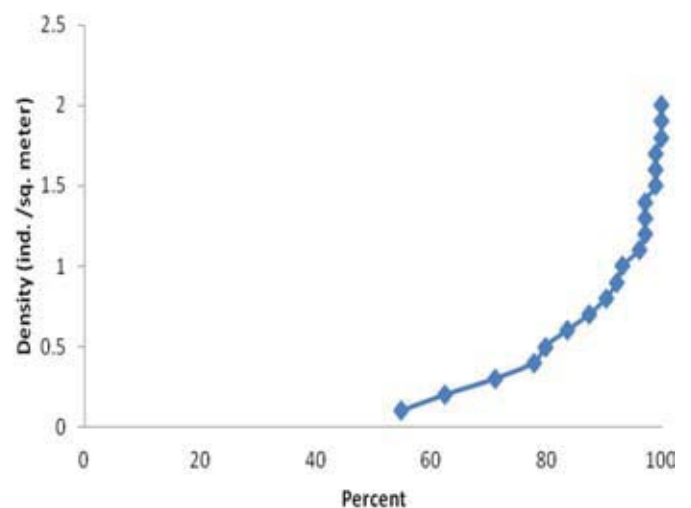


FIGURE 8

Frequency of predator size classes. Larger predators were generally solitary; smaller predators were the most common and occurred in larger groups.

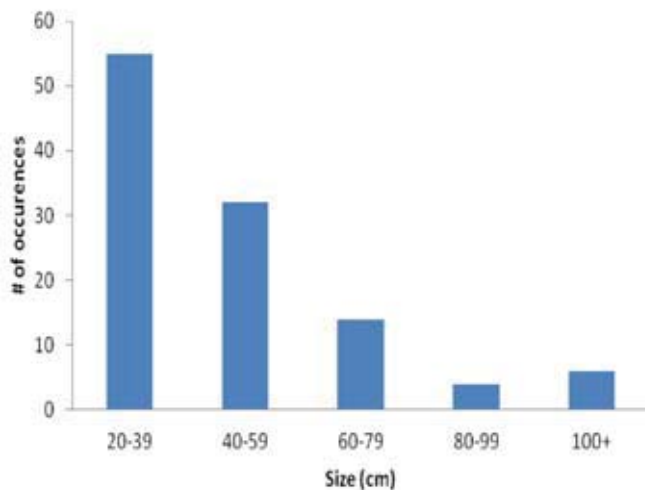
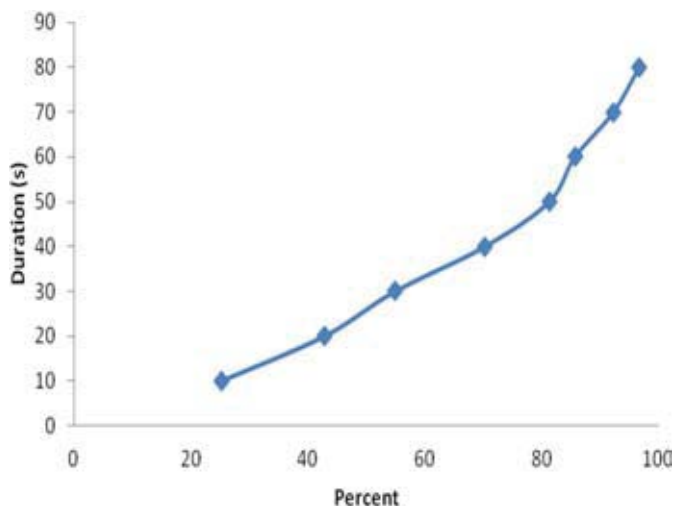


FIGURE 9

Distribution of PRE duration. Events were typically under 1 min in duration.



vertically. An arrangement of multiple sensors for simultaneous observations within and between habitat features also would resolve the issue of the optimal volume required for sampling (and perhaps reduce the number of samples required for comparisons).

Interesting relationships that were found to be statistically significant also prompt the need for further explanation. The negative relationship

between predation rate and the extent of prey response as well as positive relationships between predator group size, duration of the event, and number of attacks per event may lend clues about prey group response to the intensity of attacks as well as dynamics within the predator group.

Resolving the issue of measures of prey response to predators has long been of interest to ecologists. The use

of DIDSON may allow us to better address this problem, encompassing both predation behavior, as well as how prey species assess risk (e.g., behavior modifications in response to predation risk, deemed “risk effects”; Heithaus, 2008). Clemente et al. (2011) observed that areas closed to fishing positively affected predator assemblages, enhancing the intensity of predatory interactions compared to unprotected areas. Testing whether such patterns emerge in multiple regions and ecological settings as well as under different management scenarios would be a particularly useful application of this technology.

Increasing awareness of the utility of these types of sonar systems for studies of behavioral ecology will yield concomitant advances in analytical approaches. For example, Boswell et al. (2008) developed methods for autonomous analysis of large data sets from DIDSON records in order to measure fish size, biomass, swimming speed and direction. Mueller et al. (2010) used Echoview software (Myriax Echoview and Eonfusion, Hobart, Tasmania, Australia) to quantify species-specific tailbeat frequencies of two salmonids in a river in Alaska. Such approaches can then be used in sonar studies of migration behaviors addressing issues such as timing of upstream movements and patterns of habitat use. Automated approaches for quantifying the metrics we described here would greatly facilitate future studies given the predicted sample sizes required for comparisons. Concrete species identification remains elusive with acoustic work; however, the high-resolution imagery provided by DIDSON can lend information on body morphology, flexion, swimming behavior, and tail beat frequencies. These attributes, combined with the

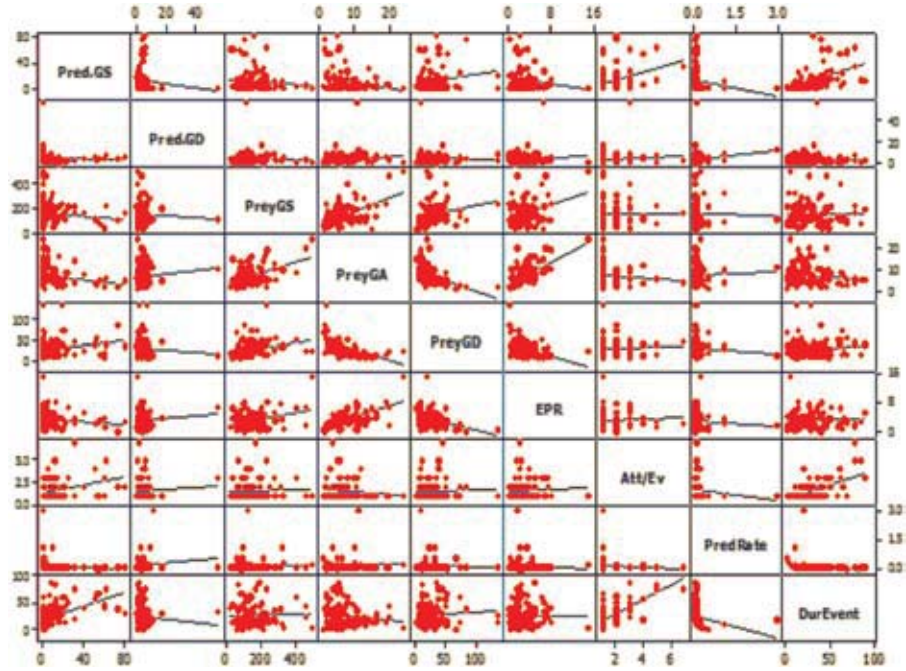
TABLE 3

Correlation matrix of continuous metrics (Pearson's *r* value is top number).

	Predator Group Size	Predator Group Density	Prey Group Size	Prey Group Area	Prey Group Density	Extent of Prey Response	#Attacks/Event	Predation Rate (events/s)
Predator group size	****							
Predator group density	-0.0990, <i>p</i> = 0.306	****						
Prey group size	-0.105, <i>p</i> = 0.277	-0.047, <i>p</i> = 0.629	****					
Prey group area	-0.226, <i>p</i> = 0.018	0.080, <i>p</i> = 0.404	0.489, <i>p</i> < 0.001	****				
Prey group density	0.182, <i>p</i> = 0.058	-0.078, <i>p</i> = 0.419	0.265, <i>p</i> = 0.005	-0.495, <i>p</i> < 0.001	****			
Extent of prey Response	-0.125, <i>p</i> = 0.194	0.093, <i>p</i> =0.335	0.338, <i>p</i> < 0.001	0.636, <i>p</i> < 0.001	-0.366, <i>p</i> < 0.001	****		
#Attacks/Event	0.376, <i>p</i> < 0.001	0.061, <i>p</i> = 0.527	0.033, <i>p</i> = 0.733	-0.099, <i>p</i> = 0.305	0.045, <i>p</i> = 0.641	0.075, <i>p</i> = 0.437	****	
Predation Rate (events/s)	-0.123, <i>p</i> = 0.137	0.130, <i>p</i> = 0.134	-0.071, <i>p</i> = 0.869	0.101, <i>p</i> = 0.635	-0.093, <i>p</i> = 0.487	-0.097, <i>p</i> = 0.0400	-0.093, <i>p</i> = 0.288	****
Duration of event (s)	0.547, <i>p</i> < 0.001	-0.086, <i>p</i> = 0.373	0.044, <i>p</i> = 0.652	0.124, <i>p</i> = 0.198	0.098, <i>p</i> = 0.313	0.022, <i>p</i> = 0.822	0.643, <i>p</i> < 0.001	-0.224, <i>p</i> = 0.019

FIGURE 10

Regression matrix plot of paired metrics with continuous data plotting both x on y and y on x . A general lack of linearity suggests there may be a polynomial model that may be more descriptive of these relationships. Pred. GS = predator group size; Pred. GD = predator group density; Prey GS = prey group size; Prey GA = prey group area; Prey GD = prey group density; EPR = extent of prey response; Att/Ev = number of attacks/event; PredRate = global predation rate; DurEvent = duration of event.



knowledge of species typically present in the area, may allow for the development of techniques to identify fish at least to species groups (such as jack, grouper, and sea bass).

Split-beam hydroacoustics provide a snapshot of fish distribution over a large spatial scale. However, key to understanding processes that result in this spatial variation are the real-time interactions that occur at the level of individual animals. DIDSON allows for the collection of continuous behavior data at a specific location over a long temporal period. Characterizing predation at multiple sites will allow statistical comparisons between sites and increase understanding of variation in species interactions as a whole. Developing effective and consistent data acquisition and analysis techniques for use of sonar records from DIDSON will allow for incorporation of variation in predation rates and predation intensity across habitats into population models so that spatially explicit demographic processes can be incorporated.

FIGURE 11

Variability over time for both the number of prey (left axis) and predation rate (right axis), ranging from midmorning to midafternoon (x axis is local EDT).

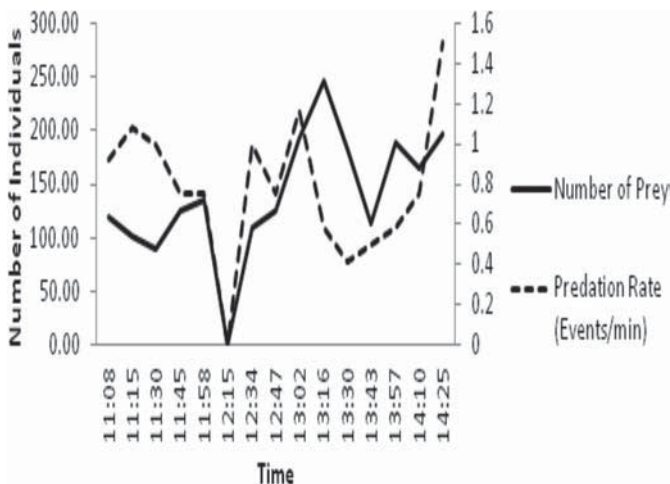


FIGURE 12

Result of two-term local quadrat variance analysis indicating that variance in predation rate is highest at a scale of 3 block units equivalent to approximately 120 min.

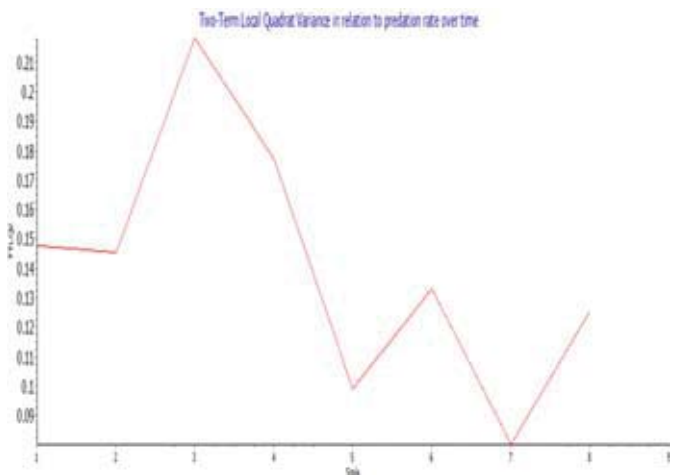


TABLE 4

Sample size requirements for a power level of 0.8 and alpha < 0.05.

Metric	Sample Size
Predator group size	856
Predator group density	858
Prey group size	859
Prey group area	859
Prey group density	859
Extent of prey response	854
Attacks/event	856
Predation rate	860
Duration of event	854

The knowledge gained from these approaches can then provide a more complete foundation for effective management and conservation strategies.

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