Journal of Experimental Marine Biology and Ecology 535 (2021) 151490

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

HotSpotter: Using a computer-driven photo-id application to identify sea turtles

Stephen G. Dunbar [a,b,c,*], Edward C. Anger [d], Jason R. Parham [e,f], Colin Kingen [e], Marsha K. Wright [a,b], Christian T. Hayes [a,b,g], Shahnaj Safi [h], Jason Holmberg [e], Lidia Salinas [b,c], Dustin S. Baumbach [a,b]

[a] *Marine Research Group, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350, United States of America*
[b] *Protective Turtle Ecology Center for Training, Outreach, Research Inc. (ProTECTOR, Inc.), Loma Linda, CA 92350, United States of America*
[c] *Protective Turtle Ecology Center for Training, Outreach, Research – Honduras (ProTECTOR - Honduras), Tegucigalpa, Honduras*
[d] *ScubaTed, Roatán, Honduras*
[e] *WildMe, Portland, OR 97217, United States of America*
[f] *Rensselear Polytechnic Institute, Troy, NY 12180, United States of America*
[g] *Division of Coastal Sciences, School of Ocean Science and Engineering, University of Southern Mississippi, Ocean Springs, MS 39564, United States of America*
[h] *School of Public Health, Loma Linda University, Loma Linda, CA 92350, United States of America*

A R T I C L E I N F O

Keywords:
Marine turtles
Photo identification
Computer-automated algorithms
Sea turtle database management

A B S T R A C T

Photo identification (PID) in animal studies has been a widely used method for identifying individuals of many species based on unique natural markings and patterns. The use of PID has facilitated investigations in which residency, home ranges, and growth rates have been assessed. However, many PID studies in the past have relied heavily on manual photo matching. More recently, computer-assisted PID programs have been used to identify individuals of different sea turtle species, and reduced time investment in identifying individuals within specific populations. Still, some computer-based PID programs require significant time investment in ensuring photos are captured at consistent angles and lighting conditions, pre-processing image manipulations, and post-processing manual matching confirmation of potential matches provided by the program. For PID to be an effective time and money saving mechanism for wildlife research and conservation, these common drawbacks need to be addressed with a computer-assisted PID program that reduces manipulation and time investment burden, and consistently provides accurate and reliable results. In this study, we evaluated the accuracy of matching individual face images using the HotSpotter (HS) PID program by building a database of 2136 images of hawksbill (*Eretmochelys imbricata*) turtles, then querying the database with 158 new images to find matches for individual turtles. Overall, we found that with almost no pre-processing manipulation, and with images from highly variable underwater conditions, qualities, and angles, HS correctly matched individuals in the first choice 80% of the time, increasing to 91% in the first six choices. When assessing in-water images only, accuracy for matching increased from 84% in the first choice, to 94% by the sixth choice. We suggest that the integration of HS technology into a global, web-based PID system will increase the ability to remotely identify individual marine organisms on a global scale, and improve usability for community scientists who may have little to no technical training.

1. Introduction

The use of photo-identification (PID) in animal research is well established and has been demonstrated to provide valuable information on individual animal movements, growth rates, and species population status (Riley et al., 2010). This is because natural markings and color patterns may both be stable over several life history stages (Carpentier et al., 2016; Van Horn et al., 2014), and unique to individual animals within a population (Gardiner et al., 2014; Vaissi et al., 2018), unlike physical tags or marks placed on individual animals by researchers. As a result, various PID techniques have been used to re-identify and track individual animals over time, including manual visual comparisons of photographs, and the use of a number of computer-assisted PID programs and processes. Several studies have used one or more of these

* Corresponding author at: Loma Linda University, Griggs Hall, 11065 Campus St., Loma Linda, CA 92350, United States of America.
E-mail address: sdunbar@llu.edu (S.G. Dunbar).

https://doi.org/10.1016/j.jembe.2020.151490
Received 23 April 2020; Received in revised form 21 September 2020; Accepted 3 November 2020
Available online 18 November 2020

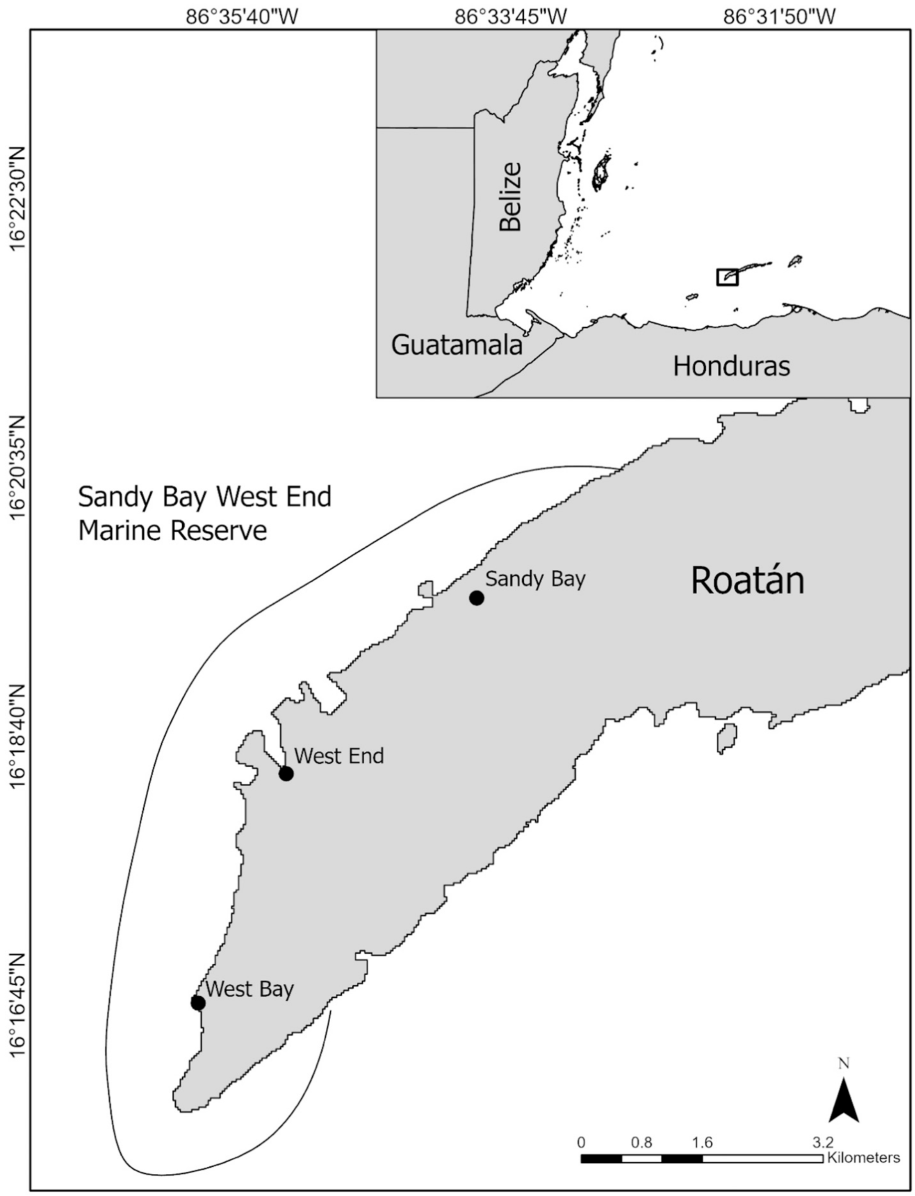

Fig. 1. Map of study area in the Sandy Bay West End Marine Reserve (SBWEMR), Bay Islands, Honduras. The black line indicates the approximate area of the SBWEMR and the inset shows the regional location of Roatán.

techniques in work with terrestrial species, such as reptiles (Gardiner et al., 2014; Knox et al., 2013; Sacchi et al., 2010; Sreekar et al., 2013), felids (McClintock et al., 2013), ursids (Anderson et al., 2010; Anderson et al., 2007), African equids (Rubenstein et al., 2018), and rhinocerids (Jewell et al., 2001), as well as dozens of marine species, such as whale sharks (Graham and Roberts, 2007; Holmberg et al., 2008; Holmberg et al., 2009; Riley et al., 2010), sharks (Towner et al., 2013), whales (Blackmer et al., 2000; Frasier et al., 2009), seals (Karlsson et al., 2005), seadragons (Martin-Smith, 2011), lionfish (Chaves et al., 2016), and several marine invertebrates (Gallardo-Escarate et al., 2007; Gosselin et al., 2007; Raj, 1998).

PID in sea turtle research is relatively new and has only recently been reported as a useful tool for the identification and conservation of sea turtle species. Possibly the first use of PID in sea turtle research was reported in 1996 by McDonald and Dutton (1996) on matching unique pineal spots on the heads of leatherback turtles (*Dermochelys coriacia*). In 1998, Richardson et al. (2000) reported manually matching videos of green turtles (*Chelonia mydas*) in Hawaii with a small number ($n = 93$) of facial scale photographs. Recently, several sea turtle studies have also used manual visual matching of photographs to understand nesting female remigration patterns (Chew et al., 2015; Valdés et al., 2014), examine population sex ratios (Su et al., 2015) and long-term differences in intersexual survival rates (Schofield et al., 2020), investigate hatchling scale pattern stability over time (Carpentier et al., 2016; Chew et al., 2015), identify individual turtles in their foraging grounds over time (Dunbar et al., 2014; Lloyd et al., 2012; Schofield et al., 2008; Su et al., 2015), and estimate flipper tag loss (Reisser et al., 2008). However, for PID investigations using manual methods, both the time and financial commitment to retrieve, assess, and determine positive matches through manual visual comparisons becomes prohibitive as the number of photographs in a database increases (Dunbar et al., 2014; Jean et al., 2010). Recent advances in computer algorithms have facilitated partial automation of PID in sea turtle research, allowing for ease in identification of individual sea turtles over time within a single study area (Carter et al., 2014; Chassagneux et al., 2013; Dunbar and Ito, 2015; Dunbar et al., 2014; Jean et al., 2010), identification of dead turtles (Long, 2016), and the identification of scale-less leatherback turtles during nesting (McDonald and Dutton, 1996; Pauwels et al., 2008).

There are, however, consistent drawbacks in the use of computer-assisted PID across animal studies. Several authors have suggested that automated matching can be hindered by the use of low-quality photographs in the computer database. For example, in her study of cheetahs over a 25-year period, Kelly (2001) found that up to 33% of matches were unreported, and also discovered matching accuracy decreased when poor quality images were used. Long (2016) found that while using the NaturePatternMatch (NPM) pattern recognition software (Stoddard et al., 2014), poor-quality underwater photos of sea turtles often resulted in no matches. Therefore, these results necessitated that new photos be manually compared with all other photos to determine if the animals had a match in the database. Likewise, Carter et al. (2014) and Calmanovici et al. (2018) suggested that using images with excessive blur, lighting changes, angle differences, and low visibility can hinder the association of images within computer PID software. Another drawback of several computerized PID programs is the requirement to utilize photographs taken from consistent angles and distances relative to the subject. For example, Chaves et al. (2016) reported that only photos of lionfish (*Pterois volitans*) taken consistently at right angles to the flank of the animals were used for identification with I^3S Pattern PID software (Den Hartog and Reijns, 2014), and that matching accuracy could be affected by photo angle variations. Similarly, Calmanovici et al. (2018) found that photos taken of turtles underwater at different angles, distances, and in different light conditions reduced the accuracy of matches using I^3S Pattern. Likewise, Long and Azmi (2017) were able to more successfully identify individual turtles through NPM if photos were taken at horizontal and vertical angles $<45^\circ$ from where face scales were visible. In a more recent study, Steinmetz et al. (2018) also found photographs taken at high vertical or horizontal angles usually resulted in poorer potential matches among photographs of nesting hawksbill (*Eretmochelys imbricata*) turtles on Mahé Island in the Seychelles. The difficulty of consistently photographing marine animals with little variation from a perpendicular angle is increased due to highly variable marine conditions at both temporal and spatial scales during diving or snorkeling.

As an additional challenge, Carter et al. (2014) described adequate software and computing power as potential limitations because of the need to analyze many thousands of photograph pixels, especially if assessing color patterns is important in providing matches. The fact that many computer-assisted PID programs require laborious preprocessing manipulations of each photograph before new photographs can be queried or matched against the photo database (Calmanovici et al., 2018; Carter et al., 2014; Chaves et al., 2016; Dunbar et al., 2014; Jean et al., 2010; Pauwels et al., 2008) means that both manual input time and expense to identify individuals increase correspondingly with increased photo entry requirements.

If PID software is to be both effective at matching individual animals, and useful for general utility by both trained scientists and community scientists, it would be best to effectively reduce or eliminate the factors that are consistently reported as drawbacks in PID studies. Reducing or eliminating these drawbacks may help decrease manipulation time and requirements for extensive user training, as well as increase tolerance to low quality data that includes varied viewpoints and photographic conditions, ultimately improving PID software for analyzing low-quality photos from a variety of angles and lighting regimes. These features are especially important if animals are to be photographed within a marine environment in which it may be nearly impossible to repeatedly photograph the animal in similar light conditions and from the same angle.

The purpose of this study was to evaluate the accuracy of the computerized PID program, HotSpotter (HS) (Crall et al., 2013) that requires almost no photographic manipulations (Dunbar et al., 2017). HS works by localizing and matching Scale-Invariant Feature Transform (SIFT) (Lowe, 2004) keypoints using the Local Naïve Bayes Nearest Neighbor (McCann and Lowe, 2012) search algorithm. We aimed to determine if turtles within an open population of juvenile hawksbills in a marine protected area could consistently be identified over a period of years from photographs taken with different photographic devices, and in variable in-, and out-of-water conditions, including lighting, angle, and annual differences.

2. Methods and materials

2.1. Study site

Our study site was within the boundaries of the Sandy Bay West End Marine Reserve (SBWEMR) on the western end of the island of Roatán, Honduras (16°20′24″N, 86°19′48″W). Roatán is the largest of the three Bay Islands with a straight-distance length of approximately 46 km, and is located approximately 52 km north of mainland Honduras (Fig. 1). The SBWEMR is a locally governed marine protected area (MPA) covering approximately 13 km of coral reefs and mangroves between the towns of West Bay and Sandy Bay. Specific details on benthic habitat in the SBWEMR are provided in Hayes et al. (2017) and Baumbach et al. (2019).

2.2. Turtle measurements and photo collection

From June to September over 2014–2019, we conducted daily in-water observations of hawksbills in the SBWEMR using SCUBA, and by following and photographing turtles during as much of each dive as possible. During in-water surveys, we collected photographs of left and right facial scale patterns, dorsal head scale patterns, and general full-body photographs of hawksbill turtles at 49 dive sites using a variety of underwater cameras (see Supplementary Table 1). All underwater photos were captured in different visibility conditions, and at random angles to turtles at a distance of 1–6 m. These methods are further detailed in Dunbar et al. (2008) and Hayes et al. (2017). Photographs collected by researchers during 2006–2011 and 2014–2018 were used to establish the photographic database with HS, while photographs collected by a collaborator during 2016–2019 were added to the database and used to test if matching photographs existed. During 2016–2019, out-of-water photographs of turtles were also taken after they were hand captured, during the process of measuring and weighing. Appropriate out-of-water photographs of the left and right sides of the face and dorsal surface of the head, were also used to populate and initialize the HS database. Photographs from all years were taken of juvenile hawksbills (with the exception of one sub-adult male in 2017) found within the boundaries of the SBWEMR. Furthermore, several hundred photographs were submitted by community scientists through an openly available web-based GIS mapping system (Baumbach and Dunbar, 2017), and were likewise used to establish the photo-database.

To further aid in our identification of hand captured turtles, we applied uniquely coded Inconel (681 Style; Archie Carr Center for Sea Turtle Research, Gainesville, FL, USA) flipper tags to the large proximal scale located on the front right flipper of each hand-captured juvenile hawksbill within the SBWEMR from 2016 to 2019. In addition, we also collected morphometric data for each turtle, including curved carapace length (CCL), curved carapace width (CCW), and weight. For those turtles that were not hand-captured, we collected in-water photographs during focal follows using SCUBA. Photographs were taken of the dorsal head surface and both sides of the face from as many angles as possible, as well as flipper tags, if present. Tag numbers were kept in a flipper tag database that could be cross-referenced with matched turtle photographs from HS.

2.3. Using HotSpotter

To standardize photo names within the HS database, we labeled photographs with the code L (Left), R (Right), and T (Top) for the left side of the face, right side of the face, and dorsal surface of the head, respectively. We initially labeled all photographs of the same animal

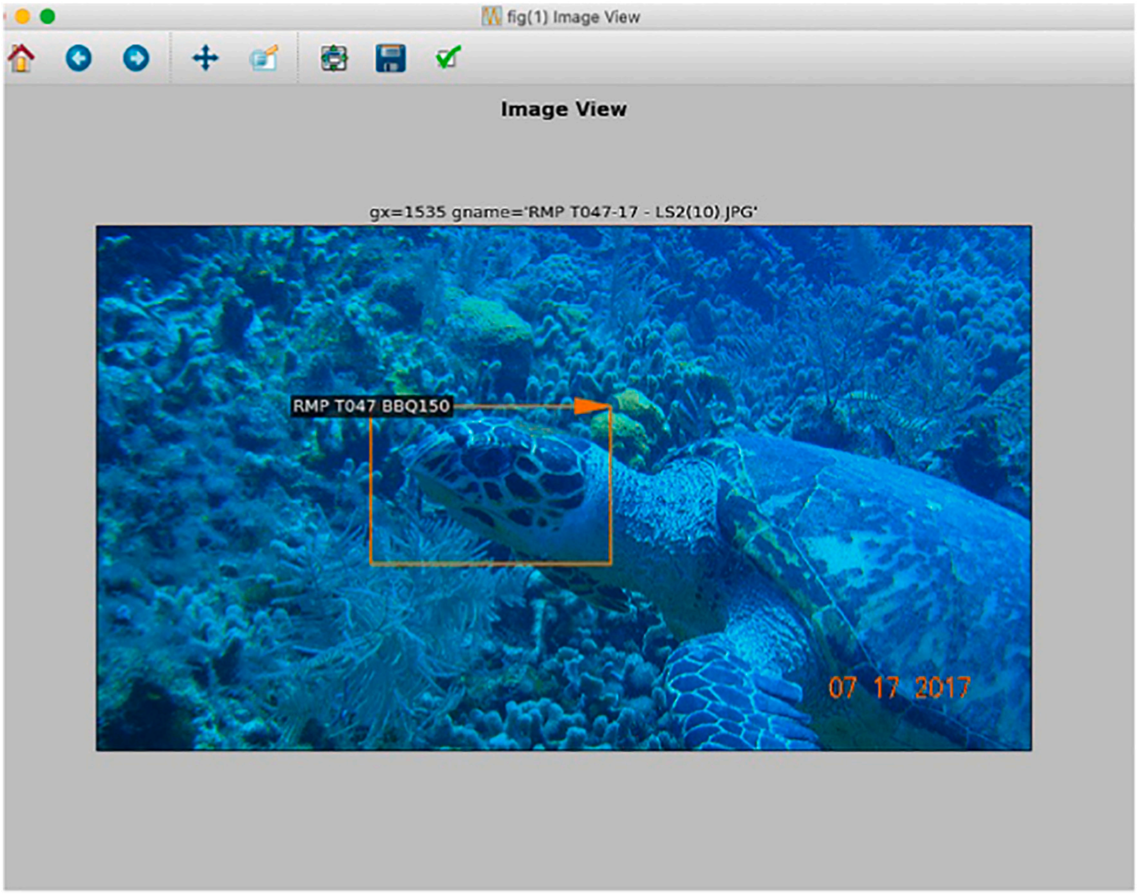

Fig. 2. An example of a "chip" made by placing digital spots on the image to the upper right and lower left of the area of interest in the image. This chip directs HS to ignore all aspects of the image that lie outside the area of interest.

with that animal's unique Turtle Identification Number (TIN) with the additional identifier of L, R, or T. These photographs were selected to be placed in a HotSpotter Turtles (HST) file folder. On opening the HS program, we selected the HST folder for the program to reference and upload all photographs in the HST folder. To create and add to the initial HS database queue, each photograph was individually selected from within HS and a chip made to select the area of the photograph the computer was to view (Fig. 2). This chip was made by adding two digital spots in horizontally and vertically opposing positions on the photograph, which were then automatically converted by the program to an 'area of interest' box, with all other information outside of this box ignored by HS. The majority of these chips required no manual manipulation, with the exception of occasionally orienting photographs to standardize head or face position within the chip. However, this entire chip creation and annotation process has recently been automated (Parham et al., 2018) through the implementation of HS into the Wildbook open source platform (Berger-Wolf et al., 2017).

Once chips were created for each image in the database, we ran queries to compare the selected image against all other photographs to determine if a match existed for an individual's top, left, or right side, thus building a series of photographs of the same animal. If multiple L, R, or T photographs were queried through HS, we labeled them with consecutive numbers (i.e. TIN035_R1; TIN035_R2, etc.). These photographs helped HS to analyze and recognize unique features of individual turtles from multiple angles and with photographs from different cameras, distances, underwater lighting, and visibility conditions.

When new photographs of turtles were acquired, we ran a query to determine if a match existed to an individual already within the database. A match score for each query image is computed by summing the similarity scores for each of its extracted Scale-Invariant Feature Transformed (SIFT) features against its nearest neighbor matched from the database. HS aggregates all closest matches for each annotation by performing a random sample consensus (RANSAC)-based spatial verification algorithm to filter out poor correspondences, then re-ranks the results.

2.4. Photo conditions for HotSpotter analysis

We conducted a subjective assessment of HS using a variety of hawksbill image angles and qualities to provide a description of successful match conditions. To assess image angles, we randomly selected images of two individual hawksbills (RMP T047 and RMP T110) from the test database that were taken of either the right or left side of the head and successfully matched to previous images already present in HS. We then selected two additional images of the same two individuals that presented large variations in angles of the right or left sides of the head (relative to the test photo) that had previously resulted in successful matches. It was beyond the scope of our study to assess specific angles between the camera and hawksbill, or between the test image and database image. To assess photo quality, we searched HS to find low-quality chips that were either blurry with little to no facial scute definition, and at the same time did not successfully match to any images in the database (RMP T050), or were semi-blurry with some definition, yet successfully matched images (RMP T054 and RMP T055). We then compared low-quality chips (presented at 72 dpi) to high-quality chips (presented at 180 or 350 dpi) of the same individual that were able to produce successful matches.

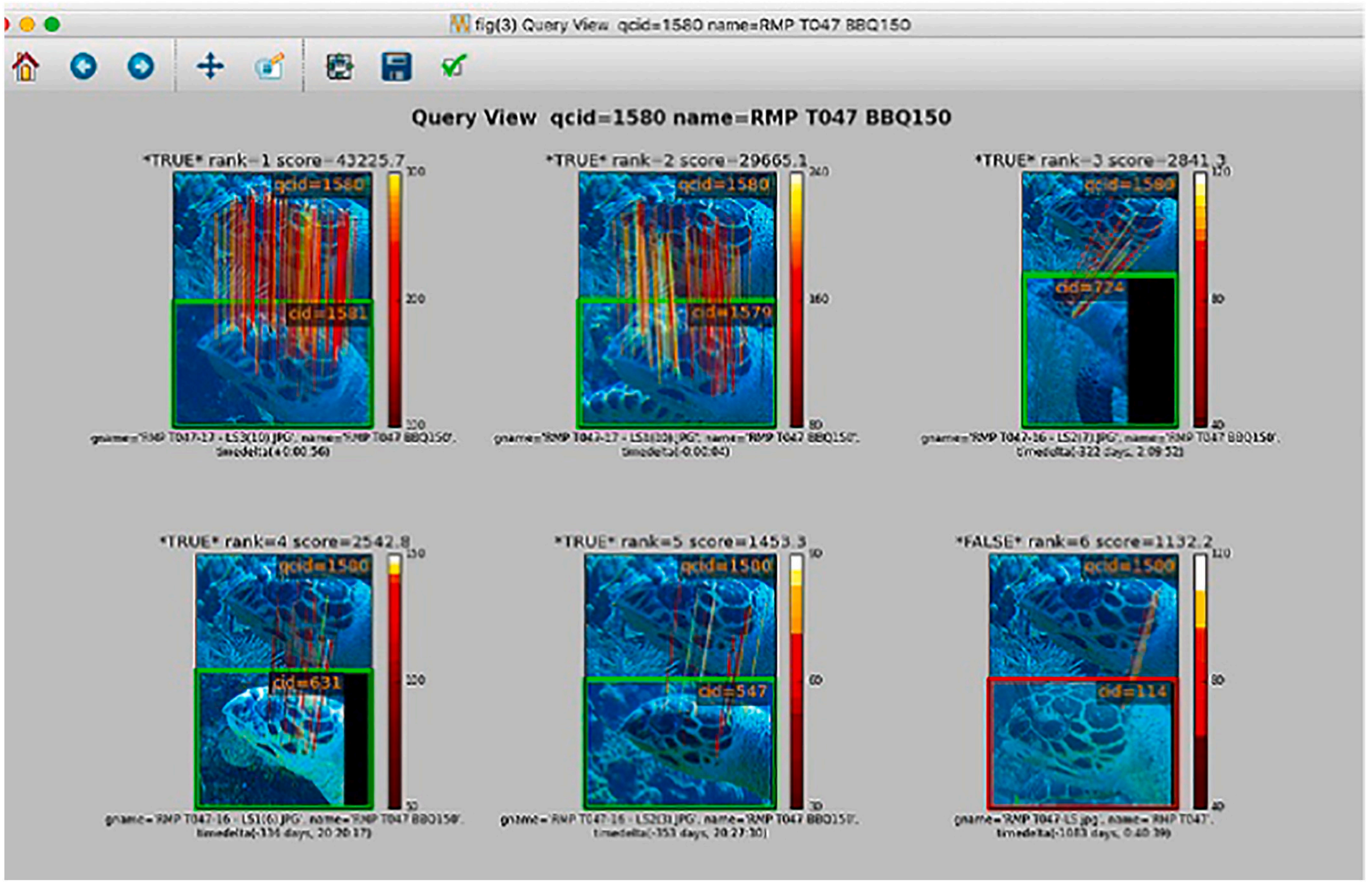

Fig. 3. The best six results of individual matches provided by HS after a query photo is run against the photo database. Match scores are used to rank the potential matches from first position (highest score = highest ranked match) to sixth position (lowest score = lowest ranked match) in descending order. Photos are queried by assigning the photo a chip identification (cid) and then querying that cid (qcid) against other cids already stored in the database. Note that in this example, the first five match choices are annotated with a '*TRUE*' label, as well as a green box around the matched image from the database, while the sixth choice is annotated with a '*FALSE*' label and a red box around the potential matched image from the database. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.5. HotSpotter vs flipper tag matching tests

To evaluate the accuracy of HS, we conducted a two-way blind test by sending photos of the R, L, and T of tagged turtles among authors. Only the sending author knew the tag numbers of photographed turtles, which were then verified by the receiving authors by choosing the best match from six HS result choices. As a default, HS is programmed to display only the six choices most likely to match the photo being queried. A report of queried turtle tag numbers was then provided to the sending author for confirmation of turtle identification.

2.6. Statistical analyses

All statistical analyses were done in SAS 9.4 (SAS Institute, Cary NC) and R 3.5 (R Core Team, 2018). Frequencies and percentages of correct matches were calculated for each of the default six potential matches provided by HS. Stratified frequencies and percentages of correct matches were also calculated for potential matches within in-water, out-of-water, and side of the turtle (i.e. right, left, and dorsal side) categories. Descriptive statistics (mean and standard deviation) were also computed for the calculated scores of all potential matches. The calculated scores for all potential matches were provided by HS and were analyzed to determine if a consistent cut-off score could be calculated for a true first choice match. Identifications provided by HS for each individual were evaluated for sensitivity and specificity by comparison to the positive ID made through the flipper tag associated with each turtle. The flipper tag number was then matched to the ID provided by HS in the first six matches. To calculate the cut-off score based on the first-choice match, we assessed sensitivity and specificity of test photo matches at each potential cut-off score, and selected the score that maximized sensitivity and specificity.

3. Results

In its default output, HS returns a panel of six potential matches ranked from the most likely (highest score) to the least likely (lowest score) positive match (Fig. 3). Scores are calculated based on both the number of similar features and the degree of similarity between the test photo and the database photos. Lines between the two photographs indicate matched features according to the similarity of that feature in both photographs. A color scale is provided with each output to show the similarity strength of each feature (Fig. 4).

We queried a total of 158 hawksbill images from within the SBWEMR against 2136 target hawksbill images in our HS photo database. Of these, 86.1% were in-water photographs, while 13.9% were out-of-water photographs. Table 1 provides the overall number of right, left, and top (dorsal) photos presented for matching, as well as the main matching results. When all 54 test photos of the right side (including in-water and out-of-water) were combined, HS accurately matched test photos 81.5% of the time in the first choice, increasing in cumulative accuracy to 96.3% by the sixth choice. We found left side matches were slightly less accurate (Table 1). When all left side test photos (including

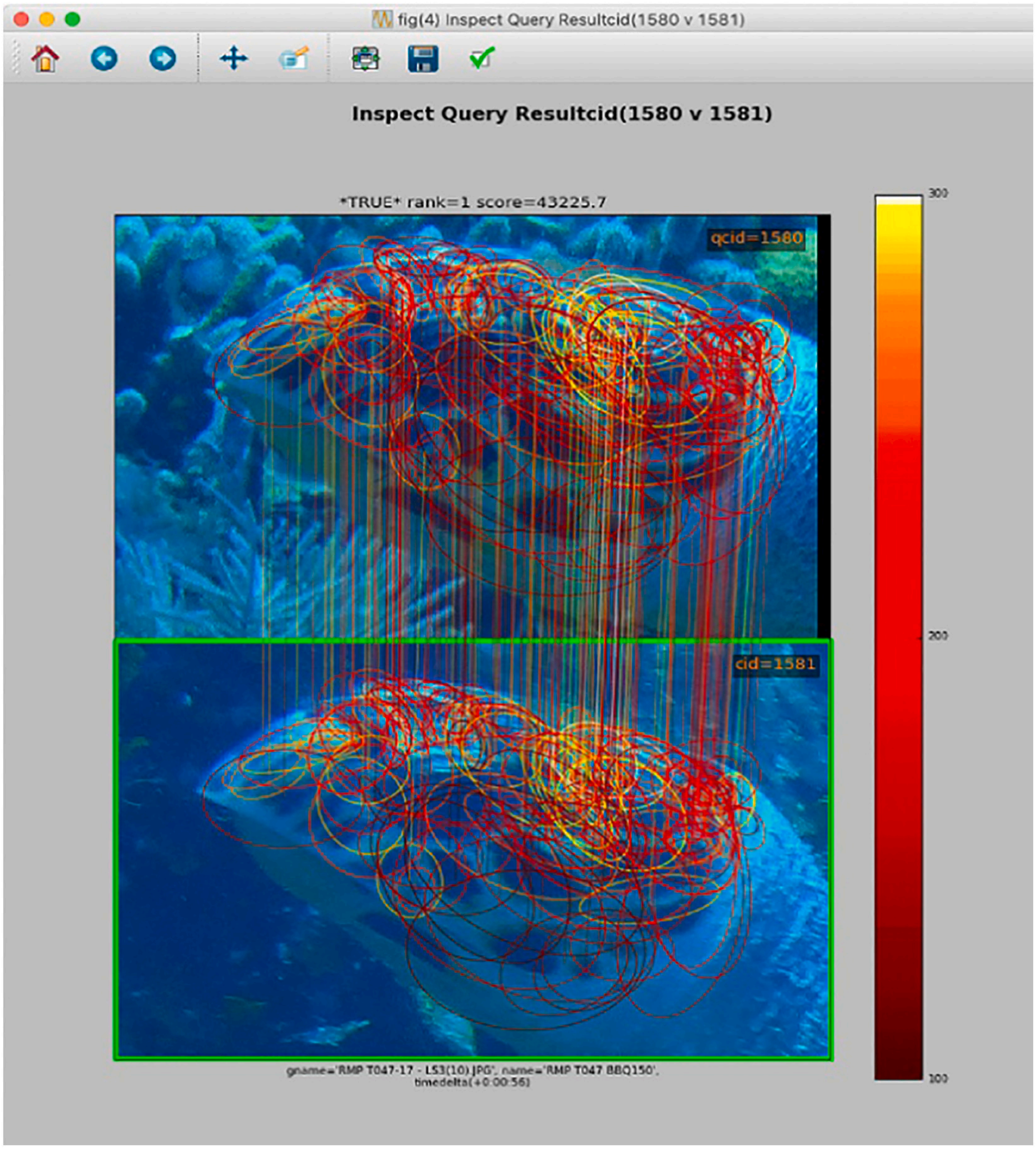

Fig. 4. A high score, first-choice match showing line indications of similarly matched features between the query image (top) and the matched image from the database (bottom). Line colors from dark red to bright yellow (in the color score bar to the right of the images) indicate increasing similarity strength scores (from 100 to 300 in this example) of each matched feature. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
The number of test photos of each side of the head along with the percentage of photos that were taken in-water or out-of-water. First-choice percentage represents the percentage of photos that were correctly matched in the first results and sixth choice represents a correct match in any of the six results.

Side	n	In-Water (%)	Out-of-Water (%)	First Choice (%)	Sixth Choice (%)
Right	54	83.3	16.7	81.5	96.3
Left	53	84.9	15.1	77.4	88.7
Top	51	90.2	9.8	80.3	88.2

in-water and out-of-water) were combined, HS increased cumulative accuracy from 77.4% in the first choice to 88.7% by the sixth choice. Of the 51 dorsal head photos tested, 90.2% were in-water, with 9.8% out-of-water. Correct matches by HS increased cumulatively from 80.3% in the first choice to 88.2% by the sixth choice.

Table 2
The numbers and percentages of matches and non-matches within a stepwise choice selection for six possible choices.

Choice number	n (%)	
	Match	Not matched
Only first choice match	126 (79.8%)	32 (20.3%)
First two choice matches	136 (88.1%)	22 (13.9%)
First three choice matches	139 (88.0%)	19 (12.0%)
First four choice matches	140 (88.6%)	18 (11.4%)
First five choice matches	143 (90.5%)	15 (9.5%)
First six choice matches	144 (91.1%)	14 (8.9%)

When evaluating HS only with in-water photos ($n = 136$), we found a high degree of match accuracy, from 83.8% in the first choice, to 94.1% by choice number six. Matching accuracy was lower when HS was evaluated with the 22 out-of-water photographs. Matching accuracy started at only 54.6% with the first choice, and increased to only 72.7%

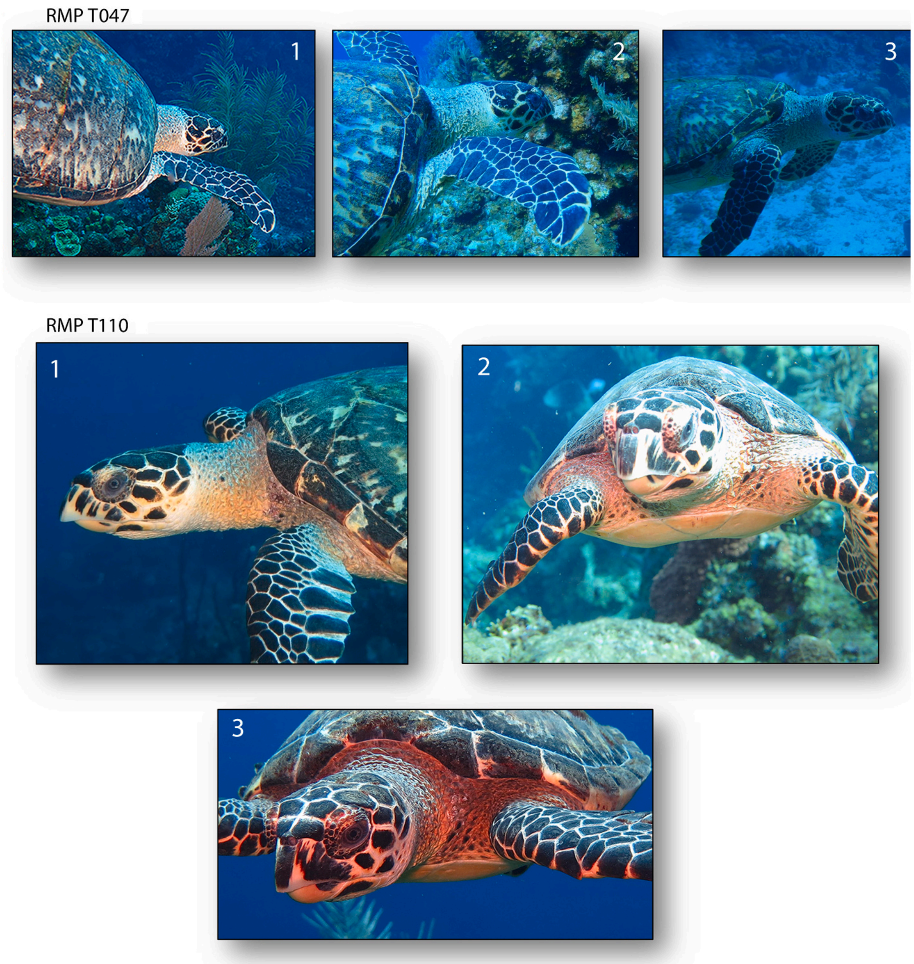

Fig. 5. Examples of photo angle variations for the turtles RMP T047 and RMP T110. In both cases, photo 1 was the test photo for both RMP T047 and RMP 110, respectively. Photos 2 and 3 are previously captured photos that show wide variances in vertical and horizontal angles that resulted in successful matches when queried respectively. Additionally, we note the variation in brightness, color, and conditions among photos that nevertheless resulted in successful matches of the right side for RMP T047, and the left side for RMP T110.

by the sixth match choice.

Overall, when we considered the cumulative match percentages across all images (face views, head views, and in- and out-of-water), HS was able to correctly match test photos 79.8% of times in the first choice and up to 91.1% of times within the first 6 choices presented to the user. Table 2 provides cumulative stepwise matches for the six choices, ranging from first choice only, to all six choices.

Our qualitative analyses of image angle variances demonstrated that HS was capable of consistently identifying individual turtles even when substantial differences in both horizontal and vertical angles exist among captured images (Fig. 5). Matching power is known to decline with severity of the angular difference according to the limitations of the underlying Scale-Invariant Feature Transformed (SIFT) algorithm, which is roughly estimated at 50% match probability loss at 50 degrees (Lowe, 2004). This is sufficient tolerance for our real-world application. In Fig. 6, we present two variations of low-quality (blurry, 72 dpi) verses high-quality (clear, 180 or 350 dpi) images that were tested in HS. We found that only the lowest-quality, blurry images in which individual scutes were indistinguishable were unable to be matched by HS. In contrast, HS was able to correctly match moderately blurry images (Fig. 6).

On analyzing the match scores for all six HS choices (which ranged from 0 to 51,009), the average scores ranged from 5438.3 (first choice) to 575.6 (sixth choice) (Fig. 7). A cut-off value of 1850 (lower than the average score) for the first-choice match provided the most optimal accuracy (84.2%), sensitivity (84.1%), and specificity (87.5%) values. As the cut-off value decreased from the mean score, sensitivity increased from 31.0 to 86.5%, while specificity decreased from 100 to 78.1% (Fig. 8).

4. Discussion

The HotSpotter photo ID software has a configurable number of matches it will return for a query. In this study, we used the default output of only six potential matches. We found the limited number of the default output of this program to be a distinct advantage over other programs, such as I^3S that provide tens to hundreds of possible match outcomes that potentially require further manual verification or rejection (Calmanovici et al., 2018; Dunbar et al., 2014; Sacchi et al., 2010). In a recent study on face recognition of 118 in-water photos of 32 greens and 1 hawksbill by Calmanovici et al. (2018) they found I^3S Pattern correctly matched 86% of images within the top 20 ranked photos, with 48% ($n = 56$) of these matched in the first position. In comparison, we found HotSpotter to have a higher correct matching result of 94% for in-water test images within the 6 matches of the default output, with 84% of these matches in the first-choice position.

Results appear to be similarly accurate for left, right, and top images, although left images had slightly lower cumulative match percentages in the first choice. These differences in match scores are likely due to small differences in image viewpoints, due to data variance.

We found matching accuracy was lower with photos taken out-of-water than in-water. In contrast, Dunbar et al. (2014) found good matching results using I^3S Classic for a small set of turtle tests using out-of-water photos, but stated that the program was reliant on photos taken from similar angles and in similar light and distance conditions. Those authors also used a relatively small database of approximately 600

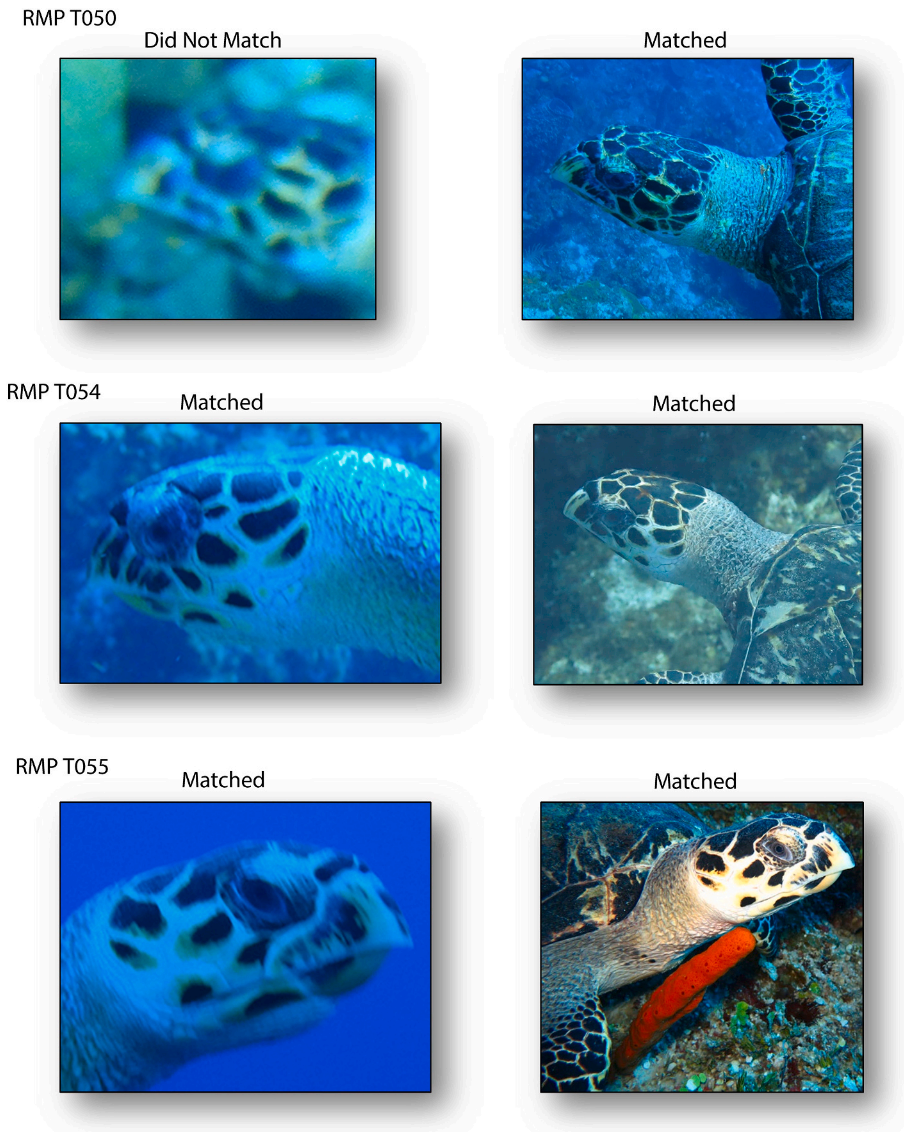

Fig. 6. Examples of photo quality and resolution. Photo quality varied widely, from slight to extreme blurriness. Only extremely blurry photos (RMP T050) were not able to be matched in HotSpotter. Photo resolution varied from 72 to 350 dpi. Although match success was higher with high-quality photos, HotSpotter was also able to match low-quality photos with minimal individual facial scute definition.

photographs and only tested images of two turtles. Likewise, several studies report that matching accuracy of I^3S decreased, or was likely to decrease when variability in photo angle, light, and distance (typical variability of in-water conditions) were factors (Calmanovici et al., 2018; Chaves et al., 2016; Sacchi et al., 2010). We found HS able to consistently match images that had relatively wide variations in individual or combined horizontal and vertical angles. Additionally, HS was able to take advantage of even low-quality, blurry images to make successful matches of individual turtles, although we found very low-quality images which do not provide any scute definition are unable to be accurately matched. These features provide valuable advantages of HS over other PID processing software in that images collected during highly variable in-water conditions (including pitch and roll of both the photographer and the turtle) are useful for both populating the database, as well as reducing limitations on correctly matching individuals.

In contrast to results by Calmanovici et al. (2018), our current results show greater accuracy with the highly variable conditions of photos taken in-water than those taken out-of-water. It is highly likely that with an increased number of out-of-water photos taken in variable angle, light, and distance conditions, accuracy of out-of-water matching would greatly improve. Crall et al. (2013) also found that HS matching accuracy improved when numbers of photos per individual zebra increased.

Match scores provided by HS represent a sense of visual similarity between the query image and the background image. In general, the scores for a match will be higher when: 1) there are few but very similar features between the two images and/or 2) there are very many, but weakly similar features. Both conditions could signify a potential match. The advantage of these scores is that they can be used to calculate a cut-off value for the first choice match (score of 1850), above which the accuracy is 84% that the first-choice is a true match. Although we sought a cut-off value only for the first-choice match to be able to minimize the need to review all other potential matches, users may be able to calculate cut-off scores for any match choice position available.

4.1. Conclusion

In this study we have demonstrated the highly accurate matching of hawksbill photos in both in-water and out-of-water conditions with the nearly fully automated HotSpotter PID program. HotSpotter is based on proven feature extractors that are robust to scale, illumination, and in

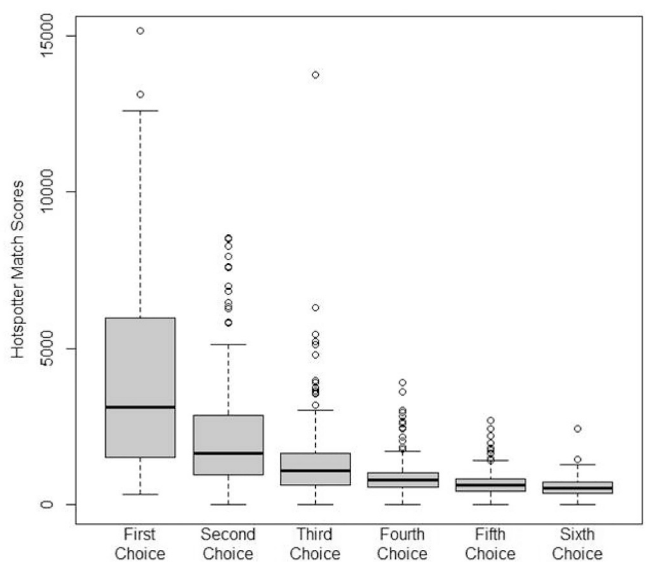

Fig. 7. Boxplots showing the minimum and maximum HS match scores along with the median and interquartile range for the top 6 match choices.

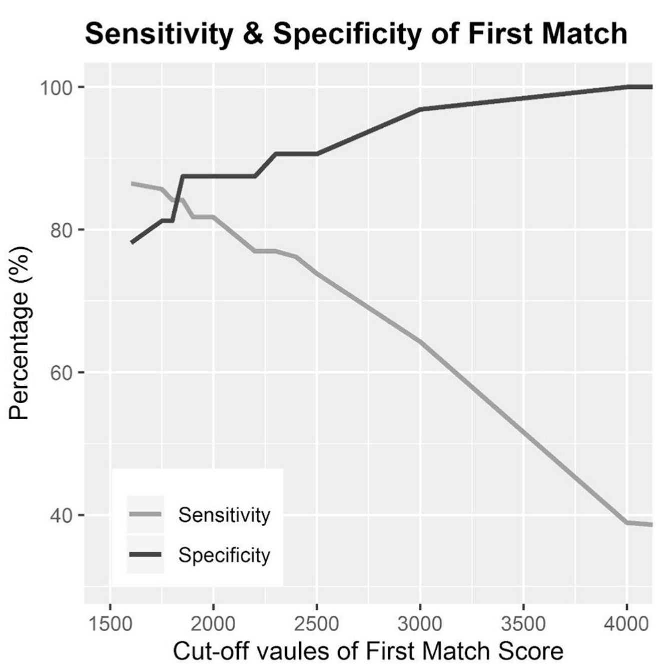

Fig. 8. A plot of sensitivity and specificity values used to identify optimal cut-off values for first choice match scores.

some cases, mild distortions, and variations in quality and photo angle, making it an ideal candidate for finding high-quality matches. Additionally, HotSpotter, unlike some computer-based PID programs, benefits from a suite of post-processing algorithms to reduce obvious false matches, reduce the importance of background textures not belonging to an animal, and intelligently rank the best matches for the user to review. This is an obvious and important advantage if photos are to be gathered by community scientists who contribute their images to research projects, or if photos are harvested from Internet sources. The integration of HS into the Wildbook-based Internet of Turtles[1] (Berger-Wolf et al., 2017; Leslie et al., 2015) is likely to increase the potential for remotely identifying individuals of all marine turtle species on a global scale. As a result, these technologies are likely to spawn new mechanisms for tracking individuals, furthering our understanding of sea turtle movements and habits, gathering information on population dynamics, and highlighting population hotspots for future investigations.

Some investigators have recognized the potential limitations of computing power to analyze PID datasets (Carter et al., 2014). We also concede there are additional factors to be considered when running PID programs on different forms of hardware. However, we suggested that while challenges to computing hardware power are likely to be resolved in the near future, the more systemic challenge both now and in the future, will be the development of more robust algorithms that are able to maintain matching accuracy while assessing very large photo databases (i.e. >100,000 images). Nevertheless, with additional advances in computer processing and software-specific developments, there will doubtless be new developments in the application of computer-driven PID for ever-widening suites of marine taxa.

CRediT authorship contribution statement

Stephen G. Dunbar: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing. **Edward C. Anger**: Conceptualization, Methodology, Investigation, Writing - review & editing. **Jason R. Parham**: Software, Writing - review & editing. **Colin Kingen**: Software, Writing - original draft, Writing - review & editing. **Marsha K. Wright**: Investigation, Writing - review & editing. **Christian T. Hayes**: Conceptualization, Methodology, Writing - review & editing. **Shahnaj Safi**: Formal analysis. **Jason Holmberg**: Software, Writing - review & editing. **Lidia Salinas**: Conceptualization, Methodology, Writing - review & editing. **Dustin S. Baumbach**: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing.

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.

Acknowlegements

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. We wish to extend our deepest thanks to ProTECTOR, Inc. Interns: Tori Bolin, Mark Oliinik, Walker Johnson, Miranda Wredberg, Zoe Aguila, Ashley Morrow, and Ashlyn Lewis, and ProTECTOR, Inc. Volunteers: Razvan Orban, Voicu and Sebastian Tulai, who assisted with gathering photographs of turtles. We are grateful to the citizen-scientists who submitted photographs through the TURT smartphone app and the Roatán web-based map, including Leah Pomedli, Joachim Muth, Tom Gillham, Gregory Phillips, Christopher Torres, Kathy O'Hara, Ofri Weiss Lipshitz, Marion Hinoux, Shelley Armas, Lisanne Sweere, Kevin Bates, Ronald Halley, Sanae Halley, Brian McGuire, and Kal Lin. Thanks to the members of the Marine Research Group (LLU) and to three anonymous reviewers, all of whom provided many thoughtful comments and suggestions for improving the manuscript. We are especially grateful to Rafael Brioso, Paulo Shikanai, Kathy Berner, and their dive team at Splash Inn for their continuing support for sea turtle research and conservation in the Bay Islands of Honduras. This is Contribution No. 36 of the Marine Research Group (LLU) and Contribution No. 18 of ProTECTOR, Inc.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.

[1] https://iot.wildbook.org

org/10.1016/j.jembe.2020.151490.

References

Anderson, C.J.R., Roth, J.D., Waterman, J.M., 2007. Can whisker spot patterns be used to identify individual polar bears? J. Zool. 273, 333–339. https://doi.org/10.1111/j.1469-7998.2007.00340.x.

Anderson, C.J.R., Da Vitoria Lobo, N., Roth, J.D., Waterman, J.M., 2010. Computer-aided photo-identification system with an application to polar bears based on whisker spot patterns. J. Mammal. 91, 1350–1359. https://doi.org/10.1644/09-MAMM-A-425.1.

Baumbach, D.S., Dunbar, S.G., 2017. Animal mapping using a citizen-science web-based GIS in the Bay Islands, Honduras. Mar. Turt. Newsl. 152, 16–19.

Baumbach, D.S., Anger, E.C., Collado, N.A., Dunbar, S.G., 2019. Identifying Sea turtle home ranges utilizing citizen-science data from novel web-based and smartphone GIS applications. Chelonian Conserv. Biol. 18 (2), 133–144. https://doi.org/10.2744/CCB-1355.1.

Berger-Wolf, T.Y., Rubenstein, D., Stewart, C.V., Holmberg, J.A., Parham, J., Menon, S., Crall, J., Van Oast, J., Kiciman, E., Joppa, L., 2017. Wildbook: Crowdsourcing, Computer Vision, and Data Science for Conservation. Bloomberg Data for Good Exchange Conference, Illinois, pp. 1–8.

Blackmer, A.L., Anderson, S.K., Weinrich, M.T., 2000. Temporal variability in features used to photo-identify humpback whales (*Megaptera novaeangliae*). Mar. Mamm. Sci. 16, 338–354. https://doi.org/10.1111/j.1748-7692.2000.tb00929.x.

Calmanovici, B., Waayers, D., Reisser, J., Clifton, J., Proietti, M., 2018. I^{3}S pattern as a mark-recapture tool to identify captured and free-swimming sea turtles: an assessment. Mar. Ecol. Prog. Ser. 589, 263–268. https://doi.org/10.3354/meps12483.

Carpentier, A.S., Jean, C., Barret, M., Chassagneux, A., Ciccione, S., 2016. Stability of facial scale patterns on green sea turtles Chelonia mydas over time: a validation for the use of a photo-identification method. J. Exp. Mar. Biol. Ecol. 476, 15–21. https://doi.org/10.1016/j.jembe.2015.12.003.

Carter, S.J.B., Bell, I.P., Miller, J.J., Gash, P.P., 2014. Automated marine turtle photograph identification using artificial neural networks, with application to green turtles. J. Exp. Mar. Biol. Ecol. 452, 105–110. https://doi.org/10.1016/j.jembe.2013.12.010.

Chassagneux, A., Jean, C., Bourjea, J., Ciccione, S., 2013. Unraveling behavioral patterns of foraging hawksbill and green turtles using photo-identification. Mar. Turt. Newsl. 137, 1–5.

Chaves, L.C.T., Hall, J., Feitosa, J.L.L., Côté, I.M., 2016. Photo-identification as a simple tool for studying invasive lionfish *Pterois volitans* populations. J. Fish Biol. 88, 800–804. https://doi.org/10.1111/jfb.12857.

Chew, V.Y.-C., Liew, H.-C., Joseph, J., 2015. Photographic identification of green turtles (*Chelonia mydas*) at Redang Island, Malaysia. Mar. Turt. Newsl. 146, 1–6.

Crall, J.P., Stewart, C.V., Berger-Wolf, T.Y., Rubenstein, D.I., Sundaresan, S.R., 2013. HotSpotter – Patterned species instance recognition. In: 2013 IEEE Workshop on Applications of Computer Vision (WACV), Florida, pp. 230–237.

Den Hartog, J., Reijns, R., 2014. I^{3}S Pattern manual – Interactive Individual Identification System. www.reijns.com/i3s/downloads/I3S%20Pattern.pdf.

Dunbar, S.G., Ito, H.E., 2015. Picture perfect: Photography for hands-off turtle monitoring. In: The State of the World's Sea Turtles (SWOT), 10, pp. 10–11.

Dunbar, S.G., Salinas, L., Stevenson, L., 2008. In-water observations of recently-released juvenile hawksbills (*Eretmochelys imbricata*). Mar. Turt. Newsl. 121, 5–9.

Dunbar, S.G., Ito, H.E., K, B., Dehom, S., Salinas, L., 2014. Recognition of juvenile hawksbills *Eretmochelys imbricata* through face scale digitization and automated searching. Endanger. Species Res. 26, 137–146. https://doi.org/10.3354/esr00637.

Dunbar, S.G., Baumbach, D.S., Wright, M.K., Hayes, C.T., Holmberg, J., Crall, J.P., Berger-Wolf, T.Y., Stewart, C.V., 2017. HotSpotter: less manipulating, more learning, and better vision for turtle photo identification. In: 37th Annual Symposium on Sea Turtle Biology and Conservation, Nevada, p. 77.

Frasier, T.R., Hamilton, P.K., Brown, M.W., Kraus, S.D., White, B.N., 2009. Sources and rates of errors in methods of individual identification for North Atlantic Right Whales. J. Mammal. 90, 1246–1255. https://doi.org/10.1644/08-MAMM-A-328.1.

Gallardo-Escarate, C., Goldstein-Vasquez, J., Thiel, M., 2007. Individual identification of decapod crustaceans I: color patterns in rock shrimp (*Rhynchocinetes typus*). J. Crustac. Biol. 27, 393–398. https://doi.org/10.1651/S-2773.1.

Gardiner, R.Z., Doran, E., Strickland, K., Carpenter-Bundhoo, L., Frère, C., 2014. A face in the crowd: a non-invasive and cost effective photo-identification methodology to understand the fine scale movement of eastern water dragons. PLoS One 9, e96992. https://doi.org/10.1371/journal.pone.0096992.

Gosselin, T., Sainte-Marie, B., Sevigny, J.M., 2007. Individual identification of decapod crustaceans II: natural and genetic markers in snow crab (*Chionoecetes opilio*). J. Crustac. Biol. 27, 399–403. https://doi.org/10.1651/S-2771.1.

Graham, R.T., Roberts, C.M., 2007. Assessing the size, growth rate and structure of a seasonal population of whale sharks (*Rhincodon typus* Smith 1828) using conventional tagging and photo identification. Fish. Res. 84 (1), 71–80. https://doi.org/10.1016/j.fishres.2006.11.026.

Hayes, C.T., Baumbach, D.S., Juma, D., Dunbar, S.G., 2017. Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area. J. Sustain. Tour. 25, 1–17. https://doi.org/10.1080/09669582.2016.1174246.

Holmberg, J., Norman, B., Arzoumanian, Z., 2008. Robust, comparable population metrics through collaborative photo-monitoring of whale sharks *Rhincodon typus*. Ecol. Appl. 18, 222–233. https://doi.org/10.1890/07-0315.1.

Holmberg, J., Norman, B., Arzoumanian, Z., 2009. Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. Endanger. Species Res. 7, 39–53. https://doi.org/10.3354/esr00186.

Jean, C., Ciccione, S., Talma, E., Ballorain, K., Bourjea, J., 2010. Photo-identification method for green and hawksbill turtles - first results from Reunion. Indian Ocean Turtle Newsl. 11, 8–13.

Jewell, Z.C., Alibhai, S.K., Law, P.R., 2001. Censusing and monitoring black rhino (*Diceros bicornis*) using an objective spoor (footprint) identification technique. J. Zool. 254 (1), 1–16. https://doi.org/10.1017/S0952836901000516.

Karlsson, O., Hiby, L., Lundberg, T., Jüssi, M., Jüssi, I., Helander, B., 2005. Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. AMBIO 34, 628–634. https://doi.org/10.1579/0044-7447-34.8.628.

Kelly, M.J., 2001. Computer-aided photograph matching in studies using individual identification: an example from Serengeti cheetahs. J. Mammal. 82 (2), 440–449. https://doi.org/10.1644/1545-1542(2001)082<0440:CAPMIS>2.0.CO;2.

Knox, C.D., Cree, A., Seddon, P.J., 2013. Accurate identification of individual geckos (*Naultinus gemmeus*) through dorsal pattern differentiation. N. Z. J. Ecol. 37, 60–66.

Leslie, A., Hof, C., Amoracho, D., Berger-Wolf, T.Y., Holmberg, J., Stewart, C.V., Dunbar, S.G., Jean, C., 2015. The Internet of Turtles. The State of the World's Sea Turtles (SWOT), 11, pp. 12–13.

Lloyd, J.R., Maldanado, M.A., Stafford, R., 2012. Methods of developing user-friendly keys to identify Green Sea turtles (*Chelonia mydas* L.) from photographs. Int. J. Zool. 2012, 1–7. https://doi.org/10.1155/2012/317568.

Long, S.L., 2016. Identification of a dead green turtle (*Chelonia mydas*) using photographic identification. Mar. Turt. Newsl. 150, 4–6.

Long, S.L., Azmi, N.A., 2017. Using photographic identification to monitor sea turtle populations at Perhentian Islands Marine Park in Malaysia. Herpetol. Conserv. Biol. 12, 350–366.

Lowe, D.G., 2004. Distinctive image features from scale-invariant keypoints. Int. J. Comput. Vis. 60 (2), 91–110. https://doi.org/10.1023/b:visi.0000029664.99615.94.

Martin-Smith, K.M., 2011. Photo-identification of individual weedy seadragons *Phyllopteryx taeniolatus* and its application in estimating population dynamics. J. Fish Biol. 78, 1757–1768. https://doi.org/10.1111/j.1095-8649.2011.02966.x.

McCann, S., Lowe, D.G., 2012. Local Naive Bayes Nearest Neighbor for image classification. In: 2012 IEEE Conference on Computer Vision and Pattern Recognition, Rhode Island, pp. 3650–3656.

McClintock, B.T., Conn, P.B., Alonso, R.S., Crooks, K.R., 2013. Integrated modeling of bilateral photo-identification data in mark–recapture analyses. Ecology 94, 1464–1471. https://doi.org/10.1890/12-1613.1.

McDonald, D.L., Dutton, P.H., 1996. Use of PIT tags and photoidentification to revise remigration estimates of leatherback turtles (*Dermochelys coriacea*) nesting in St. Croix, U.S. Virgin Islands, 1979-1995. Chelonian Conserv. Biol. 2, 148–152.

Parham, J., Crall, J., Rubenstein, D., Holmberg, J., Berger-Wolf, T., Stewart, C., 2018. An animal detection pipeline for identification. In: 2018 IEEE Winter Conference on Applications of Computer Vision (WACV), California, pp. 1–9.

Pauwels, E.J., de Zeeuw, P.M., Bounantony, D.M., 2008. Leatherbacks matching by automated image recognition. In: Perner, P. (Ed.), Advances in Data Mining. Medical Applications, E-Commerce, Marketing, and Theoretical Aspects. Springer, Berlin, Heidelberg, pp. 417–425.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raj, L., 1998. Photo-identification of *Stichopus mollis*. SPC Beche-de mer Inf. Bull. 10, 29–31.

Reisser, J., Proietti, M., Kinas, P., Sazima, I., 2008. Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. Endanger. Species Res. 5, 73–82. https://doi.org/10.3354/esr00113.

Richardson, A., Herbst, L.H., Bennett, P.A., Bennett, U.K., 2000. Photo-identification of Hawaiian green sea turtles. In: Eighteenth International Sea Turtle Symposium. National Marine Fisheries Service, Sinaloa, México, p. 316.

Riley, M.J., Hale, M.S., Harman, A., Rees, R.G., 2010. Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. Aquat. Biol. 8, 145–150. https://doi.org/10.3354/ab00215.

Rubenstein, D., Parham, J., Stewart, C., Berger-Wolf, T., Holmberg, J., Crall, J., Mackey, B., Funnel, S., Cockerill, K., Davidson, Z., Mate, L., Nzomo, C., Warungu, R., Martins, D., Ontita, V., Omulupi, J., Weston, J., Anyona, G., Chege, G., Kimiti, D., Tombak, K., Gersick, A., Rubenstein, N., 2018. The State of Kenya's Grevy's Zebras and Reticulated Giraffes: Results of the Great Grevy's Rally 2018 (Technical Report). Grevy's Zebra Trust, Nairobi, Kenya, p. 7.

Sacchi, R., Scali, S., Pellitteri-Rosa, D., Pupin, F., Gentilli, A., Tettamanti, S., Cavigioli, L., Racina, L., Maiocchi, V., Galeotti, P., Fasola, M., 2010. Photographic identification in reptiles: a matter of scales. Amphib.-Reptil. 31, 489–502. https://doi.org/10.1163/017353710X521546.

Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., 2008. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. J. Exp. Mar. Biol. Ecol. 360, 103–108. https://doi.org/10.1016/j.jembe.2008.04.005.

Schofield, G., Klaassen, M., Papafitsoros, K., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2020. Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. Ecology 101, e03027. https://doi.org/10.1002/ecy.3027.

Sreekar, R., Purushotham, C.B., Saini, K., Rao, S.N., Pelletier, S., Chaplod, S., 2013. Photographic capture-recapture sampling for assessing populations of the Indian gliding lizard *Draco dussumieri*. PLoS One 8 (2), e55935. https://doi.org/10.1371/journal.pone.0055935.

Steinmetz, K., Webster, I., Rowat, D., Bluemel, J.K., 2018. Evaluating the software I3S pattern for photo-identification of nesting hawksbill turtles (*Eretmochelys imbricata*). Mar. Turt. Newsl. 155, 15–19.

Stoddard, M.C., Kilner, R.M., Town, C., 2014. Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. Nat. Commun. 5, 4117. https://doi.org/10.1038/ncomms5117.

Su, C.-M., Huang, C.-T., Cheng, I.J., 2015. Applying a fast, effective and reliable photographic identification system for green turtles in the waters near Luichiu Island, Taiwan. J. Exp. Mar. Biol. Ecol. 467, 115–120. https://doi.org/10.1016/j.jembe.2015.03.003.

Towner, A.V., Wcisel, M.A., Reisinger, R.R., Edwards, D., Jewell, O.J.D., 2013. Gauging the threat: the first population estimate for white sharks in South Africa using photo identification and automated software. PLoS One 8, e66035. https://doi.org/10.1371/journal.pone.0066035.

Vaissi, S., Farassat, H., Akmali, V., Sharifi, M., 2018. Consistency of coloriation pattern and applicability of photo identification method as a tool to identify Kaiser's mountain newt, *Neurergus kaiseri*. Russ. J. Herpetol. 25, 311–321. https://doi.org/10.30906/1026-2296-2018-25-4-311-321.

Valdés, Y.A., Ricardo, J.A., Trelles, F.B., Abad, O.E., 2014. First assay of photo-identification in marine turtles' nesting population. Rev. Investig. Mar. 32, 43–51.

Van Horn, R.C., Zug, B., LaCombe, C., Velez-Liendo, X., Paisley, S., 2014. Human visual identification of individual Andean bears *Tremarctos ornatus*. Wildl. Biol. 20 (5), 291–300. https://doi.org/10.2981/wlb.00023.