An Approach For Use of Dual Frequency Identification Sonar (DIDSON) to Quantify Behavioral Aspects of Piscivory at Ecologically Relevant Time and Space Scales

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An Approach for the Use of Dual-Frequency Identification Sonar (DIDSON) to Quantify Behavioral Aspects of Piscivory at Ecologically Relevant Time and Space Scales

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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 (<10m radius) and large-scale hydroacoustic surveys (10s - 100s km²) are traditional approaches. 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 out to 30 m range. This technology can be used to observe predator-prey interactions at ecologically relevant space and time scales often missed by traditional methods. Here I 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 non-random use of landscape features by both predator and prey are described, relationships between patterns in these attributes are tested, and issues regarding sampling strategies for future studies are discussed. Approaches combining direct visual observation and acoustic sampling at multiple scales are required to gain a greater understanding of variation in such relationships across underwater landscapes and the role such relationships play in the demographics of fish populations and communities.
**Introduction**

Predation plays a critical role in the structure of reef fish communities (Tupper and Boutilier 1997, Carr et al. 2002, Hixon and Beets 2003). In addition to direct effects on mortality of constituent 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 using indirect methods such as stomach content sampling and survivorship experiments, without regard for the more complex interactions between competing predators as well as between predators and prey and their surrounding habitat. However, these indirect methods cannot identify other important variables that influence predation dynamics and the impacts that they have on population and community structure (Dill et al. 2003) such as predator group composition, effects of predator abundance, variation in functional roles, 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 time and space 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 the 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, in review). Cosner (1999) suggests that predation rates are therefore density dependent for both predator and prey as competition between predators increases.

The importance of intra- and inter-specific 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. 2009), is unknown in most ecological settings in the ocean. However, 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 and Pitman 1986, Ribic et al. 1997, Safina 1990, Clua and Grosvalet 2001, Robinson and Tetley 2007). Auster et al (2009) observed predation by single and mixed-species groups of midwater piscivores at sub-tropical reefs off the southeast United States, where the forcing of prey species to retreat to the sea floor resulted in high density patches of prey which were then attacked by single and mixed-species groups of demersal piscivores. In a subsequent study with larger sample sizes conducted at reefs off the southeast US as well as northeast Gulf of Mexico (Auster et al. in review) only 11% of 379 predation events involved only a single piscivore. All other events involved single and mixed species groups (67% of 274 events off the southeast US and 28% of 105 events in the northeast Gulf of Mexico involving facilitated interactions between midwater and demersal predators). 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 population and community
structure. Such data will contribute to the foundation for developing effective
conservation and management strategies.

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., <10 m horizontal radius, < 30 m depth and
<1 hr observation time). Hydroacoustic approaches can be used to expand such
observations in both space and time. For example, multibeam sonar has been used to
investigate schooling behavior in response to predation (Gerlatto et al. 2006, Brierly and
Cox 2010) as well as 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., 10s to 100s km$^2$) but lack the spatio-temporal
resolution necessary to capture individual predation events as they occur. Use of sonar
technology at intermediate space and time scales, in the ecological realm in which
predation events occur (e.g., at the scale of individual landscape features and single
predation events), can provide a more comprehensive picture of the mechanics and
outcomes of predation events at the level of individual animals in particular
environmental settings.
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. The higher frequency provides a much higher resolution image than lower-frequency systems used previously (i.e., kHz range). This allows the observation of the movement and behavior of individual animals. Previously, DIDSON sonar has been used for fish counts (e.g., salmonids passing particular areas in a river) and size estimates (Boswell 2007, Maxwell and Gove 2007). DIDSON has also been used in abundance estimates in turbid waters, such as mangrove channels, where diver observations are not practical or possible (Frias-Torres and Luo, 2009). DIDSON ensonifies a region ranging from 1-30m from the transducer (the spatial envelope in which most predation events unfold) and can be deployed by hardwire or autonomously for hours to days. This allows the collection of data at ecologically relevant space and time scales, capturing the fine-grain characteristics of predation. Some basic behavioral work has also been done using DIDSON to investigate the spawning behaviors of chum salmon (Tiffan et al, 2010); this success illustrates the potential to investigate behavior on a larger, more complex level required for predation studies. Because the use of DIDSON for behavioral observations is still exploratory, however, there is a need to first develop metrics and approaches to quantify attributes of predator-prey interactions from sonar records. Here I 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, across habitats, and within and between ecosystems.
Materials & Methods

I. DIDSON System Characteristics

I used a DIDSON standard model 300M in this study. This is a high-resolution sonar unit that operates at a 1.1 or 1.8 MHz, producing video-like images (Figure 1a, b). For this study the system was set to 1.8 MHz with a 2-11 m horizontal range. The transducer produces 96 beams with a 28.8°x12° field of view. Data were collected continuously at a rate of 8 frames s⁻¹ with data files parsed into 12 minute 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).

II. Study Site

Anchor Ledge (31° 37.7’ N, 80° 34.6’ W; depth 25 m), located approximately 20 miles off the coast of Georgia, is part of a large network of sub-tropical sandstone ledge (reef) habitat representing approximately 5% of the continental shelf off the southeast United States (Powles and Barans 1980, Parker et al. 1983). Emergent ledges are up to 3m in height surrounded by sand plains and exposed flat hard substratum. Hard substratum is dominated by suspension feeding organisms such as coral and sponge (Kendall et al. 2007). This complex environment provides shelter for prey and subsequently mediates distribution patterns of fishes which affects spatial patterns of predator-prey interactions (Figure 1d; Sedberry and Van Dolah 1984). Common mid-water piscivores at these reefs include bar jack Carangoides ruber, blue runner Caranx

III. 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, in review) considered discrete predation events as sample units and this approach is continued here for analysis. Small and large fish were present and moving through the ensonified volume in most records, however this by itself does not indicate predation related behaviors. I first established decision criteria to determine from observed behavior if a predation-related event (PRE) was occurring (Figure 2). Both predator and prey need to be present in the field of view for a PRE to occur. I assumed that predator reaction to prey was evident by a rapid change in predator trajectory. 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 ensonified region. However, I 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 which 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, just prior to the PRE, and at the moment predators reacted to prey (i.e., at the time of a rapid change in predator trajectory). Sixteen metrics (13 based on measures with continuous data and 3 based on 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 in large part due to image resolution and animal orientation. While still a viable measure, in this study I binned individuals by 20 cm size classes instead. Number of prey groups and number of predator groups varied little and are presented in numerical classes.

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 format with the low and high contrast threshold set to 30 and 255 respectively, essentially enhancing the contrast between fish and background. These values were determined based on a set of iterations to eliminate background and facilitate counts and measurements. Length and area were measured in Image J based on an inter-calibration of a known length acquired from an image. That is, a one meter measured distance normal to the transducer at a 6 m range was translated to 57.4 pixels using the
Image J Set Scale tool. While there is a decrease in resolution with increasing distance from the transducer, measurements taken at 6 m do not differ by more than 2 cm across the 1m-12m range.

Density and numbers of individuals for both predators and prey were then counted using the particle counting tool for objects over 5 cm in image 1. Areal measurements of prey school size (using image 1) and extent of prey response were made using the distance measurement tool. The areal extent of prey response was measured as the difference in prey school area just prior to and during the PRE by comparing images 2 and 3 (Figure 4). Predation rate was measured both by individual event (i.e. the number of attacks/duration of the PRE) as well as by the total PRE rate per file (i.e. the number of events per 12 minute file). The duration of events (in seconds), number of attacks, and number of groups were also recorded.

Sizes of predators in each PRE were binned by size class. 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 or across (intersecting) the reef from an off reef position. Predator behavior was also classified based on shape of aggregations and orientation within or outside of prey schools. Predators were either multiple individuals moving in a distinctly linear formation, as a circular-like group (or polygon) with individuals three or more deep, or as a single individual. 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 5 a, b). 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.

To determine if patterns of predation are patchy over time, that is multiple predation events tend to occur together, a two-term local quadrat variance (TTLQV) analysis was performed. The TTLQV was originally developed to assess spatial patterns of patchiness from quadrat data, but in this case temporal samples in lieu of quadrats were used to assess patchiness in predation rates. Here global predation rate based on each 12-minute file was the sample unit versus a spatial quadrat for which the statistical procedure was originally designed. 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 between blocks (Rosenberg and Anderson, 2011).

Because this was an exploratory effort to assess approaches for future research, I also performed a post-hoc power analysis to determine approximate sample sizes needed for future studies, assuming data are distributed in similar fashion.
Results

A total of 192 minutes of sonar data (parsed in sixteen 12-minute record files) were recorded at Anchor Ledge from 1551 – 1836 UTC on 17 June 2009, a clear and sunny day with calm seas. 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, has a normal distribution based on the Anderson-Darling test for normality (p > 0.05). All others are 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).

There was a pattern of small predator group size (<20 individuals; Figure 6), and groups were relatively low in 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 20-39 cm in length and groups always contained like-sized individuals. Five percent of predators were over 100 cm in length and these individuals were always solitary (Figure 8). Ninety percent of events were under one minute in duration (Figure 9). Table 3 contrasts the relationships in metrics based on continuous data; only 12 pairs were significant. Interestingly, the relationship between predator group size (mean 10.4 individuals, SD=16.8) and extent of prey response (mean 2.99 m², SD=2.16) was not significant (p=0.99, r²=0.1197). A significant negative relationship was found between prey group area and predator group size (p=0.018, r²=0.0514) and predation rate and
extent of prey response (p=0.04, r²=0.070) as well as a positive relationship between the number of attacks per event and predator group size (p<0.001, r²=0.1420) and event duration and predator group size (p<0.001, r²=0.2990) As expected, prey group area and, density, and the extent of prey response were strongly correlated (p<0.05, r²=04060, 0.1341, 0.2460 respectively), as well as the duration of event, number of attacks, and predation rate (p<0.01, r²=0.4104, 0.0500, 0.0110, respectively) The regression matrix (Figure 10) illustrates that even with significant r values few pairs show any linear relationship, suggesting some polynomial relationship is required to describe those that had significant correlations.

Predation rate and prey group size varied over time (Figure 11); with a pattern of higher activity in the morning and afternoon with a minima at mid-day. The relationship between predation rate and prey group size was marginally significant (p=-0.0713, r²=0.0020). The two-term local quadrat variance analysis of global predation rate revealed that variance was highest over time at a scale of 3 blocked sample units (30% of the total sample time, or 57.6 minutes). 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 minutes (Figure 12). Over the entire observation period, mean predation rate was 0.485 events min⁻¹, ranging from 0.0 - 1.25 events min⁻¹.

A post-hoc power analysis, assuming variation in the data for each metric is similar for future observations revealed that in order to detect differences in samples at a 95% confidence level (power coefficient = 0.80), a minimum sample size of roughly 859 events will be necessary (table 4).
Discussion

This study demonstrates 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. These approaches can now be implemented to answer important ecological questions. This is a powerful tool for collecting data over long periods within and between sites irrespective of bottom time, depth and visibility which typically impose severe limitations for data collection by divers. 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 large sample sizes (ca. n = 800) will be needed to test for differences across treatments. If three hours of observation yields approximately 100 PREs, then a 24 hour deployment per station could produce sufficient sample sizes for appropriate statistical contrasts.

The general trends in metrics provided by DIDSON supported observations made by divers related to variability in numbers and sizes of predators, coordinated group behaviors, patchy prey distribution localized to ledge features, and movement patterns oriented along the axis of reefs (Auster et al 2009, in review). However, the limitation of the sonar records is the inability to discern species. Here there is a need for coordinated observations by divers or remote video to link size and behavior discernible from sonar records to species or species groups (e.g., midwater or demersal prey species, midwater or demersal pscivores).
The lack of statistical significance in the relationships between paired metrics raises many questions for further investigation regarding whether this pattern is due to limitations based on the region ensonified 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 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. Another alternative is that activities of both predator and prey groups may be occurring outside the ensonified region as well as in acoustic shadows cast by landscape features. While I assumed that behaviors observed in the ensonified 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.

Development of sampling methods to address spatial variation in the ensonified region, such as placing the DIDSON on a pan-tilt unit and conducting timed samples over pre-set positions, may produce a more complete picture. An arrangement of multiple sensors for simultaneous observations within and between habitat features 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 study. A negative relationship between prey group area and predator group size may indicate a response by prey to predators not yet seen in the field of view,
as areal measurements were taken prior to the presence of predators. 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 will 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 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 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).

There is also potential for the use of acoustic camera systems alone or in conjunction with passive acoustics and optical video in ocean observatory systems (e.g., as a component of IOOS- Integrated Ocean Observation System), allowing for long-term monitoring of vagile fauna at specific sites or in specific habitats (Barans et al. 2005, Brehmer 2007, Hahn and Thomas 2009, Paquette et al. 2009). The extremely large size of data files and limited internal memory are currently limiting factors for autonomous use. Compression of data and remote storage would be necessary for such an application while a system cabled to shore would have no such limitations.

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 has the potential 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 such factors as
variable predation rates and variation in predation intensity across habitats into population models so that spatially explicit demographic processes can be incorporated. The knowledge gained from these approaches can then provide a more complete foundation for effective management and conservation strategies.
Table 1. Description of metrics based on continuous and categorical data.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Measures with Continuous Data</strong></td>
<td></td>
</tr>
<tr>
<td>Size of predators</td>
<td>Direct length measure of individual animals</td>
</tr>
<tr>
<td>Predator Group Size</td>
<td>The number of individuals in a school of predators</td>
</tr>
<tr>
<td>Predator group density</td>
<td>Number of individuals/area of group</td>
</tr>
<tr>
<td>Prey group size</td>
<td>Number of individuals in a school of prey fish</td>
</tr>
<tr>
<td>Prey group density</td>
<td>Number of individuals/Area of group</td>
</tr>
<tr>
<td>Prey group area</td>
<td>Area of prey group</td>
</tr>
<tr>
<td>Areal extent of prey response</td>
<td>Measurement of change in prey group area during predation related event</td>
</tr>
<tr>
<td>Duration of event</td>
<td>Time elapsed from first reaction to prey to end of reaction to prey</td>
</tr>
<tr>
<td>Predation rate</td>
<td>Number of attacks min(^{-1}) within each event</td>
</tr>
<tr>
<td>Number of attacks event(^{-1})</td>
<td>The number of times all predator schools attacked a prey school</td>
</tr>
<tr>
<td>Number of prey groups</td>
<td>Number of schools of prey</td>
</tr>
<tr>
<td>Number of predator groups</td>
<td>Number of schools of predators</td>
</tr>
<tr>
<td>Global predation rate</td>
<td>Number of attacks per 12-minute file</td>
</tr>
<tr>
<td><strong>Categorical Data</strong></td>
<td></td>
</tr>
<tr>
<td>Size class of predators</td>
<td>The average size of predators in the school; 20 cm increments</td>
</tr>
<tr>
<td>Formation of predators relative to prey school</td>
<td>Singular, Linear, Circular: Along prey group or within prey group</td>
</tr>
<tr>
<td>Trajectory of predators across field of view</td>
<td>Across or along field of view</td>
</tr>
</tbody>
</table>
Table 2: Descriptive statistics of metrics based on continuous data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>StDev</th>
<th>Minimum</th>
<th>Q1</th>
<th>Median</th>
<th>Q3</th>
<th>Maximum</th>
<th>Skewness</th>
<th>Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predator Group Size (count)</td>
<td>10.47</td>
<td>16.89</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>12.5</td>
<td>81</td>
<td>2.48</td>
<td>5.81</td>
</tr>
<tr>
<td>Predator Group Density (m-2)</td>
<td>4.579</td>
<td>5.617</td>
<td>0.043</td>
<td>2.211</td>
<td>3.887</td>
<td>5.398</td>
<td>55.556</td>
<td>7.17</td>
<td>63.69</td>
</tr>
<tr>
<td>Prey Group Size (count)</td>
<td>155.84</td>
<td>89.09</td>
<td>24</td>
<td>95.5</td>
<td>136</td>
<td>199.5</td>
<td>501</td>
<td>1.66</td>
<td>3.65</td>
</tr>
<tr>
<td>Prey Group Area (m2)</td>
<td>7.1</td>
<td>4.46</td>
<td>0.897</td>
<td>4.353</td>
<td>5.833</td>
<td>9.325</td>
<td>24.29</td>
<td>1.36</td>
<td>2.08</td>
</tr>
<tr>
<td>Prey Group Density (m-2)</td>
<td>28.72</td>
<td>21.94</td>
<td>2.27</td>
<td>14.43</td>
<td>22.52</td>
<td>34.58</td>
<td>134.75</td>
<td>2.52</td>
<td>8.94</td>
</tr>
<tr>
<td>Extent of Prey Response (m2)</td>
<td>2.944</td>
<td>2.146</td>
<td>0.013</td>
<td>1.426</td>
<td>2.445</td>
<td>3.854</td>
<td>14.85</td>
<td>2.01</td>
<td>7.81</td>
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<tr>
<td>Attacks per event</td>
<td>1.5138</td>
<td>1.0239</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>7</td>
<td>2.68</td>
<td>8.78</td>
</tr>
<tr>
<td>Predation Rate (events s-1)</td>
<td>0.1428</td>
<td>0.3209</td>
<td>0.0147</td>
<td>0.0436</td>
<td>0.0667</td>
<td>0.125</td>
<td>3</td>
<td>7.19</td>
<td>60.06</td>
</tr>
<tr>
<td>Duration of event (s)</td>
<td>25.94</td>
<td>20.62</td>
<td>2</td>
<td>9</td>
<td>19</td>
<td>39.5</td>
<td>90</td>
<td>1.08</td>
<td>0.56</td>
</tr>
</tbody>
</table>
Table 3: Correlation matrix of metrics with continuous data (Pearson's r value at top, p value for each contrast at bottom, significant correlations in bold)

<table>
<thead>
<tr>
<th></th>
<th>Predator Group Size</th>
<th>Predator Group Density</th>
<th>Prey Group Size</th>
<th>Prey Group Area</th>
<th>Prey Group Density</th>
<th>Extent of Prey Response</th>
<th>#Attacks /Event</th>
<th>Predation Rate (events/sec)</th>
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</thead>
<tbody>
<tr>
<td>Predator Group Size</td>
<td>*****</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Predator Group Density</td>
<td>-0.0990, p=0.306</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Prey Group Size</td>
<td>-0.105, p=0.277</td>
<td>-0.047, ****</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size</td>
<td>p=0.018</td>
<td>p=0.018</td>
<td></td>
<td></td>
<td>p&lt;0.001</td>
<td></td>
<td></td>
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<tr>
<td>Prey Group Area</td>
<td>0.182, p=0.058</td>
<td>-0.078, 0.265, -0.495, ****</td>
<td></td>
<td></td>
<td>p=0.005</td>
<td>p&lt;0.001</td>
<td></td>
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</tr>
<tr>
<td>Prey Group Density</td>
<td>-0.125, 0.093, 0.338, 0.636, -0.366, ****</td>
<td></td>
<td></td>
<td></td>
<td>p=0.001</td>
<td>p&lt;0.001</td>
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<tr>
<td>Extent of Prey Response</td>
<td>0.194, p=0.058</td>
<td>0.335, p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
<td>p&lt;0.001</td>
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<tr>
<td>#Attacks/Event</td>
<td>0.376, p=0.001</td>
<td>0.061, 0.033, -0.099, 0.045, 0.075, ****</td>
<td></td>
<td></td>
<td>p=0.001</td>
<td>p=0.001</td>
<td></td>
<td></td>
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<tr>
<td>Predation Rate (events/sec)</td>
<td>-0.123, p=0.137</td>
<td>0.130, -0.071, 0.101, -0.093, -0.097, -0.093, ****</td>
<td></td>
<td></td>
<td>p=0.001</td>
<td>p=0.001</td>
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<tr>
<td>Duration of Event (s)</td>
<td>0.547, p=0.001</td>
<td>-0.086, 0.044, 0.124, 0.098, 0.022, 0.643, -0.224,</td>
<td></td>
<td></td>
<td>p=0.001</td>
<td>p=0.001</td>
<td></td>
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</tr>
<tr>
<td>Event (s)</td>
<td>p=0.001</td>
<td>p=0.373</td>
<td>p=0.652</td>
<td>p=0.198</td>
<td>p=0.313</td>
<td>p=0.822</td>
<td>p&lt;0.001</td>
<td>p=0.019</td>
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Table 4: Sample size requirements for a power level of 0.8 and alpha <0.05

<table>
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<tr>
<th>Metric</th>
<th>Sample Size</th>
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<tbody>
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<td>Predator Group Size</td>
<td>856</td>
</tr>
<tr>
<td>Predator Group Density</td>
<td>858</td>
</tr>
<tr>
<td>Prey Group Size</td>
<td>859</td>
</tr>
<tr>
<td>Prey Group Area</td>
<td>859</td>
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<tr>
<td>Prey Group Density</td>
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</tr>
<tr>
<td>Extent of Prey Response</td>
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<tr>
<td>Attacks/Event</td>
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<td>Predation Rate</td>
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<tr>
<td>Duration of Event</td>
<td>854</td>
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</tbody>
</table>
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.
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).
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.
Figure 5. Example (top) 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). Illustration of categories for predator group orientation to prey (bottom).
Figure 6. Distribution of predator group size. Predator schools were predominantly under 20 individuals in size, though groups ranged from 1-100+ 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 one minute in duration.
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 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.
Figure 11. Variability over time for both the number of prey (left axis) and predation rate (right axis), ranging from mid-morning to mid-afternoon (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. See text for details.
References


Kendall, M., Bauer, L., Jeffrey, C. 2007. Characterization of the benthos, marine debris and bottom fish at Gray’s Reef National Marine Sanctuary. NOAA Tech Mem NOS NCCOS 50. 82p. + Appendices. NOAA, Silver Spring, Maryland, USA.


Tiffan, K., Haskell, C., Kock, T. 2010. Quantifying the behavioral response of spawning chum salmon to elevated discharges from Bonneville Dam, Columbia River, USA. River Research and Applications. 26:81-101