TITLE: A low-cost, long-term underwater camera trap network coupled with deep residual learning image analysis

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ABSTRACT

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1. Understanding long-term trends in marine ecosystems requires accurate and repeatable counts of fishes and other aquatic organisms on spatial and temporal scales that are difficult or impossible to achieve with diver-based surveys. Long-term, spatially distributed cameras, like those used in terrestrial camera trapping, have not been successfully applied in marine systems due to limitations of the aquatic environment.
2. Here, we develop methodology for a system of low-cost, long-term camera traps (**Dispersed Environment Aquatic Cameras**), deployable over large spatial scales in remote marine environments. We use machine learning to classify the large volume of images collected by the cameras. We present a case study of these combined techniques' use by addressing fish movement and feeding behavior related to grazing halos, a well-documented benthic pattern in shallow tropical reefscares.
3. Cameras proved able to function continuously underwater at deployed depths (up to 7 m, with later versions deployed to 40 m) with no maintenance or monitoring for over five months, and collected time-lapse images during daylight hours for a total of over 100,000 images. Our ResNet-50-based deep learning model achieved 92.5% overall accuracy in sorting images with and without fish, and diver surveys revealed that the camera images accurately represented local fish communities.
4. The cameras and machine learning classification represent the first successful method for broad-scale underwater camera trap deployment, and our case study

41 demonstrates the cameras' potential for addressing questions of marine animal
42 behavior, distributions, and large-scale spatial patterns.

43 KEYWORDS: Behavior, camera trap, image classification, long-term, machine learning,
44 marine, underwater, reefscape, deep learning, landscape of fear

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46 INTRODUCTION

47 Terrestrial camera trapping is a growing field and a technique increasingly applied
48 in global biodiversity monitoring (e.g., Steenweg et al. 2017). Camera traps are remotely
49 activated cameras that rely on motion and heat sensors to trigger when an animal passes
50 by. They are used to study species richness (Rowcliffe 2017) and the distribution,
51 abundance, habitat use, and behavior of wildlife around the world, with many studies
52 surveying more than one species at a time (Burton et al. 2015). Most camera traps are small,
53 relatively inexpensive, and often deployed in groups or networks over a wide area for
54 months at a time. They are typically less invasive and more reliable than comparable
55 observation techniques (Cutler and Swann 1999). Because they trigger based on the
56 difference between background radiation and a warm-bodied animal passing through the
57 sensor's field, camera traps have typically been used to study mammals and birds, although
58 the field is now expanding to include some ectotherms (Rowcliffe 2017).

59 Comparable techniques for monitoring underwater species face several technical
60 challenges, chiefly the attenuation of infrared radiation in water, which renders a standard
61 commercial camera trap unlikely to trigger underwater, except at very close range (Giles
62 and Bankman 2005), and the rigors of operating in the marine environment where water
63 intrusion and algal and faunal fouling are persistent issues. The fact that most fish are

ectotherms further complicates use of the traditional heat-triggered infrared sensor technology used in most terrestrial camera traps. Far-red illumination invisible to most fish provides one potential alternative to infrared (Williams et al. 2014), although far-red light still attenuates over short distances underwater. Given the ability of sound to propagate well underwater, acoustic techniques provide another possible alternative to infrared sensing (Giles and Bankman 2005). Acoustic cameras have been used in the past to image sharks and other fish in low-light, turbid environments, replacing light-based imaging entirely (McCauley et al. 2016). This suggests that acoustic techniques could also be used to trigger conventional optical cameras.

Due to the power requirements of active triggering (far-red light, sonar) and recording methods, current underwater fish monitoring and measurement techniques are either limited by short battery life and operate on the scale of hours, as with baited remote underwater video (BRUV) and similar short-term recording devices (Cappo et al. 2004, Colton and Swearer 2010, Brooks et al. 2011, Williams et al. 2014, Boussarie et al. 2016) or require a tethered, external power source (Boom et al. 2014, Marini et al. 2018). Because of this, the spatial extent, number of cameras, and duration of monitoring for marine systems are vastly smaller in scope than terrestrial efforts (compare Williams et al. 2014 and Siddiqui et al. 2018 to the TEAM or Snapshot Serengeti datasets described in Beaudrot et al. 2016, Norouzzadeh et al. 2018, respectively). Even long-term underwater monitoring with an external power supply may be limited to recording images or video during daylight hours (e.g., Boom et al. 2014) due to the difficulties of avoiding reflected particulate matter in underwater images taken at night with direct illumination. Without a side-mounted or similarly external flash, both white light and infrared images will be obscured by the

illumination of biotic and abiotic particulates suspended in the water column, and continuous illumination may also attract fish and other marine organisms, depending on the color of the light (Ko et al. 2018). Thus, most long-term underwater observations are limited with regard to both power and nighttime illumination, and solutions can be costly and prohibit deployment of underwater cameras in remote locations without access to external power or consistent upkeep.

A related challenge faced by both terrestrial and marine camera traps is the time cost related to processing and analyzing large photosets obtained from multiple cameras over the course of months or years (Norouzzadeh et al. 2018). While computer vision techniques are not yet widespread in the field of camera trapping, they have the potential to reduce time cost (Rowcliffe 2017) and have already been successfully applied to the extensive Snapshot Serengeti camera trap dataset (Norouzzadeh et al. 2018) as well as video frames from cabled or short-term marine cameras (Boom et al. 2014, Siddiqui et al. 2018, Marini et al. 2018, Villon et al. 2018).

Here we present a simple design for an affordable, long-running, autonomous underwater camera based on an existing commercially-available terrestrial model. We outline the deployment of our Dispersed Environment Aquatic Cameras (DEACs) across a 270 km² tropical reefscape, our testing, and our subsequent analysis of the 100,000+ images obtained by implementing a deep convolutional neural network (CNN) technique for image classification. To demonstrate both the efficacy of our design and the value of long-term unmanned underwater observations to marine ecology research, we present a case-study in fish feeding behavior as it relates to a well-documented benthic pattern at Lighthouse Reef Atoll, Belize.

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METHODS

112 **Design**

113 *Camera Selection*

114 Cuddeback Silver Series scouting cameras, model 1231 (Cuddeback, Green Bay,
115 WI, USA), were chosen for their compact size, their relatively high 20 megapixel (MP)
116 image resolution, and their time-lapse function, which allows images to be taken at pre-
117 programmed time intervals and certain light levels without requiring the use of additional
118 video or motion-triggered image settings. This programming flexibility, especially
119 regarding the time-lapse feature, is not included in multiple similar cameras from other
120 manufacturers. The cameras were programmed to take 20 MP images every 15 minutes
121 whenever ambient light levels were high enough to allow for color photography without
122 flash, using the “Day” setting. Nighttime images and video and all infrared sensor-triggered
123 images and video were disabled to conserve both power and memory space because initial
124 field tests showed that few or no additional usable images were captured using the infrared,
125 low-light “Night” setting.

126 Cameras were synchronized to record photos on the hour and every 15 minutes
127 following to ensure that images from different cameras and sites were captured at the same
128 time of day and under the same local conditions. The 15-minute interval was chosen to
129 balance the need for regular observations of reef and seagrass communities that may
130 include transient fish species and the constraints of storing and processing thousands of
131 high-resolution images collected by multiple cameras over a months-long deployment. The

132 ability of this interval to adequately capture the community composition and species
133 present at a given reef was validated using in-person diver surveys (described below).

134 Memory cards were 32 GB SanDisk (Western Digital Corporation, Milpitas, CA,
135 USA) or Kingston (Kingston Technology Corporation, Fountain Valley, CA, USA)
136 microSD cards with adapters, capable of holding over 25,000 20 MP color images each.
137 Each camera required eight Energizer Ultimate Lithium AA batteries (Energizer Holdings,
138 Inc., St. Louis, MO, USA), which provided enough power for over five months of
139 continuous function under the settings described here.

140 The total cost of each camera, including the batteries and SD card, came to just
141 \$125 per unit with the housing (discussed below). The use of pre-built commercial trail
142 cameras, which are designed for energy efficiency over long deployments, significantly
143 reduced both material and energy costs, relative to constructing a similar camera from
144 scratch using components like a Raspberry Pi (Raspberry Pi Foundation, Cambridgeshire,
145 UK) and GoPro (GoPro, Inc., San Mateo, CA, USA), Canon (Canon, Inc., Ota City, Tokyo,
146 Japan), or Sony (Sony Corporation, Minato City, Tokyo, Japan) cameras, as used in
147 previous underwater camera applications (e.g., Brooks et al. 2011, Williams et al. 2014,
148 Boussarie et al. 2016, Siddiqui et al. 2018, Villon et al. 2018).

149

150 *Housing Construction*

151 Two different housings were tested in the field, both based on commercially
152 available junction box enclosures. Housing 1, based on item DS-AT-1217-1 available from
153 “Saipwell” (Saip Electric Group Co., Ltd, Wenzhou, China), has thinner walls (2.4 - 3.9
154 mm) made of an unspecified plastic. The top secures with specially-shaped plastic screws

155 and it contains an O-ring like insert made of foam. Housing 2, based on model ML-
 156 47F*1508 from Polycase, Inc. (Avon, OH, USA), is a thick-walled (3.5 - 4.0 mm) design
 157 made of polycarbonate resin secured with stainless steel screws and a silicon rubber gasket.
 158 Both housings had a 2 inch diameter hole drilled in the faceplate and a 3 inch disk of 1/8
 159 inch thick acrylic epoxied to the opening with MarineWeld (J-B Weld Company, Atlanta,
 160 GA, USA) to act as a window. Since both housings used identical acrylic windows and
 161 contained the same cameras, images collected using each design were indistinguishable;
 162 the chief difference between the housings was their pressure tolerance and leakage at depth.
 163 Each housing cost approximately \$30 for all components (included in the total price given
 164 above). Ablative antifouling boat paint was applied to the housing exterior, excluding the
 165 back and acrylic window, of a subset of cameras with Housing 2 to reduce biofouling.

166 Cameras were programmed, armed, and packed inside their housings with
 167 cardboard spacers. Housings were sealed with Star brite marine silicone sealant (Star brite,
 168 Fort Lauderdale, FL, USA) around the seam of the enclosure lid. Silicone sealant was also
 169 used to reinforce the edges of the epoxy seal around the lens window, both inside and
 170 outside.

171

172 *Field Installation*

173 Cameras were secured to four-legged bent rebar stands with plastic cable ties
 174 threaded through mounting holes pre-built into the housings (Fig 1). Due to their buoyancy,
 175 camera housings were placed underneath the crossed rebar forming the top of each stand
 176 and secured laterally to the four legs, which were sunk into the sediment to keep the stands
 177 upright. Lightweight plastic or polystyrene buoys were tethered to a small subset of

178 cameras and stands located in particularly shallow water (2 m or less) to prevent collision
179 by boats.

180

181

182 **Figure 1.** DEACs were deployed on four-legged rebar stands in the field. Plastic cable ties
183 attached to the camera housing and to the legs were used to secure buoyant cameras in
184 housings below the crossed rebar at the top of each stand. Bottom left inset: A detailed
185 front view of a camera in Housing 1 underwater.

186

187 Deployment

188 Study System and Question

189 Lighthouse Reef Atoll off the coast of Belize is primarily a shallow (1-8 m depth)
190 lagoon environment, dominated by scattered patch reefs interspersed with a mosaic of
191 seagrass, macroalgae, and sand. Although relatively isolated from the mainland, the atoll

192 is subject to heavy local fishing pressure for conch, lobster, and certain fish species. A
 193 small no-take marine protected area (MPA) surrounds the island of Half Moon Caye in the
 194 southeastern corner of the atoll. Because of its shallow benthos, wide variety of benthic
 195 cover types, and spatial variation in protected status, Lighthouse Reef provides an ideal
 196 location to test our DEACs under a variety of conditions. The shallow marine grazing
 197 system of Lighthouse Reef and similar Caribbean locations is in many ways analogous to
 198 terrestrial grazing systems like the African savanna (Burkepile 2013), where camera trap
 199 networks have been effectively deployed for years (e.g., Norouzzadeh et al. 2018).

200 To structure our testing and demonstrate the utility of the DEACs for addressing
 201 ecological questions at large spatial scales, we organized our deployments around a
 202 widespread benthic pattern particularly prominent at Lighthouse Reef: grazing halos.
 203 Grazing halos consist of a bare sand or lightly vegetated border surrounding a coral patch
 204 or similar underwater structure that separates the reef from surrounding dense vegetation
 205 (i.e. seagrass or algae). The heightened grazing observed inside these halos could be due
 206 to a landscape of fear (e.g., Hammerschlag et al. 2015), where herbivores are afraid to
 207 venture past a threshold distance from the reef due to predation risk (Madin et al. 2011).
 208 At Lighthouse Reef, grazers are mostly large parrotfishes (Scaridae) and surgeonfishes
 209 (Acanthuridae). However, this threshold of fish density could also be due simply to the
 210 natural dispersion of grazers as they venture farther from the reef, which serves as a central
 211 aggregating structure for many fish (Sale and Douglas 1984, Bohnsack 1989, Layman et
 212 al. 2013). We proposed that if a strong landscape of fear is in effect, herbivorous species
 213 observed and photographed in the halo will never venture out into the surrounding seagrass,
 214 except perhaps when traveling in schools. However, a simple drop-off in fish density with

215 distance would still result in the occasional grazing reef fish being seen by our cameras,
216 and if reef fishes are food limited rather than predator limited, they should forage widely
217 in the seagrass, which is a preferred food (Bilodeau 2019). Therefore, regular detection of
218 reef herbivores out in the seagrass over multiple months could be taken as evidence refuting
219 the landscape of fear at Lighthouse Reef.

220

221 *Spatial Arrangement*

222 Cameras were deployed in pairs at 21 patch reef sites within Lighthouse Reef Atoll.
223 DEAC sites were distributed evenly inside and outside of the Half Moon Caye Natural
224 Monument MPA in the southeastern corner of the atoll. Seven sites (3 inside the MPA, 4
225 outside) featured predominantly algal bottom cover; the rest were in areas surrounded by
226 seagrass, primarily *Thalassia testudinum*. Patch reef sites for camera deployment were
227 chosen via random point placement using satellite imagery and a depth map of the atoll
228 (courtesy of the Carnegie Airborne Observatory), which allowed sites to be evenly
229 stratified across depths from 2-7 m.

230 Sites deeper than 4 m were initially avoided due to leakage of Housing 1 past this
231 depth, although depths of up to 7 m (maximum depth required in the study) were
232 successfully achieved with Housing 2, which was used for initial deployments in March
233 2018 and all deployments from August 2018 onward. Cameras were deployed in sets of
234 two, one camera located at the edge of the sandy halo surrounding a patch reef and the
235 other located at least twice the halo's width away from the edge in the surrounding seagrass
236 or algal benthic cover (Fig 2). In the case of particularly narrow halos, "control" cameras
237 were placed a minimum of 15 m from the halo edge. This allowed control cameras a view

238 of the same bottom cover (seagrass or macroalgae) as that adjacent to the halo but placed
 239 them well beyond the fish density thresholds observed by Layman et al. (2013), while also
 240 accounting for the possibility that larger halos could represent reefs with larger or farther-
 241 ranging fish populations. “Halo” cameras had a relatively wide field of view, as is typical
 242 of terrestrial trail cameras, which included both the halo in front of them and the patch reef
 243 beyond. Both cameras were pointed toward the reef, although the edge of the halo was
 244 beyond the range of view for the grass (“control”) camera at most sites.

245

246 **Figure 2.** Camera arrangement at a patch reef site. One camera was placed on the edge
 247 of the halo facing in toward the reef (“Halo Cam”), while the second (“Control Cam”)
 248 was placed twice the halo’s width away in the surrounding seagrass or algal cover, in line
 249 with the first camera.

250

251 *Monitoring and Secondary Deployments*

252 Camera deployments occurred in stages, with the first cameras deployed in March
 253 2018 and the last cameras collected in March 2019 (Fig S1). The longest-running DEACs
 254 remained continuously active underwater from August 2018 to January 2019, a five-month
 255 interval, and were still operating at retrieval. Initial deployment of cameras in March 2018
 256 included one camera at the edge of a halo and a second camera pointed at the first in order
 257 to assess whether the presence of the camera and stand had any effect on the presence or
 258 behavior of marine animals. Given that no effects of camera presence were noted in this
 259 initial test, doubling of cameras in this manner was discontinued for future deployments,
 260 with the two cameras at each site positioned to monitor different benthic environments and
 261 unable to see each other. During the summer of 2018 (June to August), cameras were
 262 consistently checked every 1-2 weeks for leakage, algal overgrowth, or stand displacement.
 263 Cameras deployed at longer intervals from March to June 2018, August 2018 to January
 264 2019, and January to March 2019 were unmonitored during these periods in order to test
 265 long-term underwater function and determine the effects of biofouling on housings and
 266 image quality in the absence of cleaning or regular adjustments.

267

268 *Diver Observations*

269 In-water observations were conducted by a team of 2-3 divers at each camera site
 270 and at several additional locations in order to validate the camera's ability to detect fish
 271 and other animals. Observations consisted of all divers sitting directly behind each camera
 272 for 15 minutes and recording the presence and abundance of all fish and other animals

273 observed on the reef, in the halo, or in the grass to the genus or species level, when possible.

274 Divers faced forward toward the reef and recorded all fish observed within the halo or on

275 the reef itself, as this was the primary field of view of the camera. In the seagrass or

276 macroalgae, divers again faced toward the reef and recorded only fish that swam in front

277 of them and the camera. Divers remained stationary for the entire observation period at

278 each camera, and their presence did not have any observable effects on fish within the

279 camera's view, with multiple fish of different species swimming quite close to divers

280 during the observations. Fish species and counts were determined by a consensus of all the

281 divers present at each observation. A non-metric multidimensional scaling (NMDS)

282 analysis was run on species communities inside and outside of the halo using data from

283 diver observations at 20 camera locations and species counts from 54 additional images

284 taken in the 15-minute intervals before, during, and after the diver observations at 18 of

285 those locations. Only images from immediately before, after, and during diver observations

286 were used for comparison in order to control for natural variation in fish communities over

287 time, since the main goal of the comparison was to assess the ability of the cameras to

288 capture known community composition at a given location and time. All fish in this subset

289 of images were identified to the genus or species level by the same researchers who

290 conducted the in-water diver observations. To determine whether divers had any effect on

291 fish presence, counts from images captured before, during, and after diver observations

292 were compared using a nonparametric Friedman rank sum test and a Wilcoxon signed rank

293 test for pairwise comparisons. All analyses were conducted using R statistical software

294 version 4.0.3 (R Core Team 2020) with packages qdap (Rinker 2019), reshape (Wickham

295 2007), rstatix (Kassambara 2020), and vegan (Oksanen et al. 2018).

296 **Image Analysis**

297 *Image Sorting*

298 Images were initially named and sorted by location, time, and date using the
 299 camtrapR (Niedballa et al. 2016) package in R (R Core Team 2020). A subset of over
 300 13,000 images were sorted by trained undergraduate student volunteers into categories
 301 containing at least one visible fish (“Fish”) and without any visible fish (“NoFish”). To
 302 ensure consistency, all volunteers were initially trained on the same subset of ~300
 303 images drawn from multiple different cameras and their accuracy assessed by the
 304 research team before they were assigned a larger subset of images to sort individually.
 305 Due to the nature of timed rather than motion or heat triggered photos, many images did
 306 not contain fish.

307

308 *Model Choice*

309 In order to streamline future analyses of fish photos and identification and avoid
 310 manual redundancy in discriminating fish existence in pictures, we built and trained a
 311 Convolutional Neural Network (CNN) based on ImageNet pretrained ResNet-50 (He et al.
 312 2016), a deep residual network widely used in image classification. We chose ResNet as
 313 our base structure because we wanted conservative results in classifying fish pictures.
 314 ResNet is powerful at preventing overfitting, making it less likely to omit pictures
 315 containing fish. The reproducible code was implemented in Pytorch (He et al. 2016, Paszke
 316 et al. 2017, Howard et al. 2018) to identify images with animals (Fig 3).

317

Figure 3. Empty (left) and fish-filled (right) images captured at the same camera site within 24 hours. The empty or “NoFish” photo was assigned only a 0.09 probability of containing a fish by our ResNet-50 model, whereas the model predicted a 0.88 probability of the second photo containing at least one fish, hence its “Fish” designation. Probabilities like these were used to sort images into “Fish” and “NoFish” categories to streamline further analysis.

Training and Validation

Our model was trained on a sample of 10,727 images sorted by our team of trained volunteers and then run on 75,470 additional images to sort them into “Fish” and “NoFish” categories. To augment the training set, we preprocessed the fish images with spatial transformations, cropping and lightening variation, and used focal loss (Lin et al. 2017) as an objective function to address the problem of imbalanced labels.

Image Analysis

Images with a “Fish” probability of 0.4 or above were used to determine the relative presence of fish at camera sites inside and outside of the Half Moon Caye MPA. A cutoff of 0.4 was chosen based on the model’s reduced ability to correctly identify fish presence, compared to fish absence. This analysis of fish occupancy was conducted based on the

relative proportions of the total images classified that did or did not contain fish inside and outside of the MPA and at patch reef and seagrass/algae locations.

RESULTS

Camera Performance in the Field

Cameras and Housings

Housing 1 proved vulnerable to flooding at depths exceeding 4 m and prone to leaking even at shallower depths. This appears to be due primarily to the thin nature of Housing 1's walls and lid, which deformed substantially under pressure, breaking the epoxy seal with the lens and allowing water to enter. Housing 2 proved far more robust to pressure and had minimal leakage even at a maximum deployed depth of 7 m over multiple months. Further testing with this housing will be necessary to determine its maximum functional depth, but preliminary tests with a revised housing design have reached depths of 40 m.

The cameras themselves proved resilient to flooding and were typically still armed and taking photos when extracted from partially-flooded housings. However, many cameras recovered from flooded housings were unable to be redeployed due to lasting damage to their internal systems. Batteries were sufficient to power the cameras past the five month extraction date of our longest deployment, with all non-flooded cameras still displaying the starting battery status of "OK" (not "LOW" or "DEAD"). Maximum water temperature measured at any of our deployment sites, which could affect battery life, was 30° C (86° F). Cuddeback advertises that their cameras can operate up to 12 months continuously with efficient battery usage. Memory cards were

361 more than sufficient to store images on the schedule that they were collected during this
362 period (approximately 8.5 GB of images over 5 months), suggesting that image frequency
363 could be doubled or tripled in future deployments, assuming that processing of these
364 additional images is sufficiently streamlined with the use of computer vision or similar
365 techniques.

366

367 *Environmental Variability*

368 Different benthic environments and camera positioning affected the quality and
369 interpretability or classification of images. In shallow seagrass and macroalgal
370 environments, suspended organic matter in the water column reduced visibility,
371 especially at certain times of day under specific light conditions. Suspended organics may
372 also have contributed to high biofouling in these benthic environments (discussed below).
373 Camera orientation with regard to compass direction was varied between sites during
374 deployment, although both cameras at any given location were oriented in the same
375 direction. While visibility due to the direction and angle of sunlight varied throughout the
376 day at all locations, some orientations produced a greater number of poorly-lit images or
377 images with strong light reflection off of suspended particles in the water column,
378 reducing the overall image quality or number of usable images for those sites.

379

380 *Biofouling*

381 The most significant impediment to long-term camera function at our sites was
382 biofouling, the growth of marine organisms over the camera housing and stands. Image
383 quality declined rapidly due to biofouling, making fish identification impractical in as

384 little as one month depending on site conditions (Fig S2), with a median value of two
385 months endurance, although imagery from some cameras remained usable up to four or
386 five months after deployment. This biofouling decreased both fish detections in images
387 and the ability of our model to accurately classify images taken by biofouled cameras
388 (Fig S3, S4). Algal grazing by fish was an important factor reducing fouling on cameras
389 and stands placed near patch reefs, while cameras placed in seagrass or algae beds away
390 from patch reefs were overgrown with algae over the same deployment period that halo
391 cameras remained relatively unobstructed (Fig 4). The addition of antifouling boat paint
392 to the camera housings before the August 2019 deployment appeared to be only a minor
393 deterrent to organisms growing on the housing in general and did not prevent the camera
394 lens window from being almost completely obscured 2-3 months after deployment. In
395 addition to biofouling, camera function was also limited by reduced visibility at certain
396 sites, which varied based on local turbidity and light availability, and by depth.
397 Preliminary tests of a similar camera design in Hawai'i suggest that the extreme
398 biofouling observed at Lighthouse Reef is not representative of all such reef
399 environments and may be related to especially high productivity and suspended organic
400 matter in the water column at this location.

401

Figure 4. Comparison of biofouling and algal overgrowth of structures placed at the edge of the halo, adjacent to seagrass (left), and in middle of the surrounding seagrass (right) after a month. Similar results seen across all camera sites suggest that reef-based herbivores help to control algal growth both within and at the edges of the halo but do not graze heavily, if at all, on algae and related marine organisms in the surrounding algal or seagrass beds.

Image Classification and Accuracy

Of the 130,621 images collected, 88,899 were deemed usable (68%) based on a visual examination, despite some level of biofouling in many of these. Our ResNet-50-based model had an overall accuracy of 92.5% when classifying these images into “Fish” or “NoFish” categories, with higher accuracy in identifying empty or “NoFish” photos due to the increased number of these in the training dataset (Table 1).

Table 1. Accuracy of model predictions. Accuracy is determined by comparing the computer’s prediction for each image with the actual label of “Fish” (image contains at least one fish or similar animal) or “NoFish” (image is empty) assigned to the photo by a team of trained volunteers. The model was trained on 10,727 images classified by volunteers and then validated with an additional 2,702 human-sorted images, the results of which are shown in this table. Prediction accuracy is higher for “NoFish” (empty) images, likely due to the higher proportion of this type of image in both the training and validation datasets.

True Image Designation	Correct Predictions	Incorrect Predictions	Percent Accuracy (%)
<i>Fish</i>	444	165	72.9
<i>NoFish</i>	2057	36	98.3
All images	2501	201	92.5

Community Composition

Comparison with Diver Observations

Large compositional differences were identified between the halo/reef and seagrass/algae fish communities but no obvious difference between the communities constructed from diver species observations and those from camera images (NMDS; Fig 5), although individual images consistently contained fewer fish than were observed by divers during a 15-minute period at the same site (Fig S5). An ANOSIM conducted on the NMDS output showed a significant difference between the halo/reef and seagrass/algae communities ($R=0.66$, $p<0.001$), which was reflected in both the camera and diver species observations. Overall, there was a small but significant effect of time (before, during, or after diver presence) on fish counts (Friedman rank sum test $p=0.0089$, Kendall’s $W = 0.24$). Fish counts were significantly higher during diver observations compared to before (WSRT adj. $p=0.021$), but there were no significant differences between the before and after time points (WSRT adj. $p=0.83$) or during and after (WSRT

443 adj. $p=0.34$), which suggests that divers did not have a consistent measurable effect on
444 fish presence during these short observational periods.

445
446 **Figure 5.** Non-metric multidimensional scaling (NMDS) based on 20 diver observations
447 and an additional 54 camera images from the same sites. Points represent individual site
448 observations or images and are colored yellow for halo/reef cameras and dark green for
449 seagrass or algae cameras. ANOSIM of this NMDS output found a significant difference
450 between halo/reef (yellow) and seagrass/algae (green) communities ($R=0.66$, $p<0.001$).
451 Dots represent diver observations, while triangles represent camera images. Most image-
452 based points fall within the same area as those from diver observations, illustrating that
453 the cameras accurately captured the two different fish community types.
454

455 Fish Distributions

456 The fish detection counts based on camera data revealed that the proportion of
457 images with fish was 4.8 times higher in halos (0.38 ± 0.002) as compared to seagrass or
458 algae camera locations (0.08 ± 0.002). MPA status also had a significant effect, with an

18% increase in the proportion of photos with fish within the MPA (0.26 ± 0.002), compared to outside the MPA (0.22 ± 0.002). Detailed analysis of camera locations relative to both benthic cover (i.e. reef/halo or algae/seagrass) and protection status (inside or outside MPA) revealed that fish detection is higher in halos outside of the MPA, relative to inside, but lower in seagrass communities outside of the MPA, relative to inside (Fig 6).

Figure 6. Proportion of images containing fish at halo and grass/algae sites inside and outside of the Half Moon Caye MPA. Proportions calculated to two significant figures are indicated above each bar. Error bars represent ± 1 standard error of the mean from the binomial distribution (≤ 0.004).

A preliminary analysis of diver observations from 20 camera locations as well as an additional 60 images from those sites did not contain a single instance of an herbivorous reef fish (surgeonfish and all adult parrotfish except for *Sparisoma radians*) outside of a halo.

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DISCUSSION

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Camera Performance

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Deployment Duration and Function

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Underwater camera traps proved to be energy-efficient, durable, and capable of producing large volumes of quality images representative of the fish communities at their locations. The DEAC camera trap design is a reliable, cost-effective, and easy-to-implement solution allowing the expansion of terrestrial camera trapping techniques to shallow marine environments. The set-up can easily be used to vastly expand the capability of BRUVs and associated techniques (Cappo, Speare, & De'ath, 2004; Colton & Swearer, 2010; Brooks, Sloman, Sims, & Danylchuk, 2011), and can also provide marine observations over periods of months. In addition to being long-term and more scalable, un-baited camera traps such as these may be more accurate than BRUVs in their estimation of population and community composition (Mccoy et al. 2011) and allow the use of random encounter models for occupancy that are widely used with terrestrial camera traps (Rowcliffe et al. 2014).

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Camera placement and orientation is an important consideration when deploying DEACs in the field, and the ideal placement may vary with geographic location, season, target time of day, water quality, and shading from local structures like patch reefs or docks. The cameras have no observable effect on the behavior of marine animals and may therefore be used to document species that typically evade divers. Even cameras that are “cleaned” by herbivorous fish in the halo do not appear to attract any more attention than natural patches of algae or coral rubble. They are also capable of remaining

underwater at depth for long periods and recording high volumes of photo or video observations—our longest running cameras were deployed for 5 months, captured over 7,500 images each, and still had battery life to extend to a year. The exceptional duration and the ability to capture vast numbers of images, and to automatically recognize photos with fish (see below) gives the capability to not only provide a continuous record of rare species behaviors or visits by transient species that divers would miss or only observe by chance, but to also, for the first time, to record changes in behavior, relative abundance, and migrations across seasons and lunar phases.

Comparison to Existing Methods

DEACs offer significant advantages over existing underwater camera options, as well as surveys by divers. These underwater camera traps record similar data to that gathered by in-person observations, with a few notable exceptions. While the longer time interval chosen for our extended duration field tests did not capture as many individual fish in each image as divers recorded during the same 15-minute period corresponding to a single photo, the cameras did accurately capture the composition of the community during that time, with regard to both species presence and abundance (Fig 5). Analysis of synchronous diver and camera observations at different sites reflected obvious differences in community composition between different benthic environments. These compositional differences also support the placement of the halo and control cameras at each site, suggesting that the cameras were separated enough to capture these different adjacent community types while remaining close enough to control for local site conditions. The only group of animals observed by divers that were not well captured by

521 DEAC images were schools of roving juvenile fish and small parrotfish that camouflage
522 well within seagrass and algal environments and are best detected through movement.
523 The inability of the camera images and corresponding CNN to identify these fish may be
524 due to a combination of more limited image quality in these turbid environments and the
525 inability of human sorters (on whose data the CNN was trained) to distinguish these small
526 fish later in a static image. Since these species are neither significant grazers (in terms of
527 biomass consumed) nor threatening predators, their detection or inclusion in fish
528 community composition was relatively unimportant for addressing the question used here
529 to assess DEAC utility. However, for applications where detection of these species or
530 similarly small or cryptic organisms is important, use of short video clips in place of still
531 images (an option readily enabled with the DEAC design) could increase the ability of
532 both humans and machines to detect these animals through motion.

533 The current duration of camera operation is over an order of magnitude longer
534 than the operational duration achieved by other non-tethered underwater cameras (e.g.
535 Williams et al., 2014; Siddiqui et al., 2018), even with biofouling seriously impairing
536 image quality after 1-2 months (Fig S2). To the best of our knowledge, these are the first
537 underwater camera traps to be affordable, power-efficient (therefore deployable over the
538 span of months) and also self-contained, without the challenges imposed by a surface-
539 tethered external power source, which typically limits deployment in remote regions and
540 at multiple sites over large areas.

541

542 *Future Improvements*

543 The greatest immediate limitation to the camera design was the inability to
544 prevent or seriously reduce biofouling without periodic manual cleaning of the cameras,
545 although the magnitude of this challenge may be location-specific. Biofouling is a
546 common problem with unsupervised underwater monitoring equipment (Delauney &
547 Compère, 2009), with multiple solutions proposed to control it, including local
548 chlorination (Delauney & Compère, 2009; Xue et al., 2015), copper sheeting and mesh,
549 and UV radiation (Patil, Kimoto, Kimoto, & Saino, 2007). Ongoing tests of camera and
550 housing design are incorporating these methods to reduce biofouling by marine
551 organisms and extend the functional life of the lens window to better reflect the power
552 and storage capabilities of the camera.

553 While both the batteries and memory cards we employed were sufficient for the
554 deployment duration and image capture frequency tested, the inability to utilize memory
555 cards with greater than 32GB of storage in Cuddeback cameras is problematic with a
556 more frequent time lapse interval or in the case of short videos collected in place of single
557 images. Therefore, optimizing and expanding both power and data storage capacity of
558 these cameras via commercial means (cameras with larger SD storage capability) or
559 noncommercial modifications is another potentially valuable direction for future research.
560 For example, SD Ultra Capacity (SDUC) storage media currently affords 2 TB of
561 storage, vastly expanding the capability of underwater camera traps for either smaller
562 time intervals between images or multi-year deployments. Indeed, large storage capacity
563 may obviate the need for camera triggering, making time-lapse or video with on-board

564 object recognition a superior alternative, giving the ability to capture even rare or
565 transient species while effectively using the millions of potential images generated.

566 Design improvements currently in progress focus on reducing biofouling,
567 extending the depth range of the camera housings to over 50 m, and implementing an
568 external flash or other nighttime illumination.

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570 **Image Analysis**

571 The success of our initial image sorting using the CNN ResNet-50 illustrates the
572 power of machine learning and computer vision techniques to drastically reduce time and
573 cost when dealing with large image sets. Our ability to use this trained model to pre-sort
574 images with high accuracy before attempting further analysis via manual or autonomous
575 machine-learning based methods also reduces the cost of the most disadvantageous
576 aspect of our timed image capture method: the number of frames with no objects of
577 interest to the current study. Now that datasets obtained from this and similar shallow
578 marine environments can be easily sorted to exclude non-target images, future
579 underwater camera trap projects using a similar time-lapse method will be able to quickly
580 remove the majority of empty frames, while retaining the ability to measure frequency of
581 detection events and variations in fish presence by time of day, season, or other
582 environmental variables by comparison of occupied and empty images. Expansion of the
583 deep neural network model to focus on identification of individual species, functional
584 groups, and/or the sizes of different individuals, as has been done in similar image
585 analyses (Boom et al. 2014, Boussarie et al. 2016, Siddiqui et al. 2018, Norouzzadeh et
586 al. 2018), will further streamline the analysis of this and related large image datasets.

587 Our community composition analysis also demonstrates that the 15 minute photo
588 interval of our cameras was sufficient to capture species representative of the same fish
589 community observed by divers in the water. This suggests that while a single image does
590 not capture every fish active in the area during the 15 minute period it represents, the
591 collection of images from any given site are representative of the community at that
592 location and are likely to accurately reflect changes in species behavior, abundance, or
593 diversity at the site over a range of time scales (e.g. daily vs. seasonal changes). Further
594 study of camera captures vs. diver observations regarding species known to be wary of
595 divers, either those using traditional open-circuit SCUBA or closed-circuit rebreathers, is
596 an important line of future investigation to understand true reef fish occupancy and
597 abundance.

598 Our analysis of the number of images with fish collected at different groups of
599 cameras revealed a difference undetected by the fish counts from our diver observations,
600 showing that fish were detected by cameras more frequently (and are therefore likely to
601 have higher occupancy) in halos outside of the MPA, while fish were detected in seagrass
602 or algal habitats more frequently inside of the MPA. The results of this apparent
603 interaction between benthic cover and protected status illustrate the complexity of
604 patterns and variation within the benthos and the fish communities at Lighthouse Reef.
605 Further image analysis and modeling may help to distinguish the underlying causes of
606 such variation. The inability of traditional diver surveys alone to detect these differences
607 at all reinforces the value of spatially-distributed, long-term datasets like the images
608 collected from our cameras. The observed differences in fish detection between halo and
609 grass/algae control sites also reinforce diver observations of both less fish and a different

610 fish community in the algae or seagrass beds away from the reef and support the results
611 of the community composition analysis (Fig 5).

612

613 **Case-Study and Future Applications**

614 We obtained a large volume of usable images from sites with a variety of depths
615 and benthic cover types, subjected to different fishing pressures inside and outside of a
616 local MPA, and monitored over the course different seasons. This allows us to reasonably
617 conclude that our observations are likely representative of fish presence and behavior at
618 patch reef sites within Lighthouse Reef Atoll as a whole. The complete lack of grazing
619 reef fish observed outside of the halo region by cameras located in surrounding sea grass
620 within 30 m or less of the halo supports the idea that a predator modification of prey fish
621 behavior imposes real constraints on fish movement and that heightened grazing pressure
622 adjacent to reef structures is not simply the result of fish randomly dispersing with
623 distance from the reef. If the latter were true, the pattern would be a simple exponential
624 decrease in fish as distance from the patch reef increased, which would likely be reflected
625 in a lower (but nonzero) number of grazing fish detected at seagrass and algae camera
626 locations, compared to those at the halo edge. An alternative hypothesis is that the lack of
627 grazing fish appearing in images taken outside of the halo is due to unequal detection of
628 fish between the two environments, possibly the result of faster or more furtive
629 movements outside the relative safety of the halo. However, this explanation is refuted by
630 two pieces of evidence: First, diver observation also showed no herbivorous reef fish at
631 grass or algal camera sites, and, second, other fish species that were observed by divers to
632 move quickly through the seagrass or algal environment (e.g. bar jacks, *Caranx ruber*)

633 appear in both halo and control camera images, indicating that cameras placed in the
634 grass are very capable of photographing fish moving through that environment. It is
635 therefore more likely that the complete lack of detection of reef-based grazers outside of
636 the halo, even though their food is in much higher supply there, is due to their total or
637 near-total absence from this environment because of the combined lack of shelter and
638 exposure to predators.

639 This study demonstrates the value of long-term, spatially-distributed underwater
640 camera trap observations for addressing a subtle difference in fish communities and
641 benthic pattern generation. DEACs can be easily deployed alone or in large spatial arrays
642 for short or extended time periods, and they are capable of recording periodic still images
643 for long-term studies or short videos for detailed behavioral observations. Most
644 importantly, these cameras are highly energy-efficient and require little-to-no
645 maintenance while deployed, making them ideal for remote locations or extended
646 observations that surface-anchored systems or commercial underwater cameras with
647 limited battery life are not suitable for. Multiple networks of camera traps like TEAM
648 (Beaudrot et al. 2016) and Snapshot Serengeti (Norouzzadeh et al. 2018) have been
649 successfully deployed over large regions in terrestrial environments, and DEACs offer
650 the option to now expand such long-term, spatially-extensive monitoring efforts to the
651 marine realm. The use of a CNN makes processing the volume of images collected over
652 such a long-term study a practical option, and continuing advancements in machine
653 learning and computer vision are likely to enable further processing of similar large
654 visual datasets in the future.

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AUTHOR CONTRIBUTIONS

671 SB and MS conceived the ideas and designed the camera trap methodology. BX and VPP
672 designed and trained the machine learning model. SB, AS, and MS collected the data. SB
673 and BX analyzed the data. All authors contributed to the drafts and gave final approval
674 for publication.

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