



# Nocturnal surveys reveal novel insights into the community dynamics of an anchialine ecosystem from The Bahamas

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## ABSTRACT

Understanding the composition and structure of marine animal assemblages across space and time is essential in the establishment of effective management frameworks, particularly for holistic approaches to ecosystem conservation. Baited remote underwater video (BRUV) surveys are a well-established tool used in assessing relative abundances of marine fauna but are not commonly used in enclosed environments such as lakes. Sweetings Pond is an anchialine lake situated on the island of Eleuthera in The Bahamas that remains relatively undocumented, with only a single census available from 1983, yet has experienced an increase in stress from anthropogenic activity. Here, we investigated differences in community composition between sites and attempted to identify the species/benthic components driving changes using baited video surveys, before exploring differences in community structure between day-night periods. Nine species were identified over the 3780 min of BRUV footage analyzed, which was comparable to 1983 estimates. No difference in animal assemblages was seen between sites and no correlation with benthic composition was present. However, nocturnal replicates displayed higher median animal abundance and species richness than diurnal replicates, potentially resulting from a sequential food web aggregation around the light source. A number of unique, opportunistic feeding behaviors were also observed which opens avenues for future study. Overall, this study presents BRUVs as a viable and streamlined tool for managers of enclosed aquatic ecosystems to rapidly assess the system's macrofauna across day-night periods, supporting the requirements of an ecosystem-based management approach.

## 1. Introduction

Holistic monitoring of ecosystems has become a valuable tool in the conservation of biodiversity as contemporary efforts shift focus from species specific management towards ecosystem-based approaches (Gavaris, 2009; Long et al., 2015). Such change has been necessitated by the apparent failure of silo-structured management strategies in marine ecosystems (Costanza et al., 1998) resulting in fishery stock collapse (Costello et al., 2008; Hambright and Shapiro, 1997), and a skewing of priorities, with 'flagship species' receiving disproportionate research effort and subsequent funding (Smith et al., 2012; Verissimo et al., 2014; Zacharias and Roff, 2001).

This shift in focus requires robust surveying techniques that are able to effectively quantify the maximum number of species and individuals present in a community (Turner, 2014). In open marine environments,

this has traditionally been achieved by underwater visual census (UVC) via SCUBA, but is often criticized for regularly underestimating counts (Edgar et al., 2004). Remote underwater video survey (RUVS) methods have thus been employed regularly over the last 20 years as an alternative to UVC, particularly when targeting areas inaccessible to SCUBA divers (Armstrong et al., 1992; D'Onghia et al., 2015), highly mobile or cryptic species (Willis and Millar, 2000), and is able to minimize observer bias by allowing all analysis to take place *ex situ*, thus further creating a permanent survey record. The current standard for RUVS involves the addition of a form of bait (BRUVs) to act as an attractant for nomadic or cryptic species (Whitmarsh et al., 2016) and now is used universally. In enclosed aquatic environments however, BRUV approaches are rarely used with only a few examples to our knowledge in the North American Great Lakes (Robinson et al., 2019), Irish loughs (Roberts et al., 2016) and an Australian estuarine lake (Lowry et al.,

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2011). This rarity may result from the typically poor water clarity expressed by these ecosystems compromising video quality due to algae bloom structure or high dissolved organic carbon levels (Lietz et al., 2015), and concerns over the influence of bait plumes in biasing observations (Heagney et al., 2007). However these are challenges that modern techniques can overcome (Morán-López and Uceda Tolosa, 2017). Baited video consequently represents a powerful surveying approach and is likely capable of supporting freshwater and marine lake monitoring if implemented more widely.

A second major requirement of ecosystem-based management is understanding the target ecosystem across time as well as space (Long et al., 2015). In marine environments, communities of reef fish are known to be influenced by the day-night cycle (Azzurro et al., 2007) with diel changes in fish assemblages having been explored relatively rarely. The majority of studies focus on diurnal surveying, particularly those utilizing BRUV survey methods (Barker et al. 2018, Harvey et al., 2012b) which are constrained by low light conditions. Restricting surveys to diurnal periods may limit our understanding of ecosystem functioning; for example, differences in diel fish assemblages have been attributed to changes in the abundance of prey (Carpentieri et al., 2005) or predators (Hammerschlag et al., 2010) and habitat/shelter availability (Harvey et al., 2012a), all of which are ambiguous in the absence of nocturnal sampling. This is especially critical in enclosed ecosystems that are considered vulnerable to extrinsic pressures and where trophic interactions remain poorly understood. Monitoring both diurnal and nocturnal animal assemblages therefore support management decision makers by establishing baseline ecosystem functioning across day-night periods, as well as potentially identifying nocturnal species absent in diurnal surveying.

Sweetings Pond is an anchialine lake located in the central Bahamas and is an example of an enclosed ecosystem susceptible to increased pressure through anthropogenic activities such as tourism, artisanal fishing and unregulated farming practices. Recently, this system has been considered with a greater management priority in response to increases in tourism operations (Bahamas National Trust) and agricultural development on land peripheral to the lake. Additionally, anchialine ecosystems in general tend to display a high proportion of introduced/invasive species (Seidel et al., 2016) which highlights their susceptibility to human introductions. In Sweetings Pond, introductions may have occurred in the form of stocking for fishing purposes which has the capability to dramatically alter the community composition of this isolated ecosystem. However, the fish community structure of this site has not been consistently surveyed, with biases in research effort targeting specific organisms, including brittlestars (Aronson and Harms, 1985), octopus (Aronson, 1986; O'Brien et al., 2020) and seahorses (Mason-jones et al., 2019; Rose et al., 2016). The remainder of the community remains essentially undescribed with Aronson and Harms (1985) presenting the sole available visual fish census, reporting nine species across the diel cycle.

The overall objective of this study was to provide a contemporary understanding of the macrofaunal communities that exist within this lake, using an underutilized surveying technique to provide empirical data to underpin and inform wider conservation strategies for lake-like environments. Specifically, we used nocturnal BRUVs to test hypotheses relating to diurnal refugia in larger predatory species and naturally occurring nocturnal species that are known to inhabit this lake. In addition, we tested relative abundance and species composition between diurnal and nocturnal periods to more accurately describe the lake assemblage, and to further validate the relevance of baited video when employing holistic methods for surveying enclosed aquatic ecosystems.

## 2. Methods

### 2.1. Field-site description

This study was conducted in June and July 2019 and 2020 at

Sweetings Pond on the island of Eleuthera in The Bahamas (25°21'40"N, 76°30'40"W) (Fig. 1). Sweetings Pond is a tidal anchialine lake, 1.6 km long by 0.8 km wide with a mean depth of 6.6 m, ranging from 0.5 m at its edge to approximately 13 m at its center (Masonjones et al., 2019). A 'patch zone' is evident around the shallow periphery of the lake which consists of sponges, coral colonies, bivalve colonies and calcareous rubble (Aronson, 1986; O'Brien et al., 2020). The lake itself is separated from the wider marine environment of the Great Bahama Banks by a porous limestone basin, which acts as a migration barrier for adult animals (Masonjones et al., 2019). Despite this physical barrier to movement, there has been historical stocking of the lake by local residents, evidenced by the appearance of relatively large fish species, such as Nassau grouper, *Epinephelus striatus*, and white grunts, *Haemulon plumieri*. Three sampling sites ('Emmas', 'Grouper Cave' and 'Quarry') were selected for ecological and logistical reasons: 'Grouper Cave' represents a relatively undisturbed site with a comparatively distinct benthic habitat (O'Brien et al., 2020), 'Emmas' (f.k.a as 'Octopus Den') exhibits a higher level of disturbance due to the presence of agricultural activity on its shoreline, whilst 'Quarry' is a public access point to the system. These historic site names refer to identifying landmarks or features of the site and consequently have no reference to differences in habitat. All three sites are situated within the patch zone of Sweetings Pond and are accessible by water from the 'Quarry' entrance, which aided with the deployment and retrieval of BRUV units.

### 2.2. BRUV design

This study used a custom made BRUV unit consisting of a single GoPro Hero 4 silver edition (gopro.com), with external battery pack in a waterproof housing, which was mounted upon a 50 cm<sup>3</sup> PVC frame. Holes were drilled through the PVC to allow flooding of the frame rendering the unit negatively buoyant. No additional weights were required due to minimal hydrodynamic activity characteristic for this lake. The GoPro camera was set to record at 1080p at 30 frames per second in a wide (170°) field-of-view. To achieve lighting, a single Big Blue AL 1200 XWP II dive torch (bigbluedivelights.com) was attached to the upright of the BRUV frame and set to illumination level III. This resulted in a 600-lumen output, 6500 K white light temperature and 120° beam angle. A Big Blue branded red filter of 620 nm wavelength was attached to the torch, and was chosen over blue and white as it facilitates higher relative abundance estimates of species compared to other wavelengths (Fitzpatrick et al., 2013), whilst simultaneously minimizing changes in natural behavior (Widder et al., 2005). This result is achieved as wavelengths of red light are thought to be beyond the visual sensitivity of many fish species (Raymond and Widder, 2007;

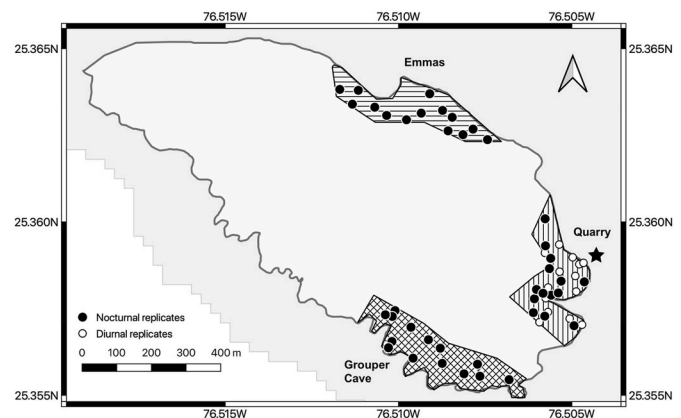


Fig. 1. Location of diurnal and nocturnal BRUV deployments within the Sweetings Pond research system and the three sampled sites. Map projected in WGS84. The point of public access to the 'Quarry' site is indicated by a black star.

Von de Emde et al., 2004).

Whilst red light does depreciate the resolution of illuminated footage (Fitzpatrick et al., 2013), the advantage of discretion that it provides further removes observer bias, and was therefore critical to achieve this study's objectives.

Each BRUV unit was baited with 0.5 kg of crushed cross-barred venus, *Chione elevata*, and Atlantic pearl-oyster, *Pinctada radiata*, collected from the lake and suspended in a plastic mist net bag 75 cm in front of the camera. These species were selected as they are known natural prey items of the Caribbean reef octopus, *Octopus briareus*, which is the only assessed predator in this system (Aronson, 1986; O'Brien et al., 2021) and the failure of previous diurnal surveys using oily teleost bait to return any abundance estimates (Masonjones, unpublished data). This is therefore a highly abundant, sustainable and non-oily bait source, which supports the need for a weaker chemical pathway and minimizes the influence of replicate BRUV surveys upon each other in a confined ecosystem.

### 2.3. BRUV deployment

Three BRUV units were built and deployed in synchrony as either diurnal or nocturnal replicates. Nocturnal BRUVs were deployed between 23:00 and 01:00 for overnight filming and collection the following day. This allowed the camera to film for the duration of its battery life with no human influence, although only 90 min of footage was analyzed following current published standards (Bond et al., 2012; Brooks et al., 2011; Gladstone et al., 2012; Whitmarsh et al., 2016). Five deployment cycles were performed, providing 14 replicates per site ( $n = 42$ ), and 3780 min of analyzed data (63 h). Additionally, 14 diurnal BRUVs were deployed at the 'Quarry' site between 09:00 and 12:00 (5 cycles) during June of 2020 in order to compare results, and validate the nocturnal sampling phases. All methodologies were identical.

Deployment coordinates were randomly generated using the 'random points in extents' research tool in QGIS (QGIS Development Team, 2019) and navigated to using a Garmin handheld GPS unit. To minimize the spatial influence of replicates in a deployment cycle upon each other, coordinates were generated with a minimum distance of 50 m between all deployments. Whilst this distance is short compared to many other BRUVs (e.g. 200m - Kelaher et al., 2014; 250 m - Galaiduk et al., 2017; 400 m - Phenix et al., 2019; Whitmarsh et al., 2018), it is sufficient in this study due to the reduction of odor dispersal caused by the choice of bait and minimal water movement exhibited in the system. Similarly, the confined nature of the system restricts the available area for deployment, whilst replicate size is an important factor to maximize the likelihood of encountering rare species.

During deployment, the BRUV unit was physically placed on the lake's benthic surface via free diving, before recording the depth of deployment and activating the camera and light. Underwater, the BRUV unit was anchored in place by its negative buoyancy and the bait arm rested on the benthos. The camera therefore had to be angled accordingly to bring the bait arm in to view, with the substrate covering approximately 2/3rds of the video frame.

### 2.4. Analytical methods

Videos were viewed in real time using QuickTime Player V10.5, by a trained observer for 95 min from the BRUV camera's activation on the bottom substrate. The first 5 min of the footage was discounted to exclude any disturbance that deployment may have caused. The relative abundance of each species and number of species (i.e. richness) was then systematically recorded as MaxN, with any interesting or unexpected behaviors (predation, aggression etc) opportunistically documented. MaxN is an index of relative abundance, estimated as the maximum number of species, or individuals of a species, on a given frame at a given time. This metric therefore avoids repeatedly counting the same individual and offers the most conservative estimate of relative abundance

(Campbell et al., 2015; Priede et al., 1994). Relative abundance estimated in this study is therefore the MaxN of each individual species per BRUVs, total abundance is the sum of MaxNs from all species and species richness is the MaxN species in a single BRUV frame. Due to the poor resolution caused by filming at night and water turbidity, only animals five cm or larger could be identified to species level. This, when combined with the filming angle and historically reported low number of fish species in Sweetings Pond (Aronson and Harms, 1985), allowed other trophically important invertebrate species to be quantified: e.g. the West Indian spider crab, *Maguithrax spinosissimus*, *O. briareus* and True Tulip, *Fasciolaria tulipa*.

To estimate benthic diversity and composition, a screenshot was taken from each replicate to act as a reference image. The reference screenshot was taken during the first 5 min of footage with fewest animals in frame to ensure an unobstructed view of the substrate. Twenty-five random points were generated in a selected area of the image via a custom macro in ImageJ (Rueden et al., 2017). This selection ensured no points were projected into the water column or non-illuminated areas. At each point, the substrate was identified, and, from the substrate abundance data, percentage cover was calculated. If a point landed upon the bait arm, the point was relocated to the nearest substrate. Simpson's diversity (Simpson, 1949) was calculated for each BRUV replicate using the 'vegan' package (Oksanen et al., 2019) in R (R Core Team, 2020), with percentage cover replacing count data (Tomascik and Sander, 1987).

Species richness and total animal abundance was first compared between day-night periods at the 'Quarry' site, using a random permutation test (Hemerik and Goeman, 2018). The absolute difference in observed median was compared to the median of the randomly resampled dataset repeated 10,000 times to allow the calculation of the two-sided p-value. This p-value is defined as the proportion of sampled permutations where the absolute difference in resampled median was greater than or equal to the observed absolute difference. A permutation test was selected due to rank ties weakening the strength of a Mann-Whitney *U* test (McGee, 2018).

To extrapolate nocturnal species richness at site and ecosystem level, a rarefaction curve with increasing sample size was generated using the 'iNEXT' package (Hsieh et al., 2016) based upon the incidence of each observed species. The influence of depth, site and benthic diversity upon relative species richness and total animal abundance was then assessed using a Poisson GLM and a negative binomial GLM respectively. A log link function was applied to both models using the 'glmmTMB' package (Brooks et al., 2017).

To test for community differences in response to site (categorical with three levels), depth and benthic Simpson's diversity (continuous), a permutational analysis of variance (PERMANOVA) was applied using the 'adonis2' function in the 'vegan' package. The Bray-Curtis index was selected to determine dissimilarity due to the high presence of zeroes in species abundances (Anderson, 2001). A constrained analysis of principal coordinates (CAP) was then run for all abundance data using the function 'capscale' in 'vegan' to identify fish species and benthic components likely to be driving differences between sites and depths. This was achieved by identifying Pearson correlations between the canonical axes and either individual animal species' MaxN or benthic percentage cover. A Principal Component Analysis (PCA) plot was then generated to visualize any community differences using the 'ggbiplot' package (Vu, 2011; Wickham, 2016) and the color-blind friendly color palette from the 'iridis' package (Garnier et al., 2021) was applied to all data visualizations.

## 3. Results

### 3.1. Species richness and abundance

Comparing total abundance and richness at 'Quarry' between day-night periods revealed significantly higher median animal abundance

(permutational  $p < 0.05$ ) and species richness (permutational  $p < 0.001$ ) in nocturnal BRUVs than diurnal (Fig. 2). Nocturnal abundance estimates were more variable than daytime estimates (Fig. 2 A, B, nocturnal: 6–101 animals; diurnal: 4–38 excluding outliers) but both periods revealed at least one animal per replicate. Similarly, diurnal BRUVs exclusively identified two species per replicate whereas nocturnal replicates ranged from one to four (Fig. 2 C, D).

In total, nine species were identified across the three sites (Table 1). At site level, eight species were observed at 'Grouper Cave' and 'Quarry', whilst nine were observed at 'Emmas'. Median nocturnal species richness was ultimately greater at 'Emmas' than the other two sites. Of these nine species, eight were observed nocturnally at all sites, with only *H. plumieri*, being observed at 'Emmas'. This species was observed however during 'Quarry's diurnal survey. The rarefaction extrapolation therefore predicts that nine species, observable by BRUVs, may be present in the lake when all data is pooled. If sites are considered individually, nocturnal species richness is extrapolated to be nine for both 'Grouper Cave' and 'Quarry' and 11 at 'Emmas' (Fig. 3). However, in reality, this site level difference is unlikely; although *H. plumieri* was not observed in nocturnal BRUV footage during this study, the species was identified at 'Quarry' diurnally and during pilot nocturnal deployments. Species richness was not found to be significantly predicted by site, depth (ranging between 0.5 and 9.0 m) or benthic Simpson's diversity in the GLM (Table 2a).

The false herring, *Harengula clupeiola*, contributed to the majority of observed animals in all sites ( $n = 1051$ ); a 1460% increase over the second most abundant species, the hardhead silverside, *Atherinomorus stipes* ( $n = 72$ , Table 1). More individual animals, as measured by MaxN, were seen at 'Quarry' followed by 'Emmas' and 'Grouper Cave' (Fig. 4). Surveys deployed in 'Quarry' consequently yielded greater MaxN abundances ( $p < 0.01$ ) than the other sites but depth and benthic

diversity had no significant effect on the probability of observing animals (Table 2b).

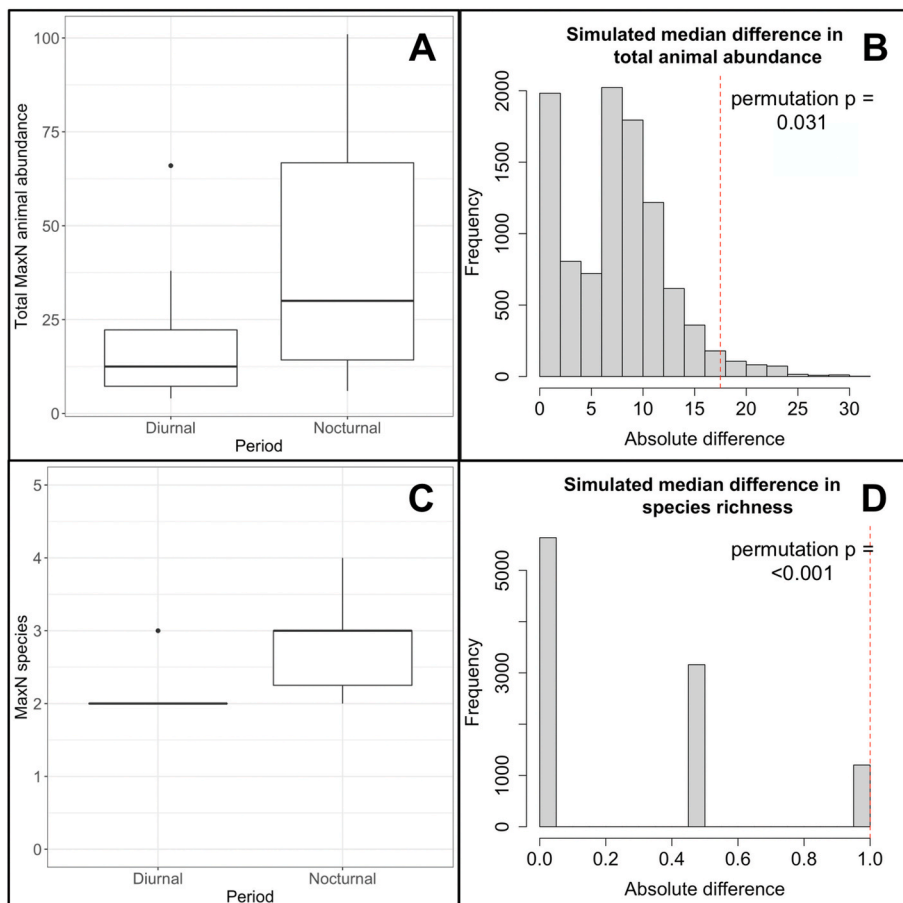
### 3.2. Sweetings Pond community structure

When visualizing the relative communities of each site using PCA, there was a high degree of overlap in animal communities among sites (Fig. 5), with *H. clupeiola* the only species contributing to the principal component axes. Formal testing via PERMANOVA found no differences in animal community structure between different sites, depths and benthic diversities (Table 3). Due to this lack of effect, the use of CAP analyses to identify species and benthic features driving patterns across Sweetings Pond was irrelevant. This being said, three species (*A. stipes*, *H. clupeiola*, and redfin needlefish, *Strongylura notata*) correlated significantly with the canonical axes (Supplementary Table 1) but only a single correlation was identified between the canonical axes and benthic components - *Mytilopsis* spp. (Supplementary Table 2).

### 3.3. Observed behavior

Three behaviors of note were observed during this study and all involved *H. clupeiola* shoals that were regularly present during BRUV footage. For example, *S. notata* were seen predating on *H. clupeiola* on six separate occasions across all three sites. Typically, an *S. notata* individual would approach from above or below the main body of the shoal before targeting prey from the greatest mass of fish (Fig. 6a). Five unsuccessful predation events were also observed in which the *S. notata* individual missed their target during approach.

*Maguimithrax spinosissimus* also exhibited predation on *H. clupeiola*, with individuals attempting 13 predation events across the 3780 min of BRUV footage. When *H. clupeiola* prey came within close enough



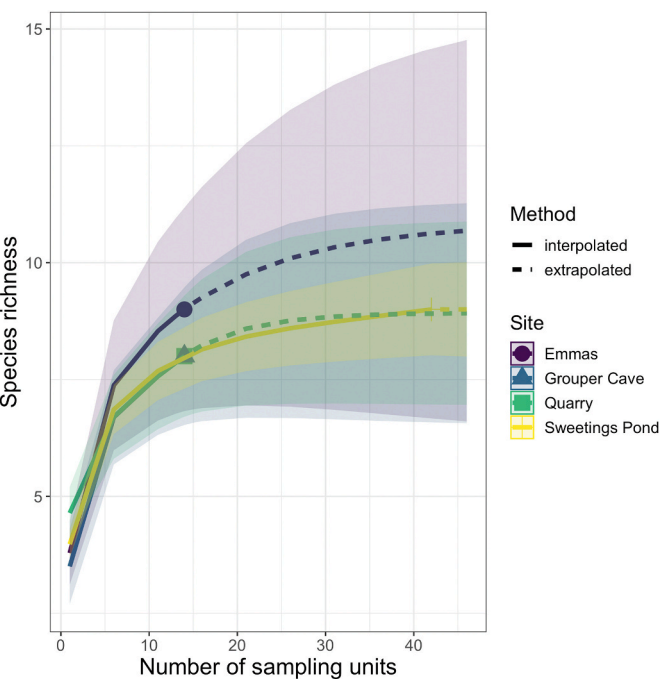
**Fig. 2.** Day-night period comparisons of total animal abundance (A,B) and species richness (C,D) in the 'Quarry' site. Raw data is presented as boxplots (A,C) where the whiskers extend 1.5 x the interquartile range of the data and the black horizontal bar indicates the median. Outliers are indicated by a black dot. Simulated permutation test results are presented as histograms (B,D) representing the frequency of absolute difference in simulated medians between day-night periods, repeated 10,000 times. The observed median difference between periods is indicated by a vertical, dashed red line. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Table 1**

Summary of the taxonomy, authority, IUCN Red List status, FO, mean MaxN per replicate and standard error of all species observed on nocturnal Sweetings Pond BRUVs. Species are ordered alphabetically by phylum.

Species	Common name	Family	Taxonomic authority	IUCN status	FO	Mean MaxN	Standard error
<b>Chordata</b>							
<i>Atherinomorus stipes</i>	Hardhead silverside	Atherinidae	Müller and Troschel, 1848	LC	0.67	1.714	0.305
<i>Eucinostomus gula</i>	Silver jenny	Gerreidae	Baird and Girard, 1855	LC	0.67	0.881	0.114
<i>Haemulon plumieri</i>	White grunt	Haemulidae	Lacepède, 1801	LC	0.02	0.024	0.024
<i>Harengula clupeiola</i>	False herring	Clupeidae	Cuvier, 1829	LC	0.93	25.023	3.824
<i>Hippocampus erectus</i>	Lined seahorse	Syngnathidae	Perry, 1810	VU	0.10	0.095	0.046
<i>Strongylura notata</i>	Redfin needlefish	Belontiidae	Poey, 1860	LC	0.75	0.786	0.121
<b>Mollusca</b>							
<i>Fasciolaria tulipa</i>	Common tulip	Fasciariidae	Linnaeus, 1758	NE	0.12	0.119	0.051
<i>Octopus briareus</i>	Caribbean reef octopus	Octopodidae	Robson, 1929	LC	0.17	0.190	0.070
<b>Arthropoda</b>							
<i>Maguithrax spinosissimus</i>	West Indian spider crab	Mithracidae	Lamarck, 1818	NE	0.74	1.167	0.160



**Fig. 3.** Rarefaction curve interpolating and extrapolating nocturnal species richness in each of the three sample sites and Sweetings Pond wide estimate. Fourteen sampling units were achieved for each site, resulting in 42 sampling units ecosystem wide when pooled. 95% confidence intervals are represented as shaded areas.

proximity, *M. spinosissimus* lifted their claws into the water column in a grabbing motion, often rising on to their rear legs to improve reach (Fig. 6b). Such feeding attempts were regularly unsuccessful with one single example of successful predation observed.

As *H. clupeiola*, were the most common species identified in Sweetings Pond, their prevalence during surveys resulted in a near constant representation in footage. This led to the identification of rare swimming behavior not observed elsewhere. Periodically, individuals performed spontaneous, circling motions in the water that resembled muscular spasms (Supplementary Video 1). Nine of these 'spasm' events were observed in separate BRUV replicates with a typical duration of 15–30 s. Fish would appear to recover after the event, returning to controlled swimming.

#### 4. Discussion

A BRUV approach was able to consistently identify animals in the

**Table 2**

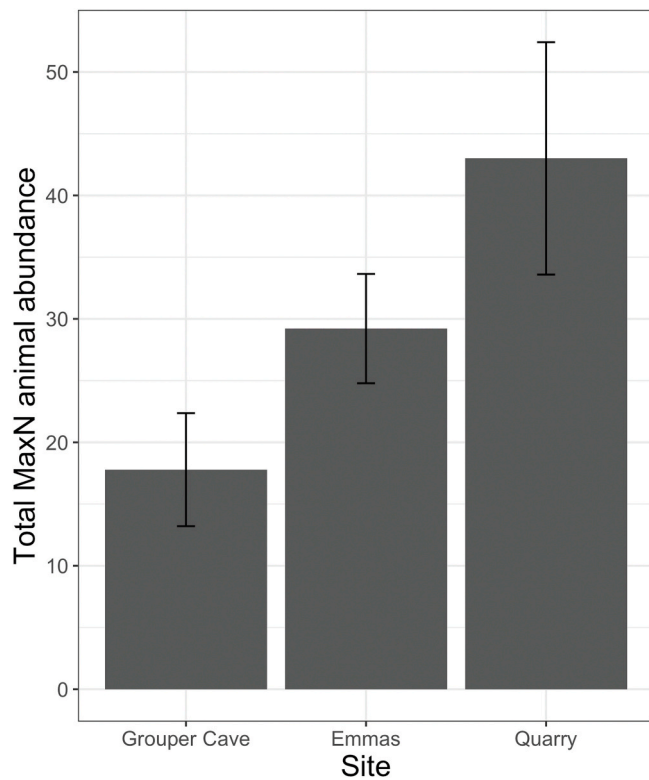
Generalised linear model parameter estimates for the response variable ~ site + depth + benthic diversity relationship. Parameter values are given on the link scale. A) Species richness response variable modelled using a Poisson distribution. B) Animal abundance response variable modelled using a negative binomial distribution.

A) Response variable: Species richness			
	Estimate	Standard error	p value
Intercept (SiteGrouperCave)	0.946	0.344	0.006**
Depth (m)	-0.023	0.061	0.706
SiteEmmas	0.136	0.248	0.584
SiteQuarry	0.175	0.266	0.509
Benthic diversity	-0.196	0.430	0.648
B) Response variable: Total animal abundance			
	Estimate	Standard error	p value
Intercept (SiteGrouperCave)	2.729	0.272	<0.001***
Depth (m)	0.093	0.078	0.231
SiteEmmas	0.493	0.311	0.113
SiteQuarry	1.035	0.320	0.001**
Benthic diversity	0.3744	0.510	0.462

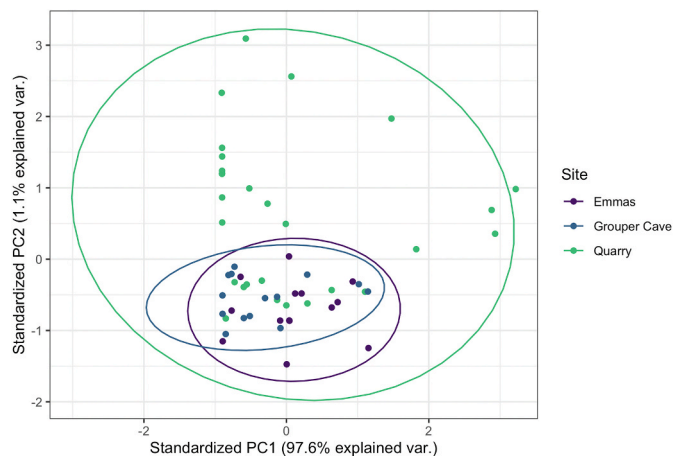
\* $p < 0.05$  \*\* $p < 0.01$  \*\*\* $p < 0.001$ .

Sweetings Pond ecosystem despite its enclosed nature and relatively small volume, and supports previous studies' suggestions that BRUV usage is viable for lake-like environments (Lowry et al., 2011; Robinson et al., 2019). Overall, the results here indicate that the animal community is stable among sites but different between day-night periods. The highest median abundance and richness of animals were seen at night which conflicts with the majority of other studies comparing day-night assemblages (for example, Azzurro et al., 2013; Cardoso et al., 2020; Harvey et al., 2012a; Myers et al., 2016; Vianna et al., 2013). Similarly, differences were evident in comparison to the 1983 UVC performed by Aronson and Harms (1985), which recorded 10 fish species.

Piscivorous fish were rare with *H. plumieri* and *S. notata* the only observed guild members. Neither of these predatory species were identified by Aronson and Harms (1985) in either diurnal or nocturnal censuses and implies that the BRUV methodology was sufficient to attract these mobile species. Stocking may have contributed to the improved *H. plumieri* representation in the assemblage, but this is unlikely for *S. notata* which has no recognized commercial value by the FAO (FAO Fisheries and Aquaculture Information and Statistics Branch) and is a common species in coastal Caribbean habitats. Conversely, this study did not observe the small bodied species commonly reported in Aronson and Harms (1985), such as the sheepshead minnow, *Cyprinodon variegatus variegatus*, and banner goby, *Microgobius microlepis*. These species were present during the course of this study but too small to be identified from footage, as justified in section 2.4. Being unable to



**Fig. 4.** The total nocturnal animal abundance observed at each of the three Sweetings Pond sites. The data is presented as a bar plot of the site mean whilst error bars represent the standard error.



**Fig. 5.** Principal component analysis plot comparing nocturnal animal communities between Sweetings Pond sites. Ellipses represent 95% confidence intervals for each multivariate mean. Arrows indicate the contribution of each animal species to the principal components.

**Table 3**

Permutational MANOVA of Bray-Curtis community dissimilarities recorded by BRUVS across Sweetings Pond sites, depths and benthic diversities.

Source	df	SS	F	p - value
Site	2	0.335	2.118	0.100
Depth	1	0.072	0.858	0.493
Benthic diversity	1	0.026	0.308	0.728
Residuals	37	3.101		
Total	41	3.554		



**Fig. 6.** Screenshot examples of feeding behaviours observed in Sweetings Pond at night. White arrows indicate the event on the frame. A – Redfin needlefish, *Strongylura notata*, preys upon a false herring, *Harengula clupeiola*. B – West Indian spider crab, *Maguimithrax spinosissimus*, attempts to catch *H. clupeiola* out of the water column.

identify small bodied species such as these is a disadvantage of utilizing BRUVS over UVCs, compounded further by the restricted field-of-view imposed by nocturnal filming. However, BRUVS provided the benefit of consistently observing both non-fish species (*M. spinosissimus*, *O. briareus* etc.) and fish shoals. For example, less than one individual of *H. clupeiola* was observed on average per UVC by Aronson and Harms (1985) compared to the ~20 individuals per BRUV replicate in this study. This consistency and identification of larger species may result from the aggregating effect of BRUVS at night.

Typically, artificial white lights drive decreases in predatory and total fish abundance in coastal and pelagic environments (Barker and Cowan, 2018; Bolton et al., 2017). However, in estuarine habitats, the occurrence of large-bodied predators appears to increase in the presence of artificial lights (Becker et al., 2013), with the authors suggesting that light can act as an aggregating device for plankton that is amplified up the trophic levels from planktivore to piscivore; the increased abundance of lower trophic levels attracts higher trophic levels. Whilst the previous studies utilized white light for nocturnal illumination, high plankton densities were observed in this study around the red light source during playback of BRUV footage. Zooplankton are attracted to the red light wavelengths applied here (Kehayias et al., 2008; Martynova and Gordeeva, 2010), with the concentration of plankton therefore likely attracting the planktivorous *H. clupeiola* and *A. stipes* (a species assumed to be referenced as ‘Minnows’ in Aronson and Harms 1985). *Harengula clupeiola* shoals arising from this abundance of prey would consequently attract the piscivorous *H. plumieri* and *S. notata*. When this observation is combined with the limited interaction of animals with the bait bag, it is this succession of aggregations exploiting zooplankton that is attractive rather than bait odor plumes. This is the first study to attempt nocturnal BRUV surveying of a lake ecosystem and, as such, it appears that using red light has the benefit of attracting higher trophic level animals that would otherwise be cryptic, whilst also minimizing

the deterrence of fish in general that occurs under white light. Zooplankton abundance has repeatedly been shown to correlate with chlorophyll/phytoplankton abundance (Gasol et al., 1997; Goldyn and Kowalczywska-Madura, 2008; Yuan and Pollard, 2018), and although no work has directly compared zooplankton abundance between enclosed-open aquatic environments, less well mixed ecosystems (e.g. lakes versus ocean - Simon et al., 1992) appear to support relatively higher phytoplankton abundance which implies a similar relationship for zooplankton. This matches our findings which suggests that nocturnal zooplankton are exploitable in enclosed ecosystems to improve fish abundance estimates during monitoring programmes.

While slight differences in animal abundance and species richness were identified between sites, community analysis highlights that Sweetings Pond supports a singular animal assemblage that migrates between the sampled sites. This is understandable due to the enclosed system and relatively small volume available to these species compared to their coastal counterparts. However, in shallow lakes, there is typically a marked difference in assemblages between either microhabitats (Kaneko et al., 2019) or littoral-pelagic zones (Cheng et al., 2012; Tang et al., 2015) not seen here. To explore these potential trends in Sweetings Pond, we recommend expanding the scope of survey to include the center of the lake which to date has been largely ignored in favor of the easily accessible littoral patch zone (Aronson and Harms, 1985; Rose et al., 2016).

The CAP analysis presented here also conflicted with the typical findings of BRUV studies (Cappo et al., 2004; Harvey et al., 2012a; Rhodes et al., 2020), in that the community did not correlate with benthic composition. Habitat complexity is known to promote biodiversity (Graham and Nash, 2013) and so this study's findings are unexpected in that context. However, the structural complexity of this specific system is limited due to dominance of calcareous rubble (dead coral skeletons and bivalve shells) and flocculant as benthic habitat (O'Brien et al., 2020). There is therefore minimal habitat interacting with the water column compared to the coastal environments where complexity-biodiversity association studies are performed (Gratwicke and Speight, 2005).

The opportunity to observe novel behaviors occurring within Sweetings Pond and lake-like environments in general, is important for driving future research questions and management considerations. For example, here *Strongylura notata* predation technique did match the kinematics of the species described by Porter and Motta (2004), but to our knowledge, there is no description of crab (*M. spinosissimus*) 'fishing' behavior in the literature. It is therefore unknown whether this is a typical behavior for these scavengers or if it is opportunistic due to prey aggregation. Opportunistic feeding is documented in seabirds (Ingraham et al., 2020), octopus (Leite et al., 2009) and sharks (Motta and Wilga, 2001) amongst others, as well as the energetic benefits of doing so (Garay et al., 2018; Garay and Móri, 2010). Ergo, the *M. spinosissimus* feeding behavior could be considered as opportunistic, and should be clarified, but may have been overlooked in the absence of video surveying approaches (Almeida and Grossman, 2012).

## 5. Conclusions

Ecosystem-based management requires an understanding of the interplay of ecology, sociology and governance at appropriate temporal and spatial scales (Long et al., 2015). This study contributes to the ecological understanding of a large anchialine lake by providing a streamlined and effective monitoring tool in the form of nocturnal BRUVs, which appear to aggregate and improve abundance estimates of the macrofauna. The rapid deployment and range of data extractable from BRUV footage therefore can provide managers of enclosed aquatic ecosystems a suite of diagnostic metrics to assess the dynamics and health of an animal assemblage at a yearly or monthly scale depending on the deployment frequency. However, the benefit of identifying larger fish species through BRUVs must be weighed against its bias against

smaller species such as *C. variegatus variegatus* in this study. Lake surveying effort should therefore consider either a two-pronged approach of UVCs for small bodied species alongside BRUVs targeting the wider assemblage, or selecting the appropriate technique to match the desired scale of monitoring. As a result, the governance of vulnerable lakes can be informed and ecosystem services maintained at sites of value to stakeholders.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107588>.

## Credit author statement

Duncan A. O'Brien: Conceptualization, Methodology, Investigation, Formal analysis, Writing- Original draft preparation, Visualization. Heather D. Masonjones: Conceptualization, Resources, Writing - Review & Editing. Enrique Bethel: Investigation, Writing - Review & Editing. Owen R. O'Shea: Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition.

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