Drivers of octopus abundance and density in an anchialine lake: a 30 year comparison

Duncan A. O'Brien [a,d*] - duncan.a.obrien@gmail.com

Michelle L. Taylor [a] - michelle.taylor@essex.ac.uk

Heather D. Masonjones [b] - hmasonjones@ut.edu

Philipp H. Boersch-Supan [c] - philipp.boerschsupan@gmail.com

Owen R. O'Shea [d] - owen@coresciences.org

[a] School of Life Sciences, University of Essex, Wivenhoe Park, Colchester, CO4 3SQ, UK

[b] Biology Department, University of Tampa, Tampa, Florida 33596, USA

[c] British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK and Department of Geography, University of Florida, Gainesville, Florida 32611, USA

[d] The Centre for Ocean Research and Education (CORE), PO Box 255-16, Gregory Town,
Eleuthera, The Bahamas

[*] Corresponding author

Abstract

Anchialine systems are isolated from the sea and often support species' populations distinct from their marine counterparts. Sweetings Pond, an anchialine lake on the island of Eleuthera in The Bahamas was identified as a site of high Caribbean reef octopus, *Octopus briareus* (Robson, 1929) density, relative to coastal populations. However, observed deterioration in local benthic habitat and increased anthropogenic influence over the last 30 years imply that this octopus population may have undergone density and distribution shifts in response to these changing conditions. Here, we assess the system wide octopus density to provide an updated estimate. We hypothesize that despite depressed habitat availability in the 1980s, it will now support octopus densities less than historical estimates because of increasing human impact on the system. Drivers of abundance were also modelled, testing ecological hypotheses of the relationship between octopus count and prey, habitat coverage, and human disturbance. *Octopus briareus* were found in 7 of 27 of surveys with a mean survey count of 0.630 ± 1.25 per 900 m^2. Octopus density did not vary significantly between sites. Octopus count was predicted to increase with increasing cover of calcareous rubble and the density of a preferred prey species, and intriguingly, counts decreased as a function of natural den abundance. System wide octopus density was comparable to earlier studies from the 1980s (1982 = 717.38 per km^2; 1983 = 282.59 per km^2; 2019 = 643.81 per km^2) with no significant difference between years. Given the ecosystem's unique and closed ecological community and the population dynamics and distribution drivers we present, Sweetings Pond has the potential to act as a 'natural laboratory' to explore further questions about marine insular systems and their influence on species populations in terms of ecological and behavioural change.

Keywords: abundance; anchialine; Bahamas; marine; octopus; *Octopus briareus*

Abbreviations

CR – Calcareous Rubble

IR – Individual Recognition

MO – *Mytilopsis* species

OR – Odds Ratio

PR – *Pinctada radiata*

RR – Incidence Rate Ratios

SPE – Sweetings Pond Ecosystem

1. Introduction

Octopus are soft-bodied cephalopod molluscs comprising a group of more than 800 extant species found globally in all seas (Jereb *et al.*, 2014). They are considered an important component of artisanal fisheries, where they contribute 3.8% mass to global landings (FAO, 2018). Due to their lack of external hard parts, octopus may display specific habitat preferences in order to establish protective dens and mitigate vulnerability to predation (Mather and Scheel, 2014) or, alternatively, to provide a sheltered area appropriate for the attachment of eggs (Hanlon and Messenger, 1996; Garci et al., 2015). Consequently, the substrate upon which their early life stages settle (Villanueva *et al.*, 2016) and adults colonise will have a significant influence on octopus survival and distribution (Hanlon and Messenger, 1996). However, there are few examples where such preferences have been identified (Hermosilla *et al.*, 2011). We hypothesize that octopus abundance and density is therefore likely to be driven by habitat quality, availability and reduced predation pressure rather than any social interaction or aggregation with conspecifics (Mather and Scheel, 2014). The Caribbean reef octopus, *Octopus briareus* Robson, is considered exempt from the common perception that octopus are typically asocial in nature, with little to no interactions with conspecifics (Hanlon and Messenger, 1996). This exemption is based upon work from The Bahamas by Aronson (1986), who presented an unexpectedly high-density population of this species compared to coastal populations, in an isolated marine lake on the island of Eleuthera.

Octopus briareus is a common tropical water cephalopod, distributed from the southeast Gulf of Mexico, through the Caribbean to the north coast of South America (Roper *et al.*, 1984). This species is ubiquitous within the littoral zone of a variety of tropical habitats, including coral reefs, seagrass meadows and soft sediment ecosystems (Roper *et al.*, 1984). In these environments, *O. briareus* functions as an important mesopredator, predating upon juvenile spiny lobster, *Panulirus argus* (Butler and Lear, 2009), coral polyps (Jereb *et al.*, 2014) and multiple bivalve species (Aronson, 1989). Although accurate fisheries data are lacking for this species, *O. briareus* supports a minor fishery in the Caribbean and Gulf of Mexico (Voss, 1971; Jereb *et al.*, 2014) and is postulated to contribute to common octopus, *Octopus vulgaris* (Cuvier, 1797) catch in the western central Atlantic fishing area (Roper *et al.*, 1984), which reported a net catch of 14,246 tonnes in 2017 (FAO, 2019).

Despite their abundance and perceived importance as mesopredators globally, very little is known of octopuses' most basic life-history and ecology. This is also true for *O. briareus* in the Caribbean, although for this species exceptions currently extend to laboratory-based research into the potential biomedical and captive mariculture uses (Borer, 1971; Cowden and Curtis, 1973; Hanlon, 1977; Hanlon and Wolterding, 1989) under laboratory conditions with few empirical data on wild populations. With limited information, the population dynamics research of Aronson (1986) on wild *O. briareus* populations in the Sweetings Pond Ecosystem (SPE) have become the benchmark for *O. briareus* ecology.

The SPE is a large anchialine lake 1.6 km long by 0.8 km wide, that displays typical subtropical environmental characteristics for a marine system (Masonjones *et al.*, 2019) and supports a dynamic community of low mobility species (Aronson and Harms, 1985), such as the lined seahorse, *Hippocampus erectus*, cross-barred venus, *Chione elevata,* and sheepshead minnow, *Cyprinodon variegatus variegatus.* Due to its isolation from the wider marine environment, linked only by small aquifers in the porous limestone basin, Sweetings Pond's species diversity is low, with the majority of the biomass provided by small invertebrate species. This is evidenced through the unusually high densities of the brittle stars *Ophiothrix oerstedii* and

Ophioderma brevispina (Aronson and Harms, 1985). In the absence of higher trophic level predators (Aronson and Harms, 1985), such as grouper or sharks, the ecosystem has also undergone the equivalent of a mesopredator release (Crooks and Soule, 1999) compared to counterpart coastal populations; although sporadic larger fish species have been observed due to a series of human introductions. The absence of apex predators has potentially led to the high octopus (max 15.2 per km^2 – Aronson, 1986) and increasing seahorse (max 0.66 per m^2 – Masonjones *et al.*, 2019) population densities observed at the site. Additionally, there have been reports of *Cladophora* algae overgrowth in the patch zone but with its rapid reversion within a year (Aronson, 1989). Such extreme changes in benthic habitat are likely to have influenced the densities of inhabiting species (Rose *et al.*, 2016) and as such, must be considered when drawing conclusions about population dynamics.

Despite the deficit in research activity at this site, the ecosystem has seen significant increases in anthropogenic incursions, specifically ecotourism, subsistence fishing, and agricultural encroachment to the water's edge. Understanding the temporal changes in density and habitat preferences of an important mesopredator in an atypical tropical ecosystem allows ecological questions to be posed to determine the ecological significance, and therefore conservation value, of similar ecosystems as sites of ecological and socio-economic importance.

The overall objective of this study was to estimate the *O. briareus* population density and spatial distribution of the SPE patch zone, providing a contemporary population estimate for the first time in over three decades. Specifically, using this system as a model for anchialine lakes, we hypothesise that the influence of depressed hard substrate availability caused by *Cladophora* overgrowth and increasing human disturbance, will result in an *O. briareus* density less than estimates during the 1980's, and that prey items' and habitat availability will drive octopus distribution. To investigate these hypotheses, we elaborated upon Aronson's (1986) survey methodology to obtain an updated density estimate, and applied modelling techniques to predict the drivers of *O. briareus* abundance across the SPE.

2. Materials and Methods

2.1. Study Area

Sweetings Pond (25°21'40''N, 76°30'40''W) is a tidal marine lake, isolated from the adjacent marine estate of the Great Bahama Banks, located on the island of Eleuthera in the central Bahamas. It is separated from the wider marine environment by a limestone ridge running north-south along its western boundary and surrounded by agriculture and largely impassable low-lying grasslands and white coppice to the north, east and south. Sampling took place from five sites originally identified and named by Aronson and Harms (1985), and further refined by Masonjones and colleagues (2019) (Figure 1). These historic site names refer to identifying landmarks or features of the site and consequently have no reference to differences in habitat or other ecological differences between sites.

Site selection provided sufficient coverage of the heterogeneous gradient of patch zone (shallow region of sponge, coral formations, bivalve clumps and calcareous rubble) identified by Masonjones *et al.* (2019) but unaccounted for by Aronson (1986). No attempt was made to sample the deeper centre of the lake due to the logistical challenge of transporting equipment and to maintain a focus on comparability with Aronson's study. Survey GPS 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.

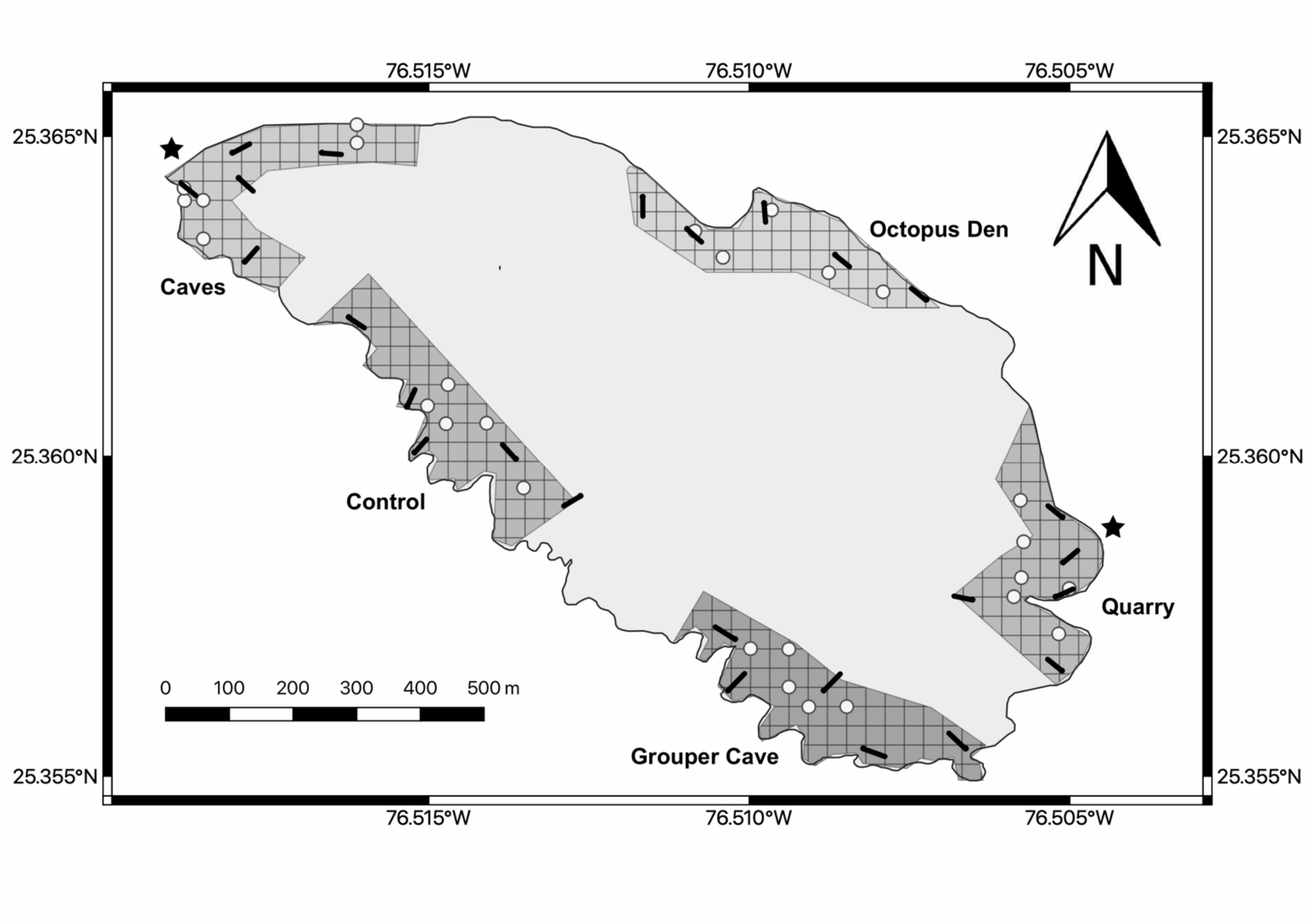

Figure 1. Location of sites within Sweetings Pond, map projected in WGS84. Grey hatched areas represent the area of patch zone designated as a site, within which survey coordinates are randomly selected. White points indicate the north-western corner of 900 m^2 (30 x 30 m) octopus survey quadrats randomly projected on to the 30 m square grid overlay. Stars represent public access points and black lines represent a 30 m ecological survey transects.

2.2 Population Survey

Octopus briareus surveys consisted of 900 m^2 quadrats (30 x 30 m) randomly replicated 5 times within each of the sites: ‘Caves’, ‘Control’ (named for continuity and not considered an ‘experimental control’), ‘Grouper Cave’, Octopus Den’ and ‘Quarry’. A minimum distance of 30 m was maintained between replicates in order to ensure spatial independence. This resulted in 27 total replicates across all sites including additional sampling effort for ‘Quarry’ and ‘Caves’ due to the presence of two lone artificial arrays currently in place for a separate study. Survey methodology elaborated upon Aronson (1986), where the 900 m^2 quadrat was gridded and bisected twice using 30 m transects in a cross pattern, creating a quadrat consisting of four sub-quadrats. The final sampled area was 24,300 m^2 and encompassed the entirety of the patch zone. In comparison, Aronson (1986) sampled 23,000 m^2 and focussed solely on the site ‘Octopus Den’.

In this study, quadrats were aligned along a north-south axis to improve the accurate alignment of quadrat borders underwater. Consequently, the random coordinates generated were used to indicate the quadrat’s north-western corner (Figure 1). Surveys involved methodical SCUBA diver swims through each sub-quadrat, scrutinising any structure for *O. briareus*. When an individual was encountered, the den type in which it was found was recorded and the animal itself photographed to provide an estimate of size. To ensure consistency with Aronson (1986), surveys were performed between 10:00 and 13:00. Doing so also ensured that the majority of octopus were residing within dens (Aronson, 1986) to improve the association of octopus count with den ecology.

Point benthic surveys were performed on the bisecting transects by recording the tape using a single GoPro Hero 7 white edition. The camera was set to film at 1080p with a wide field-ofview (270°) and 30 frames-per-second. Camera distance was maintained at 5 to 10 cm above the transect line.

Structures that could potentially be colonised were also recorded to provide an estimate of natural den availability. Four structure types were identified as potential dens based upon the literature (Aronson, 1986) and preliminary observations of octopus colonisations (Masonjones, pers.comms): sponges (e.g. *Xestospongia* spp.), holes, gastropod shells (namely *Fasciolaria tulipa*) and vegetation. Sponges were only identified as a potential den if the structure could be overturned without uprooting, as the space required for *O. briareus* colonisation is absent in well-rooted sponges. Similarly, vegetation was only recorded if the structure was distinct and elevated from the surrounding benthos to allow space underneath for *O. briareus* occupation.

2.3 Analytical Methods

'Quarry' and 'Caves' were considered disturbed sites due to their proximity to public access to the lake via footpaths and roads. 'Octopus Den' was also assumed to be disturbed owing to the performance of poor agricultural practices on the water's edge, which led to vegetation clearance and deposition into the water. The remaining sites were considered undisturbed. *Octopus briareus* counts were compared among sites and between human disturbance zones. Animal densities were estimated at both the site and lake spatial scales where density represents the total number of observed individuals divided by the area sampled. As the only overlap of sampling period between this study and Aronson (1986) were the months of May and June, the separate counts for these months were used to estimate yearly octopus density at the kilometre scale, using a negative binomial general linear model (GLM) with a log-link and an offset to account for differences in sampling area. Only two data points are available for each year as Aronson (1986) reports a single *O. briareus* count per month. Negative binomial count GLMs were also used to compare between sites and zones and to compare the influence of site and depth in influencing total natural den number. Human disturbance zone was dropped from this model as the parameter was not identifiable due to site encoding the same information. GLMs were fitted using the package 'glmmTMB' (Brooks *et al.*, 2017). The package 'DHARMa' (Hartig, 2019) was then used to assess the dispersion of model residuals and ensure these were not zero-inflated.

Regression models were then used to investigate the ecological drivers behind *O. briareus* abundance across Sweetings Pond. Total natural den availability, average quadrat depth, calcareous rubble (CR) cover, benthic diversity, preferred prey item (*Mytilopsis* spp., *C. elevata* and *P. radiata*) cover, and relative distance to public access points were the predictors of interest as these ecological factors are hypothesised to influence octopus abundance. Site was dropped to model system wide trends with the resulting models ranked by Akaike's Information Criterion (AIC), corrected for a small sample size (AICc). The final non-nested GLM involved the fixed continuous covariates, *Calcareous rubble cover, P. radiata cover* and *total natural den abundance.*

Transect video data was analysed *ex situ* in real time by trained observers using QuickTime Player V10.5. The benthic species directly below the transect tape was identified and recorded every 25 cm. The most common benthic components identified were, flocculant, sediment, calcareous rubble, *Mytilopsis* spp., *P. radiata, Laurencia* spp., *Caulerpa sertularioides*, *Hypnea* spp. and *Ecteinascidia turbinata*. The frequency data for the two bisecting transects in the octopus survey were pooled and the percentage cover of each benthic component calculated. Benthic diversity was assessed to determine differences between sites and zones of human disturbance. Diversity was calculated as Simpson's Diversity Index where percentage cover replaced count data (Tomascik and Sander, 1987). A one-way analysis of variance (ANOVA) was performed between sites and a Tukey's HSD test used to identify post-hoc differences in diversity index value. A non-metric multidimensional scaling (NMDS) ordination plot was generated to visualise benthic community differences between sites independent of the benthic diversity index. The differences were then assessed via ANOSIM (Oksanen *et al.*, 2013).

Results of statistical tests were considered significant at $p < 0.05$ with all analyses performed in R (R Core Team, 2018). Assumptions of normality were tested using Shapiro-Wilk tests and equal variances with Levene's tests. All provided uncertainties are given as the standard deviation.

3. Results

3.1 Octopus Population Density Within Sweetings Pond

Octopus briareus was the only cephalopod encountered during surveys during the two-month sampling period. In total, 17 individuals were observed during octopus surveys, with a least one octopus individual being present in 7 out of 25 surveys and a probability of observing an octopus in any one 900 m^2 of 28%. The resulting Sweetings Pond-wide mean octopus abundance was 0.630 ± 1.25 per survey (n = 27). From the GLM model, 2019 octopus density was estimated at 643.81 per km^2 (95% confidence interval: 37.75 - 13634.16) compared to 717.38 per km^2 (13.24 - 38862.50) in 1982 and 282.59 per km^2 (4.16 - 19203.52) in 1983. No significant difference was seen between the 2019 estimate and the 1980s' (GLM: $\beta_{1982} = 0.11$, $p = 0.864$; $\beta_{1983} = -0.82$, $p = 0.218$). In 2019, 'Control' displayed the highest octopus count in 2019 (Table I), followed by 'Grouper Cave' then 'Caves', with zero individuals observed at 'Octopus Den' and 'Quarry'. Octopus counts did not vary significantly between sites (Table II) and months ($\chi^2 = -1.18$, p = 0.448).

Table I. Site variation in the possible drivers of *O. briareus* abundance across Sweetings Pond. The mean for each variable is reported with the standard deviation provided in brackets.

Site	**Absolute octopus abundance per replicate (900 m^2)**	**Octopus density per km^2**	**Depth (m)**	**Benthic Simpson diversity**	**Absolute natural den abundance per replicate (900 m^2)**	***Mytilopsis* spp. Cover (%)**	***Pinctada radiata* cover (%)**
Caves	0.67 (1.63)	0.74 (1.81)	3.05 (1.64)	0.426 (0.24)	23.0 (13.9)	0.069 (0.17)	1.102 (2.70)
Control	1.60 (1.52)	1.78 (1.69)	8.27 (0.86)	0.429 (0.13)	2.0 (4.5)	2.149 (1.99)	1.736 (0.74)
Grouper Cave	1.00 (1.41)	1.11 (1.57)	6.02 (1.51)	0.584 (0.09)	29.8 (15.4)	9.835 (8.62)	4.132 (2.13)
Octopus Den	0.00 (0.00)	0.00 (0.00)	5.88 (2.94)	0.561 (0.10)	27.8 (17.2)	0.000 (0.00)	0.165 (0.23)
Quarry	0.00 (0.00)	0.00 (0.00)	2.49 (0.07)	0.241 (0.07	15.2 (7.8)	0.059 (0.17)	1.122 (1.45)

Table II. Generalised linear model parameter estimates for the octopus count ~ site + month relationship. Parameter values are given on the link scale.

	Estimate	**Standard Error**	***p* value**
Intercept (SiteControl:MonthJune)	0.470	0.624	0.452
SiteCaves	-0.581	0.999	0.561
SiteGrouper Cave	0.626	1.575	0.722
SiteOctopus Den	-24.43	714.49	1.000
SiteQuarry	-21.79	213.81	0.999
MonthMay	-1.183	1.561	0.448

Total natural den number also differed significantly between sites and depth (Table III) with ‘Control’ being significantly different to all other sites excluding ‘Quarry’; ‘Control’ displayed a den abundance 13.2% that of ‘Quarry’, the next lowest site (Figure 2). Den number was negatively related to depth ($\chi^2 = -0.202$, $p = 0.003$).

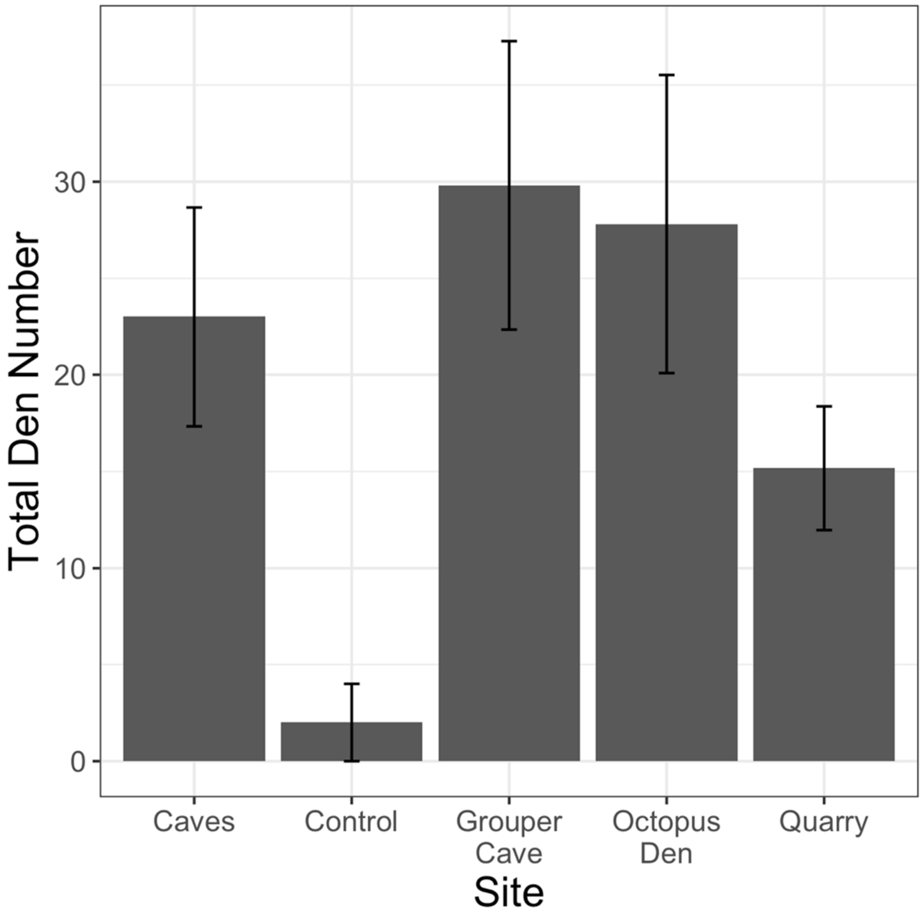

Figure 2. Overall landscape scale variation in natural den number between Sweetings Pond sites presented as bar plots. Plots represent site mean whilst error bars depict the standard error from that mean.

Table III. Generalised linear model parameter estimates for the natural den count ~ site + depth relationship. Parameter values are given on the link scale.

	Estimate	**Standard Error**	***p* value**
Intercept(SiteControl)	2.326	0.661	<0.001 ***
Depth (m)	-0.202	0.067	0.003 **
SiteCaves	1.395	0.553	0.012 *
SiteGrouper Cave	2.190	0.475	<0.001 ***
SiteOctopus Den	2.127	0.468	<0.001 ***
SiteQuarry	0.915	0.575	0.111
* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$			

3.2 Drivers of Octopus Abundance

Multi-model comparison did not provide strong evidence for an effect of human disturbance on octopus density. *Pinctada radiata* (PR) cover was retained as a predictor across the six models with the lowest AICc scores, with quadrats displaying higher PR cover yielding higher *O. briareus* counts. Calcareous rubble (CR) cover was also retained as a predictor across all models. In the optimal model (Table IV – Model 1), the three predictors influenced octopus density. If predicted coefficients are presented as incidence rate ratios (RR), an increase of 1 PR and CR

Table IV. Parameter estimates and associated standard deviations presented as model coefficients for the top ranked models predicting *Octopus briareus* abundance across Sweetings Pond. Models were ranked by AICc.

	Dependent variable: *O. briareus* count					
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Intercept	-4.234 (1.768)	-4.891 (2.087)	-4.616 (2.161)	-4.234 (1.991)	-6.813 (2.974)	-20.338 (16.561)
Average depth (m)					0.404 (0.318)	
Benthic diversity						16.000 (14.690)
CR cover (%)	0.051 (0.020)	0.061 (0.025)	0.064 (0.026)	0.048 (0.022)	0.040 (0.027)	0.179 (0.140)
MO cover (%)				0.084 (0.064)		0.064 (0.063)
PR cover (%)	0.725 (0.237)	0.480 (0.223)	0.751 (0.268)	0.817 (0.293)	0.562 (0.238)	0.988 (0.515)
Distance to public access (m)			-2.485 (2.016)			
Total den abundance	-0.066 (0.027)		-0.066 (0.027)	-0.111 (0.051)		-0.149 (0.074)
AICc	46.58	47.84	47.92	48.10	49.34	49.73
ΔAICc	0.00	1.26	1.34	1.52	2.76	3.15
Model weight	0.34	0.18	0.17	0.16	0.08	0.07

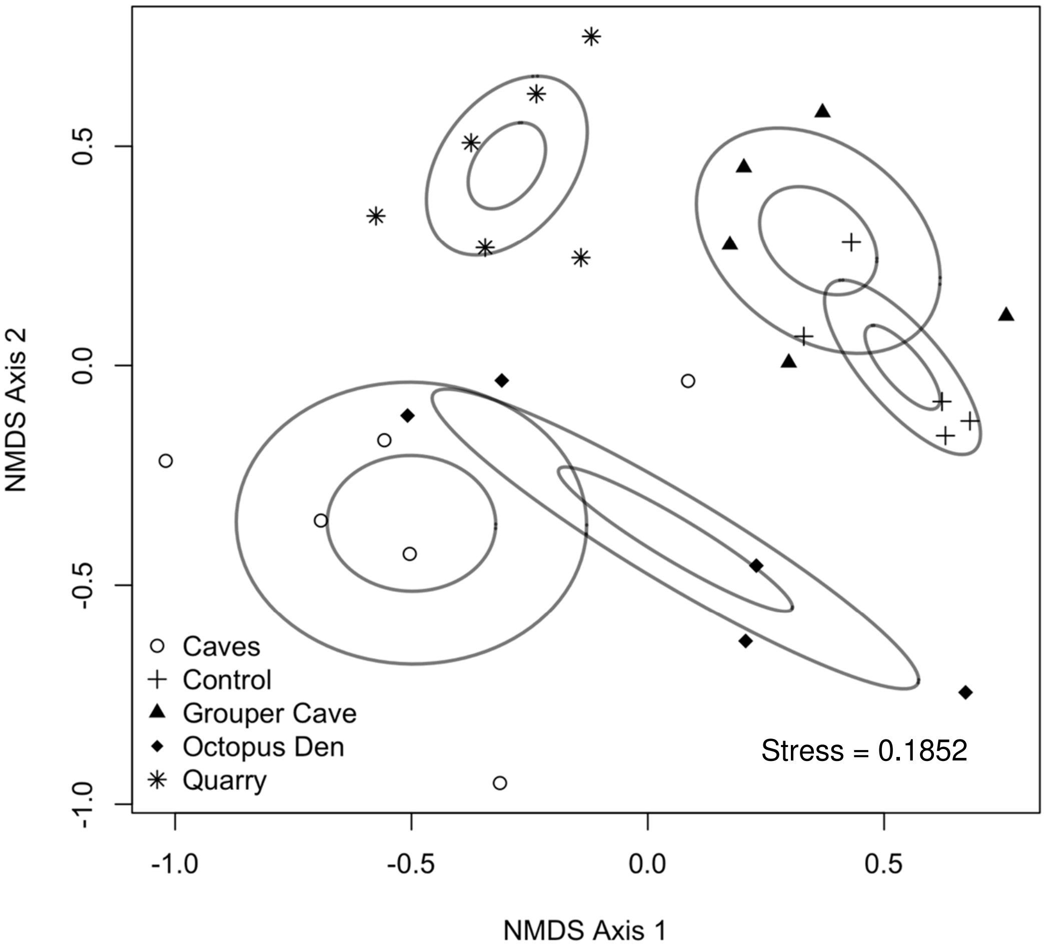

Figure 3. Non-metric multidimensional scaling plot comparing benthic species between Sweetings Pond sites. Inner ellipses represent 95% confidence intervals for each multivariate mean, based upon standard error, whilst outer ellipses represent 50%.

percentage cover unit increased the density by ~107% (RR = 2.065, $p < 0.01$) and ~5% respectively (RR = 1.052, $p < 0.05$). However, adding one den per km squared decreases the density by ~6% (RR = 0.936, $p < 0.05$).

3.3 Benthic Composition Distributions

Clear differences in benthic composition were observed between certain Sweetings Pond sites, as represented by point clustering during NMDS analysis (Figure 3). ANOSIM interrogation suggests that the ratio of within-group to between-group dissimilarities are significantly different (ANOSIM: $R^2 = 0.665$, $p < 0.001$) whilst the 95% confidence intervals of ‘Control’ and ‘Grouper Cave’ clusters overlap sufficiently to suggest their benthic communities are similar. This is also true for ‘Octopus Den’ and ‘Caves’. ‘Quarry’ has its own distinct benthic composition, a result confirmed by a significant difference in benthic diversity between sites (One-way ANOVA: $F_{4,22} = 5.02$, $p < 0.01$). A Tukey HSD post-hoc test indicated that the mean diversity score for ‘Quarry’ was significantly lower than both ‘Grouper Cave’ ($p < 0.01$) and ‘Octopus Den’ ($p < 0.01$) whilst the remaining pairwise comparisons between sites yielded no statistically significant results. The diversity differences are driven by a higher mean percentage cover of flocculant [Kruskal-Wallis test: $\chi^2 = 19.84$, df = 4, $p < 0.001$; Dunn’s Test with Bonferroni correction: ‘Quarry’ > ‘Octopus Den’ (adjusted $p < 0.001$) & ‘Control’ (adjusted $p < 0.05$)] and reduced mean calcareous rubble cover [$\chi^2 = 20.48$, df = 4, $p < 0.001$; ‘Quarry’ < ‘Grouper Cave’ (adjusted $p < 0.01$) & ‘Control’ (adjusted $p < 0.01$)] compared to the other sites.

4. Discussion

4.1 Octopus briareus Population Density

This study has shown a large population of *O. briareus* inhabiting the patch zone of the Sweetings Pond ecosystem, with estimates being comparable with earlier work by Aronson (1986) [717.38 per km^2 in 1982; 282.59 per km^2 in 1983, 643.81 per km^2 in 2019]. It is difficult to make comparisons to other populations due to a lack of data from wild *O. briareus* coastal populations. Therefore, it is necessary to draw parallels with the common octopus, *O. vulgaris*, due to it being sympatric to *O. briareus* throughout the Caribbean (Roper *et al.*, 1984), phylogenetically similar (Albertin *et al.*, 2015; Sanchez *et al.*, 2018), and likely exhibiting similar niche occupation. Thus, taking *O. vulgaris* as an exemplary, Caribbean octopus species have been observed at 918.3 per km^2 in coastal Bermuda (Mather and Odor, 1991), which is also somewhat comparable to this study and Aronson (1986).

The apparent stability of octopus density over time conflicts with fluctuations in density observed in in other octopus species (Katsanevakis and Verriopoulos, 2006), although our observation of stability is only made based upon the two data points available. It is possible that the SPE population is simply tightly linked to stable ecosystem variables as is commonplace in lake systems (Adrian *et al.*, 2009). It was expected that the population would display transient population dynamics because of an observation of anomalously early and unsuccessful egg brooding in August 1982 (Aronson, 1986) and such populations display the potential for high amplification and attenuation (transient increase and decrease in population size/density respectively) when demographic parameters or vital rates are perturbed (Stott *et al.*, 2010). *Octopus briareus* within the SPE fulfil these dynamics due to the species' ~1-year lifespan (Hanlon, 1977; Roper *et al.*, 1984) and 60–day development time of eggs (Aronson, 1989) in a system susceptible to change. However, with similar densities observed in 2019, it is unlikely to be an anomalous event, although the drivers of the unsuccessful system wide egg brooding, observed in 1982, are still unrevealed. This being said, it is appropriate to consider likely drivers/ maintainers of SPE octopus density to support management decisions regarding the site.

Vital rates are typically perturbed by density dependent effects (Ray and Hastings, 1996) acting upon ecosystem variables that the population is correlated with: e.g. abiotic factors, predation rate and prey and habitat availability. The environmental characteristics of the system assessed by Masonjones *et al*. (2019) indicate seasonal and spatial differences in surface temperature and salinity. Temperature in particular is a key environmental driver in altering cephalopod ontogeny (Rosa *et al.*, 2012), with embryonic and juvenile stages being most susceptible; for example, a 3 °C increase in temperature compared to the local mean, is sufficient to increase mortality in *O. vulgaris* juveniles by ~30% under laboratory conditions (Repolho *et al.,* 2014). The surface temperature during this study did not range more than 1.2 °C above the seasonal average (~32 ° versus 30.8 °C in Masonjones *et al*. 2019) making it unlikely to have altered octopus density. Additionally, the literature consensus is that salinity has minimal influence on *Octopus* mortality with multiple species displaying euryhaline traits: e.g. *O. vulgaris* (Delgado *et al.*, 2011) and *O. ocellatus* (Sakamoto *et al.*, 2015).

Other environmental factors that may drive patterns in octopus density and spatial distribution result from anthropogenic incursion. This is exemplified by increased public traffic to this ecosystem and the apparent harvesting of seahorses, octopus and crabs for use in the aquarium trade and subsistence fishing. Moreover, the construction of a large commercial dry dock enterprise in the neighbouring community of Hatchet Bay (~1 mile to the south-east) has the potential to induce ecotoxicity and anoxic changes. Hatchet Bay was a similar lake to Sweetings Pond until the 1920s, when it was exposed to the marine environment for use as a semi-natural harbour. Therefore, it displays the same geological topography as Sweetings Pond (Masonjones *et al.*, in prep.) and feasibly supports subterranean connectivity. This may lead to the transfer of heavy metals and antifouling compounds into the susceptible SPE. The additive effect of such pollution with litter associated with tourist traffic is known to induce mortality in aquatic organisms, alter their distribution (Koelmans *et al.*, 2013, Roldan-Wong *et al.*, 2018) and feasibly is relevant here. Expanding peripheral agriculture (2 ha yr^{-1} from 2010 – Masonjones, unpubl. data) and the associated nitrogenous compound runoff will alter oxygen availability changes as consistently shown in isolated water bodies (Jeppesen and Søndergaard, 1991; Jeppesen *et al.*, 2009). Future studies should therefore focus on ecotoxicity thresholds for this species in order to provide baseline information pertaining to ecotoxicological influence on confined ecosystems.

Alternatively, Sweetings Pond has been suggested as undergoing a mesopredator release (Aronson and Harms, 1985) where the absence of traditional apex predators enforces changes in the ecosystem's trophodynamics. Whilst no apex predators were likely ever present in sufficient densities to exert top down control, their absence in Sweetings Pond has enabled traditional mesopredators such as *O. briareus*, redfin needlefish, *Strongylura notata,* and West Indian spider crab, *Maguimithrax spinosissimus*, to inhabit the highest trophic levels (Aronson and Harms, 2085, Masonjones, pers. obs). The resulting trophodynamics of this scenario are analogous to those of mesopredator release in open marine environments. The densities observed in this study weaken this theory as octopus density is similar between the Sweetings Pond *O. briareus* population and coastal *O. vulgaris* populations, then mesopredator release can be playing no role in increasing density within Sweetings Pond. However, rather than density being driven up by such a release, the lack of predation on *O. briareus* may leave the population to be regulated by their cannibalistic tendencies (Aronson, 1989; Ibanez and Keyl, 2010). If cannibalism is only considered in the direct sense ('energy gain'), then theory predicts that cannibalism may produce population cycles and possibly chaos in the absence of other density dependent effects (Claessen *et al.*, 2004; Ibanez and Keyl, 2010). The ~1-year lifespan of *O. briareus* prevents the opportunity for adults to prey on the young-of-the-year, violating the assumptions of the alternative attractor state of population stability, based upon cannibalism as a density stabiliser (Cushing, 1992). Despite no cannibalism events being observed in this study, the combination of theory with Aronson's (1989) 6 direct observations of *O. briareus* cannibalism, suggests that cannibalism is a driver of octopus population dynamics within the SPE.

The diversity of potential drivers influencing *Octopus* abundance in Sweetings Pond further highlights the challenge of establishing robust and effective management decisions regarding this species. This is particularly true at a temporal scale, with this study the first to provide updated estimates and make comparisons to historic data to facilitate future monitoring of an important indicator species. Further study is ultimately required to investigate the relative influence of each of the previously suggested drivers and their synergistic interactions; interactions vital when assessing system responses to change (Crain *et al.*, 2008).

4.2 Octopus briareus Spatial Distribution

The spatial distribution of *O. briareus* within the SPE was solely predicted by prey availability and calcareous rubble (CR) cover. Many bivalve species recruit to empty shells which act as solid substrate in the absence of other alternatives (Fulford *et al.*, 2011; Clements *et al.*, 2018). In the patch zone of the SPE, empty shells (i.e. CR) represent the sole pool of potential substrate. It is therefore unsurprising that it and prey item cover predict octopus encounter rates. Multiple studies highlight how prey abundance and distribution drive marine predator abundance (Wirsing *et al.*, 2007, Navarro *et al.*, 2016) and it is in areas of high CR that prey bivalves aggregate and *O. briareus* are more likely to be encountered.

There were two unexpected results highlighted in the spatial analysis of octopus, although these conclusions should be qualified as being based upon 17 octopus sightings and a limited temporal dataset. Firstly, that human influence and distance to public access points have no measurable influence on octopus density. This indicates that current levels of anthropogenic disturbance are insufficient to exclude octopus from disturbed areas and as such, little management is required considering the *O. briareus* population in isolation. However, as the intensity of disturbance is increasing and conclusions can currently only be drawn over the limited temporal scale presented here, repeat monitoring is necessary. Tipping points are common in marine ecosystems (Selkoe *et al.*, 2015) and it is difficult to predict the precise amount of stress required to trigger a cascade. Consequently, there is also a need to monitor water quality in the SPE.

The second unexpected result is that total natural den number is negatively associated with octopus abundance in count models. Increasing the availability of a habitat or resource typically promotes the abundance of an organism that utilises it (Recer *et al.*, 1987; Grand and Grant, 1994, Lambert *et al.*, 2006). Here, as natural dens negatively correlate with depth, dens may be localised in areas non-optimal for octopus colonisation, be that due to lack of prey or poor habitat quality. Similarly, whilst colonised dens primarily consisted of sponges, sponge abundance was not represented in the top six optimal models

There is also the possibility that adult octopus are cryptically colonising crevices under the rock ledges of the lake edge, rather than searching for dens in the exposed areas of the patch zone randomly sampled in this study. This would cause an artefact where fewer adult octopus were encountered in natural dens than expected due to the inaccessibility of these spaces and low probability of a randomly sampled quadrat bordering the lake edge. The limited access under these ledges on standard SCUBA may be mitigated by alternative methods, including the use of cave diving equipment or baited remote underwater video (BRUV).

4.3 Management Implications

Sweetings Pond is recognised by the government of The Bahamas as having ecological significance (Bahamas National Trust, 2018), so much so that the conservation value of this site is acknowledged in a global context. A status as one of the most intriguing and important marine lakes in The Bahamas, has been justified through prominent research conducted over the last five years (Rose *et al.*, 2016; Masonjones *et al.*, 2019). Anchialine systems, as unique habitats, function as natural laboratories (Gonzalez *et al.*, 2011, Hoffman *et al.*, 2019) that allow the testing of hypotheses concerning speciation, population dynamics and behaviour, and therefore, any management effort targeting the SPE should attempt to minimise disturbance if use of the system as a natural laboratory is to be continued. Tourist traffic in particular should be a major focus due to its rapid increase, unpredictable effects in anchialine systems, and as its control will simultaneously alleviate the frequency of subsistence fishing.

From an impact perspective, the observed abundance of natural dens within the SPE implies that Aronson's (1986) suggestion of natural den limitation in the SPE is unlikely, especially as there is no consensus as to whether dens are limiting for many *Octopus* species and locations. For example, Mather (1982) determined dens were indirectly limiting for the Atlantic pygmy octopus, *Octopus joubini*, whereas the opposite was true for Mediterranean *O. vulgaris* (Guerra *et al.*, 2014). Our elaboration upon the framework provided by Aronson (1986; 1989) can simultaneously clarify this consensus and promote Sweetings Pond as a model insular system, something that is currently lacking in the Bahamas, as well as the wider regional context.

Repeated surveys using this revised methodology in conjunction with established seahorse monitoring can act as a springboard for managers to assess ecosystem health into the future.

Additionally, the lack of environmental data available for the SPE hinders holistic management decisions. An understanding of temporal or spatial changes in environmental conditions and species distributions are vital for long term planning (Samhouri *et al.*, 2010). For example, for the conservation of *O. briareus,* the protection and maintenance of the local bivalve populations (*P. radiata*, *C. elevata* and *Mytilopsis spp.*) is vital as these act as both prey and habitat, consequently correlating with octopus abundance across the SPE. Chemical pollution from antifouling paints induce larval mortality in bivalves (Ruiz *et al.*, 1995), heavy metals supress the temperature tolerance of Ostreida oysters (Lannig *et al.*, 2006) and bioaccumulation of microplastics is evident in multiple species globally (Sussarellu *et al.*, 2016, Su *et al.*, 2018). Each of these effects are probable in Sweetings Pond yet in the absence of environmental monitoring it is hard to estimate their impacts.

In conclusion, this study has demonstrated that the SPE octopus population displays consistent population density with their abundance predicted by prey and habitat availability, reiterating the ecological and evolutionary importance of Sweetings Pond and how minimisation of further human disturbance is necessary to maintain its current status. A ‘reference’ approach is required (Johnes *et al.*, 1994), establishing environmental standards of baseline lake conditions to be defined for future monitoring. Viable management strategies therefore include: limiting the timings and locations that visitors can access the SPE, guided by the seasonal and spatial use of *O. briareus*, control/catchment of visitor and agricultural nutrients/chemicals to minimise water quality degradation and licensing of tour operators to prevent overexploitation. Conservation of *O. briareus* as charismatic species in the SPE can then act as a platform to mould the entire site into a burgeoning experimental system for anchialine and insular marine environments similar to Wytham Woods, Oxford for passerine birds (Savill *et al.*, 2011) or Lake Victoria for cichlid fish (Seehausen *et al.*, 2008). As a result, The Bahamas has the opportunity to formalise the protection of a unique ecosystem and promote it as a conservation site of important evolutionary research and pride for local people.

Glossary

Anchialine – tidally-influenced subterranean estuary, facilitated by karst and volcanic terrains, that enables the penetration of seawater inland.

Patch zone – a discrete benthic region encompassing the periphery of Sweetings Pond that consists of sponge, coral formations, bivalve clumps and calcareous rubble.

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