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REPORT

Black spot syndrome in reef fishes: using archival imagery and field surveys to characterize spatial and temporal distribution in the Caribbean

Franziska Elmer[1] · Zachary F. Kohl[2,3] · Pieter T. J. Johnson[4] · Rita B. J. Peachey[1,5]

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Abstract Recently, observations of black spot syndrome (BSS) in Caribbean fishes have been linked to infection by a digenean trematode parasite, *Scaphanocephalus expansus*. Recently, This study examined the distribution of BSS over multiple spatial and temporal scales: at the island scale in Bonaire, Dutch Caribbean, using field surveys of 4885 fish belonging to three species, and across the wider Caribbean through analysis of 2112 images from Google Images searches (1985–2013). The field surveys in Bonaire indicated that the prevalence (% of individuals affected with BSS) and intensity (severity of BSS measured in 3 stages) were highest in *Acanthurus tractus* (prevalence 61.8%, including 30.1% in stage 3) followed by *Sparisoma aurofrenatum* (prevalence 48.3%, 24.1% in stage 3) and lowest in *Caranx ruber* (prevalence 38.5%, 3.3% in stage 3). Prevalence and intensity of BSS decreased significantly with survey depth (e.g., 2 m: prevalence 68.0%, 22.0% in stage 3; 18 m: prevalence 36.2%, 4.0% in stage 3) and were significantly lower in 2012 than in 2017 (prevalence: 59.3% in 2012, 68.7% in 2017; stage 3: 16.3% in 2012, 25.1% in 2017). The Southeast of Bonaire had significantly lower prevalence of BSS (16.4%) than the other four regions and lower intensity (11.7% in stage 3) than all regions but the Southwest. The Google Images searches querying for ocean surgeonfish, *A. tractus* and *A. bahianus*, identified pictures from 26 wider Caribbean locations; BSS was detected in 14 locations of which 13 were new, with the first detection dating back to 1985 in Bonaire. The Southern Caribbean had significantly higher prevalence of BSS (78.1%) than other ecoregions (0–34.6%), and Bonaire was identified as a hotspot, highlighting the utility of mining websites for archival imagery to quantify spatial and temporal patterns in disease phenomena. This study demonstrates how visible signs of parasite infection can be used to find differences in parasite prevalence and loads on a reef, island and sea scale.

Keywords Parasite · Google Images searches · Marine · Trematode · Bonaire · Picture mining · Osprey · Skin discoloration

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✉ Franziska Elmer
franziskaelmer@hotmail.com

1 CIEE Research Station Bonaire, Kralendijk, Bonaire, Caribbean Netherlands, The Netherlands

2 Department of Biological Sciences, University of North Texas, Denton, TX 76203, USA

3 Chamberlain University, Irving, TX 75063, USA

4 Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

5 Institute for Sustainable Technology, Kralendijk, Bonaire, Caribbean Netherlands, The Netherlands

Introduction

Parasites contribute significantly to the biodiversity of coral reefs, which harbor more species per square meter than any other ecosystem (Knowlton et al. 2010). Because many parasites have multiple host species, their transmission and fitness are closely interwoven with different components of the food web, being both influenced by changes in host population densities and eliciting changes in their host populations (Lafferty 1992; Skorping and Högstedt 2001; Marcogliese 2002; Dunne et al. 2013; Luong et al. 2014; Welicky et al. 2017). Despite their frequent omission from studies of marine food webs

(Lafferty et al. 2008), parasites are involved in an estimated 75% of all food web links (Dobson et al. 2008). Parasites can further affect the commercial value of fisheries (Timi and Mackenzie 2015), influence patterns of human health (Olson 1986) and function as biological indicators of pollution (Vidal-Martínez and Wunderlich 2017) or stock identification (Herrington 1939; Mosquera et al. 2003). However, the identity and distribution of marine parasites, as well as their consequences for hosts and food webs, remain comparatively understudied.

In coral reef ecosystems, patterns of parasitism have been shown to vary as a function of host identity, ecological habitat and spatial scale (Artim and Sikkel 2013; Sikkel et al. 2018; Santos and Sikkel 2019). Within the Caribbean region, *Haemohormidium*-like blood parasites in damselfishes (Pomacentridae) have low host specificity within the genus *Stegastes* and are more abundant in the Southern Caribbean, typically rare or absent in *Stegastes* species from the northern boundaries of the region (Florida Keys and the Bahamas) (Sikkel et al. 2018). On the scale of individual reefs, parasite abundance varies along reef profiles of only a few hundred meters and among adjacent reef habitats with high or low live coral cover. For blue tangs (*Acanthurus coeruleus*), a lower load of capsalid monogeneans was found at sites with higher coral cover (Sikkel et al. 2009). Gnathiid parasites were also less prevalent in areas dominated by live coral compared to dead coral (Artim and Sikkel 2013; Santos and Sikkel 2019). The Blackeye thicklip wrasse (*Hemigymnus melapterus*) had greater abundance of the monogenean ectoparasite, *Benedenia* sp., on the shallow reef flat compared with *H. melapterus* found deeper on the reef slope (Grutter 1998). Similarly, Sikkel et al. (2000) found higher crustacean ectoparasite loads on yellowtail damselfish (*Mircospathodon chrysurus*) at the shore end of a spur and groove reef compared to the seaward end of the reef. As illustrated by these examples, it is important to incorporate multiple scales from the regional to the reef scale when studying parasite prevalence in fish hosts.

In Caribbean reef ecosystems, increased observations of black spot syndrome (BSS)—a phenomenon in which fish exhibit a high frequency of conspicuous black spotting around their scales and fin rays—have recently been linked to infection by the trematode parasite, *Scaphanocephalus expansus* (Kohl et al. 2019). This parasite has a complex life cycle involving marine mollusks, tropical reef fishes and predatory birds (osprey). Although the first intermediate molluscan host of *S. expansus* remains unknown, it is likely a marine snail. A wide range of marine teleost and a few chondrichthyes fishes can function as the second intermediate hosts (Kohl et al. 2019), for which infection occurs in the superficial tissues of the dermis and fins. Encysted metacercariae of *S. expansus* mature into sexually mature adult worms only after an infected fish is consumed by an osprey, which appears to be the sole definitive host. Metacercariae are clearly visible through gross observation and necropsy as conspicuous, hyper-pigmented spots ($\sim$ 3 to 5 mm in diameter) in the integument and fin rays of infected fishes. Although spots on fishes alone cannot be exclusively prescriptive of a specific disease or parasite, Kohl et al. (2019) reported that in regions such as the island of Bonaire, both the presence and abundance of black spots correlated closely with infection by *S. expansus*. Black spot syndrome (BSS) can reach a high prevalence among species such as the ocean surgeonfish, *Acanthurus tractus* (Poey, 1860; formerly *A. bahianus*), in Caribbean regions such as Bonaire and Curacao relative to areas such as Belize and the Mexican Caribbean (e.g., Bernal et al. 2016).

The goal of this study was to investigate the spatial and historical distribution of BSS at two scales: the island of Bonaire and the broader Caribbean region. The first objective was to enhance our understanding of BSS prevalence and severity as well as any factors underlying its variation at the island-scale level in Bonaire through field-based surveys. Surveys targeted three reef fish species across depths (2, 5, 12 and 18 m), geographic locations (22 sites around the island) and through time (2012–2013 and again in 2017). The second objective was to document the historical occurrence and distribution of BSS in ocean surgeonfish throughout the wider Caribbean region using a novel technique: archival repositories of Google Images searches. Knowledge of the distribution of BSS within the region over time provides stakeholders with an indication of any spatiotemporal shifts in prevalence as well as its relevance for investigating ecological changes in the functional roles of keystone grazers, such as surgeonfish.

Materials and methods

Study sites

Bonaire is an oceanic island (288 km^2 in geographic area) located $\sim$ 58 km north of Venezuela in the Southern Caribbean Sea (Fig. 1). This island is encircled by a fringing coral reef, the reef flat and reef slope habitat encircling the island is encircled by a fringing coral reef consisting of reef flat and reef slope habitat, that provide a large geographic range to examine the distribution of BSS in reef fishes. At our study sites, the reef flat is typically 30 to 200 m in width, with the reef crest at $\sim$ 10 m depth on the western, leeward side, and $\sim$ 15 m on the eastern, windward side.

Research dives were conducted at 22 dive sites that varied in exposure to diver visitation frequency, wave

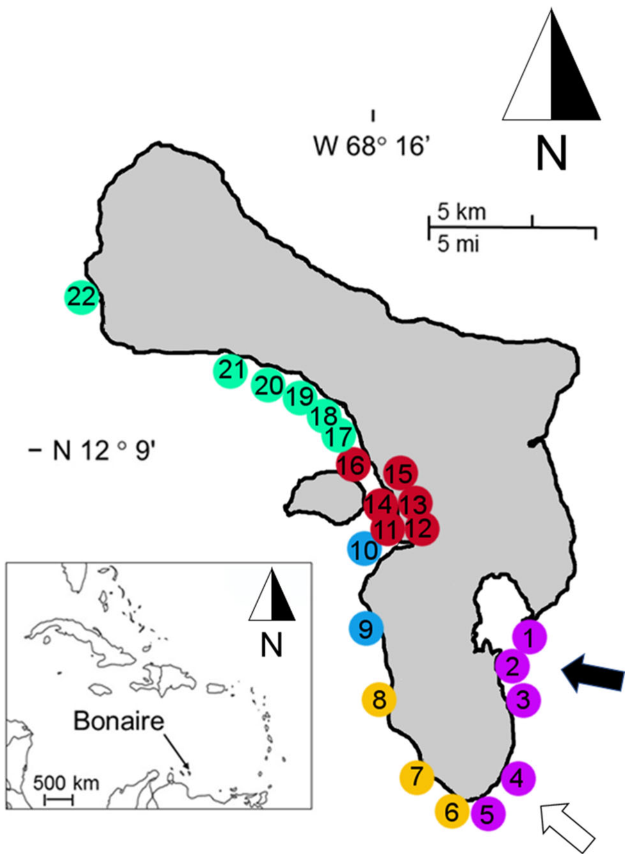

Fig. 1 Site location. The inlay shows Bonaire's location in the Caribbean region. Each number represents a study site. Study sites are color coded to indicate which regional group they belong to: Southeast (purple), Southwest (yellow), West (light blue), Kralendijk (red), Northwest (lime green). Detailed information on each study site is shown in Table 2. Black arrow indicates direction of the predominant trade winds (East/Southeast). White arrow indicates the predominant direction of the Caribbean current (South/Southeast)

energy and proximity to coastal pollution from residential areas, resorts or industry (Table 1). Parasite loads have been found to vary in response to pollution from residential areas or industry (Lafferty and Morris 1996; Vidal-Martínez et al. 2010; Palm 2011; Lacerda et al. 2018) as well as the amount of diving, with higher fish biomass on no-diving reserve sites relative to frequently visited dive sites (Hawkins et al. 1999).

The role of *Scaphanocephalus expansus* in BSS

Black spot syndrome in Caribbean reef fishes has recently been linked to the presence and abundance of metacercariae cysts of the trematode *S. expansus* (Heterophyidae) (Kohl et al. 2019). Although spotted hyperpigmentation in fish cannot be prescriptive of a specific disease or parasite, rather than some general form of injury (Matsumoto and Seikai 1990; Ottesen and Amin 2011; Lévesque et al. 2013; Noguera et al. 2013), images of fish with spots rather than asymmetric patches or scars suggest that this phenomenon is likely caused by encysting parasites. Because BSS has also been found in numerous other coral reef fish species, which were also infected with *S. expansus* (Kohl et al. 2019), we suggest that the black spots detected in the pictures analyzed in this study were caused by *S. expansus*.

Field surveys

The distribution of BSS in *A. tractus* was studied at 22 sites (Fig. 1) between September 2012 and November 2013 (hereafter referred to as "2012") and between September and November 2017. Timed-swim SCUBA surveys encompassed the reef slope, reef crest and reef flat habitats

Table 1 List of island regions including dive sites. Regions were formed based on their exposure to diver impact, wave energy, proximity to coastal pollution from residential areas and resorts, and industry which are detailed in this table

Region	Dive sites	Diver impact	Wave energy	Residential area and resorts	Industry
Southeast	Sites 1–5	Low	High	Very few residents, small windsurfing resorts	Salt industry
Southwest	Sites 6–8	High—medium	Medium	Very few residents	Salt industry
West	Sites 9–10	High	Medium	Populated with dense population on coast	Airport
Kralendijk	Sites 11–16	High	Low	Densely populated on coast and inland, > 10000 residents, several large dive resorts	Two docks used by cruise ships and commercial boats, a desalination factory
Northwest	Sites 17–22	High (except at one remote site)	Medium	Very few residents	No industry

and were conducted between 0800 and 1700 h. Divers followed the 18-m isobaths and collected data for a period of either 10 or 15 min. Sampling continued for the same time interval at 12 m, 5 m and 2 m depths, resulting in a U-shaped sampling pattern. Each observer classified all *A. tractus* within 3 m from the diver according to the number of black spots visible on the side facing the observer: stage 0 (0 black spots), stage 1 (1–4 black spots), stage 2 (5–10 black spots) and stage 3 (> 11 spots) (Fig. 2). This classification system was found to correlate positively and consistently with the number of *S. expansus* infecting the fish host (Kohl et al. 2019). No attempt was made to examine both sides of individual fish as previous observations supported the assumption that similar numbers of spots occurred on both sides of the infected fish (Peachey, unpublished data). Mixed schools of fish with *A. tractus* were photographed to ensure proper BSS classification. Although the size of fish was not recorded, individual size did not correlate significantly with BSS intensity in surgeonfishes in a previous study (Kohl et al. 2019). In surveys conducted in 2017, the method used was modified to include classification of BSS in two other fish species: bar jack (*Caranx ruber*) and redband parrotfish (*Sparisoma aurofrenatum*).

Google Images searches

Google Images searches for “ocean surgeonfish”, “*Acanthurus tractus*” and “*Acanthurus bahianus*”, were conducted to examine the distribution of BSS in the Western Atlantic, including the Caribbean and Gulf of Mexico. “Ocean surgeonfish” and “*Acanthurus bahianus”* were queried in the image search engine maintained by Google on 21 May 2013. On 26 November 2013, “*Acanthurus tractus”* was queried since Bernal and Rocha (2011) resurrected the distinct Northwestern Atlantic Ocean surgeonfish species, *A. tractus,* the year before the Google Images searches. All resulting images were saved using screen shots, and photographs that contained *A. tractus* or *A. bahianus* were logged. The search term, website, geographic location, photographer, date of photograph and individual versus school of fish were recorded. Duplicate images were identified and removed from the database. The criteria for including images in the analysis were: (1) the fish must have been photographed in the natural

Fig. 2 Examples of BSS. *Acanthurus tractus* exhibiting different stages of BSS severity: A: stage 0, no spots, B: stage 1: 1–4 black spots, C & D: stage 2: 5–10 spots, E & F: stage 3: > 11 spots

environment, and (2) more than 50% of one side of the individual must be visible in the photograph. The individuals in the selected images were visually assessed for BSS and classified as affected, unaffected or indistinguishable (e.g., due to low quality images, lighting or angles). If the picture contained more than one individual of *A. tractus* or *A. bahianus*, each fish that fit the above criteria was assessed for BSS and recorded as a nested observation within the image. In several instances, photographers were contacted for basic information regarding the place or date of the photograph.

Data analysis

Field surveys

We modeled BSS status (present or absent, distributed as a binomial variable with a logit link) using a generalized linear mixed effect model (GLMM). As fixed effects, we included fish species (*A. tractus*, *S. aurofrenatum*, or *C. ruber*), survey depth (2, 5, 12 or 18 m), region of the island (Southwest, Southeast, West, Kralendijk, Northwest) and year of survey (2012 vs. 2017). Depth was treated as a numeric variable, while each of the other fixed effects was factors. The specific study site was included as a random intercept term to account for the non-independence of surveys conducted at the same location (at different depths or in different years). Using the glmer function within the lme4 package in R (Bates et al. 2013), we used the number of affected fish relative to the number of unaffected individuals as a binomial response variable (combining the two columns using the cbind function in R). The advantage of this approach, instead of using aggregated analyses of proportion values, is that it maintains the native data distribution (binomial) and it effectively weights estimates by sample size (such that a 0.1 estimate with $n = 10$ differs from one with $n = 100$). We conducted likelihood-ratio tests to evaluate the overall significance of factor variables with more than two levels (e.g., fish species and island region) followed by Tukey's post-hoc tests for specific comparisons.

To test the effects of these same variables on the severity of BSS, we selected only fish with evident signs of infection and conducted an ordinal mixed model analysis. Specifically, we tested how the fixed effects of fish species, depth, year and island region collectively affected the distribution of BSS severity (i.e., level 1, 2 or 3, omitting any unaffected hosts) using cumulative link mixed effects models (CLMM) with the clmm function in the ordinal package (Christensen 2018). Once again, the specific study site was included as a random intercept term. This analysis aimed to determine whether, after accounting for broad-scale differences in the prevalence of affected fishes, we further detected variation in severity.

Google Images searches

We conducted a generalized linear model (GLM) for which the status of each fish (BSS present or absent) was modeled using a binomial distribution with a logit link. Because some images had multiple fish visible, our response was the number of affected fish relative to the number unaffected in a single image (these two columns were combined using the R function cbind. As fixed effects, we included the year the photograph was taken (as a numeric variable) and the geographic region (as a factor). Specific sites were broadly classified into geographic regions according to the distinctivee marine ecoregions classification of Spalding et al. (2007): Bahamian and Floridian, Eastern Caribbean, Greater Antilles, Guianan and outside of Caribbean basin (including Northeastern Brazil, Eastern Brazil, St. Helena and Ascension Islands, Bermuda), Southern Caribbean, Western and Southwestern Caribbean. The variable for year was centered and scaled prior to inclusion in the model. To help ensure that model outcomes were not driven by variation in the number of observations, we further incorporated separate fixed effects for the sample size by year and by geographic region (i.e., the total number of images in a particular year or region).

To test the overall significance of region (as a factor), we conducted a likelihood-ratio test comparing models with and without region using the anova function in R. Post hoc pairwise comparisons between specific regions were conducted using Tukey's test with the glht function in the multcomp package (Hothorn et al. 2008), which corrects significance values for multiple tests. Because no BSS was detected in one of the ecoregions (Guianan and outside of Caribbean basin), thereby precluding any pairwise comparisons, we removed these observations and reran the pairwise tests.

Results

Distribution of BSS in species of fish from field surveys in Bonaire

The grand total of fish surveyed in both years was 4885 (2865 in 2012 and 2020 in 2017), including 314 *C. ruber* (2017), 644 *S. aurofrenatum* (2017) and 3927 *A. tractus* (2865 in 2012 and 1062 in 2017). Fewer *C. ruber* were found in shallow water (17.8% at 2 m and 16.6% at 5 m), as most *C. ruber* (65.6%) were observed at greater depth (34.5% at 12 m and 31.2% at 18 m). The majority of *A. tractus* were found at shallower depths (85.2%), with nearly twice as many at 2 m (55.9%) relative to 5 m (29.3%). The remaining 14.8% of *A. tractus* were distributed between 12 m (8.9%) and 18 m (5.9%). Depth distribution of *S. aurofrenatum* was more uniform, with 17.7% being found at 2 m depth and the other 82.3% evenly distributed between 5, 12 and 18 m depth, ranging from 26.7 to 28.4% at each depth.

Of the 4885 fish surveyed, 58.5% individuals exhibited signs of BSS (Table 2). The GLMM analyses indicated that there was a significant decrease in the percentage of fish with BSS with increasing survey depth (*depth* = − 0.088 ± 0.008, $P < 0.00001$; Fig. 3) and a marginal increase over time (*year* = 0.179 ± 0.099, $P = 0.07$; Fig. 4). Patterns of prevalence of BSS varied significantly among fish species and among island regions (species likelihood ratio [LR] test, Chi-square = 59.31, $df = 2$, $P < 0.00001$; region LR test, Chi-square = 32.94, $df = 4$, $P < 0.00001$). The prevalence of BSS in *A. tractus* (61.8%) was significantly higher relative to *S. aurofrenatum* (48.3%, $P < 0.0001$) and *C. ruber* (38.5%, $P < 0.0001$), while BSS prevalence in *S. aurofrenatum* was significantly higher than *C. ruber* ($P < 0.01$; Tukey's test; Fig. 5). At the scale of the island, the Southeast region had significantly lower prevalence of BSS (16.4%) compared with each of the other four regions (52.6–81.6%, Tukey's test; all $P < 0.001$; Fig. 6). Additionally, fish in the Kralendijk region had a higher prevalence of BSS relative to the Southwest region (81.6% vs. 52.6%, $P = 0.024$).

The results were broadly similar for the analysis of BSS severity (among fishes with signs of the condition only). The severity of BSS decreased with depth (CLMM, *depth* = − 0.065 ± 0.009, $P < 0.00001$, Fig. 3) and increased with sample year (*year* = 0.238 ± 0.091, $P = 0.009$, Fig. 4). There were significant differences in BSS severity among fish species (LR test, Chi square = 65.90, $df = 2$, $P < 0.0001$). The percentage of *A. tractus* in stage 3 (30.1% of infected individuals) was higher than in *S. aurofrenatum* (24.1%) and *C. ruber* (3.3%), and the percentage of *A. tractus* in stage 1 (40.4%) was lower than in *S. aurofrenatum* (53.4%) and *C. ruber* (77.7%) (Tukey's test pairwise *P*-values comparing *A. tractus* to other species, both $P < 0.0005$). As with prevalence, severity was also higher in *S. aurofrenatum* compared to *C. ruber* ($P < 0.0001$; Fig. 5). BSS intensity differed significantly among regions (LR test, Chi-square = 22.66, $df = 4$, $P < 0.0005$; Fig. 6). Fish in the Southeastern region had fewer spots (stage 1: 77.1%, stage 3: 11.7%) compared to Kralendijk (stage 1: 33.9%, stage 3: 34.2%), the Northwest (stage 1: 40.6%, stage 3: 31.2%) and the West (stage 1: 35.4%, stage 3: 30.5%; Tukey's test pairwise *P* values comparing the Southeastern region to these three regions, all < 0.005). No significant difference in severity was found between the Southeast and the Southwest regions (stage 1: 68.3%, stage 3: 16.7%, $P = 0.89$; Fig. 6).

Wider Caribbean region spatial and temporal distribution of BSS

Of the 2112 images that were found using the Google Images search, 411 images met the criteria for inclusion in the analysis. Information on location and year was confirmed for 180 images, of which 73 were found on species identification websites, 41 on social media platforms, 25 on private websites, 20 on photograph repositories and one each on a research repository and an educational site. This classification was performed in 2018 and, unfortunately, the websites of 19 images were not online anymore and could not be classified into any of these categories (Fig. 7).

The earliest image of an *A. tractus* with BSS was from Bonaire in 1985, which is the earliest documented image of BSS in the wider Caribbean region. Twenty-two images of individual *A. tractus* were found from the years 1995 to 2004; individuals with BSS were photographed in Bonaire ($n = 2$) and the Bahamas ($n = 3$), while images of uninfected individuals came from the Bahamas ($n = 3$), British Virgin Islands ($n = 1$), Cayman Islands ($n = 2$), the Dominican Republic ($n = 1$), Florida ($n = 1$), Guadeloupe ($n = 1$), Mexico ($n = 2$), Trinidad and Tobago ($n = 5$) and the US Virgin Islands ($n = 2$). Most of the images were from the period of 2005–2013, capturing a total of 157 images and 317 fish, of which 36.9% exhibited signs of BSS. Most fish were photographed in the Greater Antilles (40.6%), followed by the Southern Caribbean (22.1%), Eastern Caribbean (14.1%), Bahamian and Floridian (9.7%), Western–Southwestern Caribbean (7.6%), and Guianan and outside of the Caribbean Basin (5.9%) ecoregions.

Results of the GLM analysis highlighted geographic variation in the detection of BSS across the Caribbean (likelihood ratio comparison of models with and without region, deviance = − 49.4, $P < 0.00001$). Based on all pairwise comparisons, the Southern Caribbean region had a highly higher prevalence of BSS (78.1%) relative to the West/Southwest (34.6%), the Eastern (29.2%), the Greater Antilles (23.2%) and Floridian–Bahamian (24.2%; all *P* values < 0.005). None of the photographed fish in the remaining region (Guianan and outside of the Caribbean basin) had BSS. Overall, there was a positive but non-significant effect of year on BSS prevalence (GLM: *scale(year)* = 0.272 ± 0.183, $P = 0.138$; Fig. 8), and this pattern was robust to nonlinear forms of analysis as well. The terms for number of observations were both significant with negative coefficients (observations per year = − 0.052 ± 0.022, $P = 0.015$; observations per region = − 0.075 ± 0.02, $P = 0.002$). Residuals from the model showed no evidence of spatial autocorrelation based on a Monte Carlo estimate of Moran's I (statistic = − 0.0134,

Table 2 List of sites that were surveyed on Bonaire, arranged clockwise from most northern east coast site to most northern west coast site. For each site the region, GPS location, amount of surveys conducted, BSS prevalence including the number of fish of each species surveyed are noted

Site no.	Site name and region	GPS location	No. of surveys	BSS prevalence (%)		
				CR	AB	SA
1	Lac Cai (SE)	N 12.99818 W − 68.223451	4	5.3% (n = 19)	20.0% (n = 195)	14.3% (n = 14)
2	Baby Beach (SE)	N 12.077182 W − 68.231111	2	29.2% (n = 24)	37.4% (n = 174)	12.5% (n = 24)
3	Salt Inlet (SE)	N 12.056636 W − 68.224975	2	10.0% (n = 10)	3.0% (n = 235)	0.0% (n = 26)
4	East Lighthouse (SE)	N 12.030570 W − 68.233498	3	30.0% (n = 10)	5.1% (n = 235)	28.0% (n = 25)
5	Lighthouse* (SE)	N 12.027813 W − 68.236885	1		31.1% (n = 103)	
6	Radio Tower (SW)	N 12.025308 W − 68.244440	2	33.3% (n = 6)	45.3% (n = 320)	12.0% (n = 25)
7	Red Slave (SW)	N 12.026504 W − 68.251602	3	48.3% (n = 29)	48.0% (n = 173)	28.8% (n = 59)
8	Tori's Reef (SW)	N 12.070679 W − 68.281956	2	42.1% (n = 19)	84.6% (n = 175)	65.5% (n = 29)
9	The Lake (W)	N 12.106461 W − 68.291026	3	33.3% (n = 15)	66.5% (n = 155)	52.6% (n = 38)
10	Donkey Beach (W)	N 12.132641 W − 68.283441	3	35.0% (n = 20)	92.2% (n = 166)	50.0% (n = 34)
11	18 Palms (K)	N 12.137894 W − 68.277222	2	35.3% (n = 17)	86.6% (n = 157)	93.3% (n = 30)
12	Cha Cha Cha (K)	N 12.145534 W − 68.277158	2	28.6% (n = 14)	89.8% (n = 176)	70.8% (n = 24)
13	Kas di Arte (K)	N 12.156256 W − 68.280309	2	50.0% (n = 8)	91.1% (n = 157)	55.6% (n = 18)
14	Something Special (K)	N 12.159667 W − 68.282496	11	57.1% (n = 7)	79.9% (n = 507)	55.6% (n = 27)
15	Bari's Reef (K)	N 12.167068 W − 68.287717	2	69.6% (n = 23)	92.8% (n = 209)	52.2% (n = 23)
16	Cliff (K)	N 12.174086 W − 68.290580	2	70.0% (n = 20)	87.1% (n = 116)	82.6% (n = 23)
17	Andrea II (NE)	N 12.191334 W − 68.298425	3	54.5% (n = 22)	82.5% (n = 63)	42.3% (n = 26)
18	Oil Slick (NE)	N 12.199975 W − 68.308777	3	28.6% (n = 7)	69.8% (n = 129)	52.9% (n = 34)
19	Weber's Joy (NE)	N 12.206185 W − 68.316940	3	50.0% (n = 6)	81.1% (n = 106)	72.7% (n = 55)
20	Tolo (NE)	N 12.214892 W − 68.337229	3	33.3% (n = 3)	66.1% (n = 109)	50.0% (n = 30)
21	Karpata (NE)	N 12.219174 W − 68.352221	3	35.3% (n = 17)	71.8% (n = 131)	59.0% (n = 39)
22	Playa Frans (NE)	N 12.245965 W − 68.414281	2	5.6% (n = 18)	80.9% (n = 136)	36.6% (n = 41)

Island regions: Southeast (SE), Southwest (SW), West (W), Kralendijk (K) and Northwest (NW). Surveys conducted in 2012 and 2013 included *Acanthurus bahianus* (AB); surveys conducted in 2017 included *Acanthurus bahianus* (AB), *Caranx ruber* (CR) and *Sparisoma aurofrenatum* (SA)

*Was not surveyed in 2017

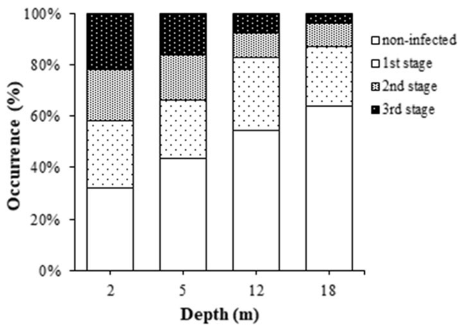

Fig. 3 Prevalence (percent with BSS) and severity (stage/load) of BSS in *Acanthurus tractus, Caranx ruber* and *Sparisoma aurofrenatum* at 2 m (n = 2365), 5 m (n = 1373), 12 m (n = 641) and 18 m (n = 506) on Bonaire (prevalence: generalized linear mixed effect model: *depth* = $-$ 0.088 $\pm$ 0.008, $P < 0.00001$; severity: cumulative link mixed effects models: *depth* = $-$ 0.065 $\pm$ 0.009, $P < 0.00001$)

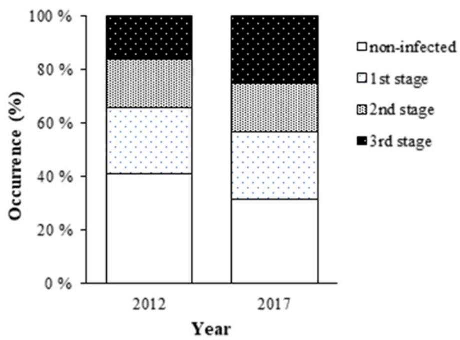

Fig. 4 Prevalence (percent with BSS) and severity (stage/load) of BSS in *Acanthurus tractus* between 2012 (n = 2865) and 2017 (n = 1062) on Bonaire (prevalence: generalized linear mixed effect model: year = 0.179 $\pm$ 0.099, P = 0.07; severity: cumulative link mixed effects models: year = 0.238 $\pm$ 0.091, P = 0.009)

P = 0.958) and visual examination of the spline correlogram (Rhodes et al. 2009).

Discussion

This study found significant differences in the distribution of BSS within Bonaire and the wider Caribbean region. Across Bonaire, the prevalence and intensity of BSS were lowest in the Southeast and within deeper waters. *Acanthurus tractus* had higher prevalence and severity of BSS compared to *S. aurofrenatum* and *C. ruber,* and there were higher prevalence and severity values of BSS in 2017 compared with earlier sampling in 2012. From the survey of archival images, the earliest occurrence of BSS in *A. tractus* was from a photograph in Bonaire in 1985. The prevalence of BSS in the Southern Caribbean ecoregion was more than double the value in other regions, likely indicative of large-scale variation in infection by *S. expansus*. There appeared to be a positive trend of

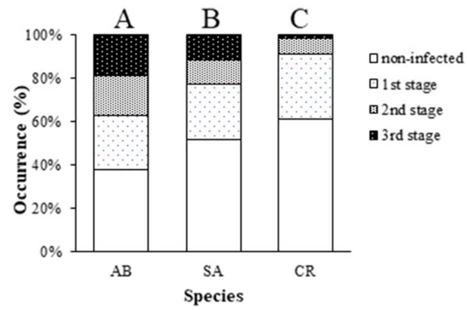

Fig. 5 Prevalence (percent with BSS) and severity (stage/load) of BSS in *Acanthurus tractus* (AB, n = 3927), Caranx ruber (CR, n = 314) and *Sparisoma aurofrenatum* (SA, n = 644) on Bonaire. Significant differences in both prevalence and severity are indicated by unique letters above the bars (prevalence: generalized linear mixed effect model: likelihood ratio [LR] test, Chi-square = 59.31, df = 2, $P < 0.00001$, severity: cumulative link mixed effects models: LR test, Chi-square = 65.90, df = 2, $P < 0.0001$)

increasing BSS observations collectively in the region from the first image in 1985 through the most recent observation in 2013, although uneven representation of images from different regions and through time limited our ability to rigorously test for temporal changes.

Spatial distribution of BSS on Bonaire

On Bonaire, the Southwest sites had a significantly lower prevalence of BSS than Kralendijk, while the Southeast sites had a significantly lower prevalence than all other regions. Furthermore, the severity of BSS (% in stage 1, 2 or 3) at the Southwest and Southeast regions was lower than in all other regions. The Southwest and Southeast sites are located adjacent to the salt production area, such that differences in anthropogenic pressure (i.e., salt industry) could drive spatial differences in BSS prevalence and intensity across Bonaire. However, the effects of the only known definitive host species—the fish-eating osprey, *P. haliatus*—on the distribution and abundance of *S. expansus* remain unknown. In these two regions, *P. haliaetus* uses the shallow reef as hunting grounds but also forages in the expansive salt production area and in a shallow tropical lagoon (Lac Bay) (Smith et al. 2012). This is a noteworthy difference to the other regions. Further investigations are needed to determine whether and how either of these factors, hunting behavior of the definitive host and anthropogenic influences, affect BSS prevalence and severity.

Distribution of BSS in adjacent coral reef habitats

In Caribbean reefs, few comparisons of fish parasite loads among adjacent habitats have been conducted (but see Fernández-Cisternas et al. 2017). In this study, the prevalence and intensity of BSS were higher in the shallow reef

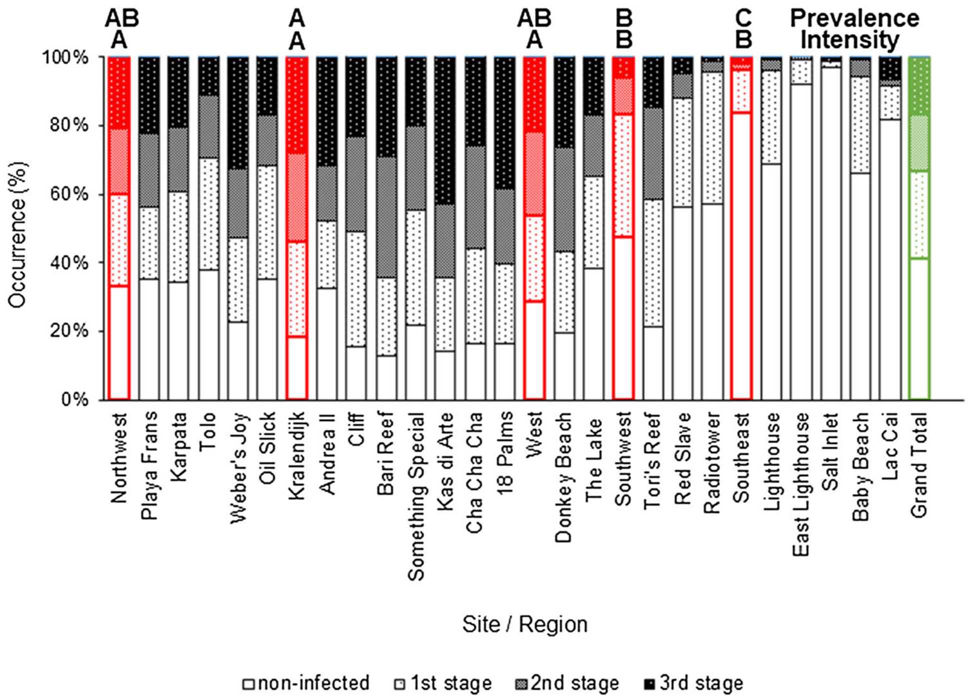

Fig. 6 Prevalence (percent with BSS) and severity (stage/load) of BSS in *Acanthurus tractus*, *Caranx ruber* and *Sparisoma aurofrenatum* across sites on Bonaire. Red bars show overall prevalence and intensities for the five areas and are followed by all sites that make up that particular area. The green bar shows the grand total for Bonaire. Sites are ordered according to the numbers in Fig. 1. Sample sizes are listed in Table 2. Significant differences in prevalence and severity are indicated by unique letters above the bars (prevalence: generalized linear mixed effect model: likelihood ratio [LR] test, Chi-square = 32.94, $df = 4$, $P < 0.00001$; severity: cumulative link mixed effects models: LR test, Chi-square = 22.66, $df = 4$, $P < 0.0005$)

flat and crest habitats (depth between 2 and 5 m) compared to the reef slope (depths between 12 and 18 m). Most previous studies of other fish parasites in tropical reef habitats have reported higher infection patterns at shallower depths and/or within areas of lower coral cover (Grutter 1998; Sikkel et al. 2000, 2009). Some of the fish species investigated in these studies, such as the yellowtail damselfish, have small home ranges, which makes it likely that they stay at the same depth after infection (Grutter 1998; Sikkel et al. 2000). For these species, it is therefore not surprising that the areas with higher abundance of parasite eggs or free-living parasites also have higher parasite infection in hosts (Sikkel et al. 2000; Artim and Sikkel 2013; Santos and Sikkel 2019). However, the host species studied here (*A. tractus, C. ruber* and *S. aurofrenatum)* and in Sikkel et al. (2009) (*A. coeruleus*) are highly mobile species with home range estimates of > 100 m (Chapman and Kramer 2000), which could be moving to a different depth after infection. Depth preference of Caribbean reef fish species has not been studied in detail, but a study from Barbados found that depth did not influence the abundance, biomass and composition of the fish population (Mallela et al. 2007), suggesting that uninfected fish of the species studied here may not show a depth preference. The depth distribution of BSS-affected fish could be caused by differences in availability of cleaner organisms between depths (Sikkel et al. 2009) or fish moving to shallower depth after infection (Barber et al. 2000). For instance, *Oncorhynchus mykiss* (rainbow trout), *Pungitius pungitius* (ninespine stickleback) and *Pimaphales promelas* (fathead minnows) swim closer to the water surface when infected by parasites (Smith and Kramer 1987; Radabaugh 1980; Gopko et al. 2017). Metacercariae of trematodes can migrate to the brain or eyes of fish hosts, altering their depth preference (Barber et al. 2000) in ways that enhance predation by the definitive host. Regardless of the specific cause, high prevalence of infected fish in shallow water is likely advantageous for the parasite as it increases the likelihood of predation by *P. haliaetus* (Swenson 1979; Kinsella et al. 1996; Foronda et al. 2009).

Observation of BSS among different fish species

Acanthurus tractus are more likely to be infected and more severely afflicted by BSS than *S. aurofrenatum* and *C. ruber*, consistent with the findings of Bernal et al. (2016) for dermal parasites (including BSS) on the nearby island of Curaçao. The proportion of infected *C. ruber* and the severity of infection for this species were significantly lower than those of *S. aurofrenatum*. According to our

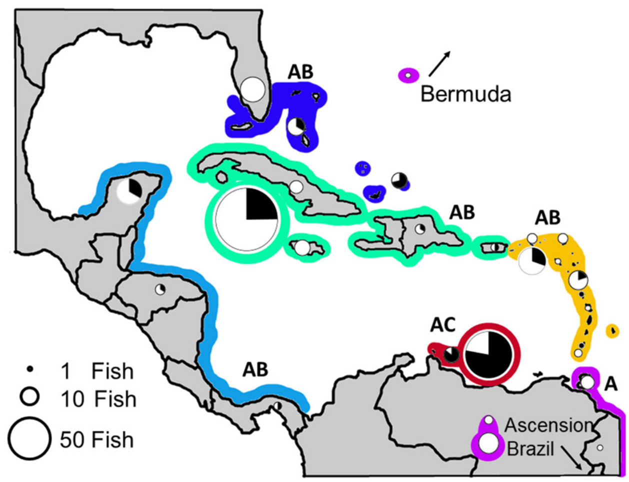

Fig. 7 Distribution of BSS in *Acanthurus tractus* and *A. bahianus* (Ocean surgeonfish) across the Caribbean derived from photographs taken between 2005 and 2013. Circle size corresponds to number of Ocean surgeonfish found on photographs, for example one fish in Bermuda, and 60 in Bonaire. White represents the percentage of fish that are uninfected, while the percentage of fish with BSS are shown in black. Ecoregion classifications are shown in color: Bahamian and Floridian (dark blue), Eastern Caribbean (yellow), Greater Antilles (lime green), Guianan and outside of Caribbean Basin (purple), Southern Caribbean (red), Western and Southwestern Caribbean (light blue). Significant differences in prevalence between ecoregions are indicated by unique letters next to the ecoregion (generalized linear mixed effect model: likelihood ratio [LR] test, deviance = − 90,033, $df = 5$, $P < 0.0005$)

survey, *A. tractus* is mainly found in the shallows (2–5 m), whereas *C. ruber* is mainly on the deeper reef (12–18 m) and *S. aurofrenatum* is distributed rather evenly among the above depths. Therefore, if infection events are more frequent in shallower depth as discussed above, it is likely that the differences in infection between species are caused by their depth preference. However, as previously stated, the fish studied here may not show a depth preference when not infected by BSS. The findings of Bernal et al. (2016) found no correlations between the presence of dermal parasites and host functional traits, including diet, mobility, schooling behavior or position in the water column, underscoring the need for more research on the depth range of these fish species and whether they have a depth preference that leads to higher infection rates.

Temporal change in distribution on both local and wider Caribbean levels

The earliest photograph of *A. tractus* from the Google Images search was of an infected individual photographed in Bonaire, demonstrating possible BSS in the local *A. tractus* population as early as 1985. Studies conducted in the 1960s and 1970s found *S. expansus* in several fish species in the Western Atlantic (Hutton 1964; Skinner 1978). *Scaphanocephalus expansus* has, therefore, been present in Western Atlantic fish before 1985. Few photographs taken before 2005 were found; however, since 2005, photographs of individuals and schools have become more common. Modeling indicates detection of BSS within the wider Caribbean did not change significantly over time, which could be due to the small and unevenly distributed samples available. Nevertheless, these findings highlight the utility of images for tracing BSS back to at least 1985, although more site-specific data are needed to gain a comprehensive understanding of changes in BSS over time.

The prevalence and severity of BSS of *A. tractus* on Bonaire increased between 2012 and 2017. Both the total number of fish with BSS and the number of fish in stage 3 increased by ∼ 9% while the number of fish classified as stages 1 and 2 remained constant. The severity of BSS increased at the same rate as the number of affected fish, likely indicating that new infections took place in

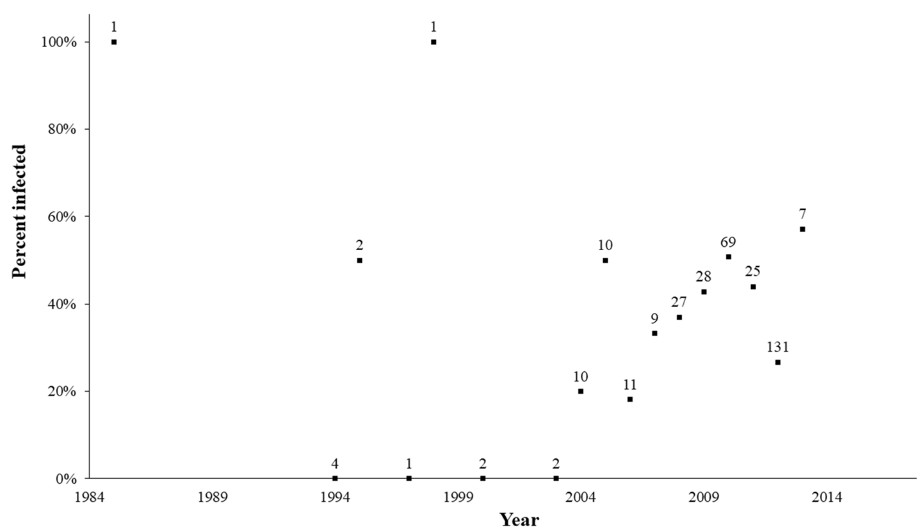

Fig. 8 Prevalence of BSS in *Acanthurus tractus* (Ocean surgeonfish) over time derived from Google Images searches collected for the wider Caribbean ("Ocean surgeonfish" and "*Acanthurus bahianus*" 21 May, 2013, "*Acanthurus tractus*" 26 November 2013). Images are from 26 locations throughout the region. Sample size (number of *A. bahianus* or *A. tractus* found on photographs) is indicated by the numbers above the data points

uninfected and infected fish. It is therefore possible that the infection does not follow over-dispersion, a phenomenon where already infected fish are more likely to get infected than non-infected fish (Anderson and Gordon 1982), although more directly collected data on parasite load per host would be needed to test this.

Wider Caribbean spatial distribution

Photographs of *A. tractus* with BSS were found in 14 of the 26 wider Caribbean regional locations. These sites were spread throughout the wider Caribbean, from the most northern location the Bahamas to St. Vincent and the Grenadines, Dominica and Guadeloupe in the east, Bonaire and Curaçao in the south and Panama, Honduras and Mexico in the west. A previous in-water survey of 80 reef fish in Mexico found no individuals infected by dermal parasites (Bernal et al. 2016); however, the results from this study show that infected *A. tractus* were present. No *A. tractus* with BSS were photographed in Bermuda and Ascension Islands, both being remote islands. Florida and Brazil were the only locations with more than 10 photographs for which no *A. tractus* with BSS were found. Haemohormidium-like blood parasites that also occur between the most southern and the most northern part of the wider Caribbean region had very low abundance in the Florida Keys and no abundance in the Bahamas, likely due to colder winters (Sikkel et al. 2018). The distribution of BSS could likely follow the same trend; however, more sampling is needed in the locations without BSS before a conclusion can be made that BSS is not present in *A. tractus* at these locations.

The detection in the Southern Caribbean (Curaçao and Bonaire; 78.7%) was significantly higher than in all other ecoregions except Guianan and outside of the Caribbean basin region. For the later ecoregion, only healthy fish were found; hence, the lack of significance is likely due to the small sample size from this region and the lack of detection of any fish with BSS. Our results align with the results of Bernal et al. (2016), who found higher dermal parasite detection in Curaçao compared to Belize and Mexico. The parasite causing BSS on Bonaire has been identified as *S. expansus* (Kohl et al. 2019) whose life cycle likely involves three hosts. Differences in BSS prevalence between regions could therefore be due to differences in host abundances. While *S. expansus* infects a wide range of fish hosts for their metacercaria stage (Kohl et al. 2019), the definitive host is always *P. haliaetus* (Jägerskiold 1904; Yamaguti 1942; Hoffman et al. 1953; Schmidt and Huber 1985; Foronda et al. 2009). The parasite is therefore reliant on the presence of a single bird species and as yet unidentified first intermediate host(s) (likely a snail). *Pandion haliaetus* are found year round on Curaçao and Bonaire (Prins et al. 2009); therefore, the prevalence in BSS could be linked to *P. haliaetus* presence at these locations. Future research should focus on finding more information on the life cycle of *S. expansus*, particularly on identification of the first intermediate host.

Google Images searches as tool for spatial and historical distribution assessment

Thirteen previously unknown locations where *A. tractus* show BSS were identified through the Google Images searches. The sample size obtained by these Google Images searches was sufficient to conduct a statistical analysis on the ecoregion level. The 78% detection frequency in *A. tractus* found for Bonaire through the Google Images searches corresponds well with the in situ observation of BSS in *A. tractus* in the areas where most diving (and therefore photography) occurs on Bonaire (Northwest 74.0%, Kralendijk 85.9%, West 79.7%). However, the 86% detection frequency found for Curaçao in this study differed greatly from the 20% in situ observation of dermal parasites in *A. tractus* found by Bernal et al. (2016). This large difference between detection frequency from pictures and in situ observation frequency is likely due to the small sample size for Curaçao. Compared to Bonaire, for which 68 photographs were found during Google Images searches, only 6 photographs were found from Curaçao. Furthermore, Bernal et al. (2016) surveyed 147 *A. tractus* in situ in Curaçao while this study surveyed 2317 *A. tractus* in Bonaire. The Google Images search a powerful tool to assess the spatial and historical distribution of dermal fish parasites; however, it is critical that a large sample size is present to reliably estimate prevalence and intensity.

Other studies have used Flickr and Panoramia to obtain primary biodiversity data (Stafford et al. 2010; Lloyd et al. 2012; Barve 2014; ElQadi et al. 2017). In this study, the Google Images search found 162 unduplicated pictures located on websites other than Flickr and Panoramia. Many other studies that mine social networking sites for geotagged pictures use the application programming interface of Flickr and Panoramia to obtain their data set (Barve 2014). While our procedure was more time-consuming, the vast number of pictures found on sites other than those two picture repositories shows that a larger sample size can be obtained with Google Images searches. This study also had additional challenges which required visual inspection of each photograph which is generally not performed when querying the application programming interface. Each picture was inspected visually for the presence of: (1) originality, (2) black spots and (3) live *A. tractus,* captured in situ. A further challenge was that aquatic photographs lack geotags, and thus, geographic information often had to be obtained from the photographer. Comparable to location information retrieved from tweets (Daume 2016), the location information found in this study was composed of different spatial scales ranging from the name of the dive site to the country where the picture was taken. Nevertheless, information on location and year was obtained for 46.7% of all photographs, which is higher than reported for geo-tagged pictures and tweets (1.8–16%; Barve 2014; Daume 2016) and slightly lower than for tweets for which location was determined using all information provided in the tweet and the tweeters user profile (46.9–69.7%; Daume 2016). In absolute numbers, the sample size obtained by this study was similar to the sample size of a study researching invasive species through twitter (Daume 2016); however, it was much smaller than of a study mining Flickr for pictures of the snowy owl and the monarch butterfly (Barve 2014). In conclusion, this method is well suited for a distribution analysis on the spatial level of countries/islands, but it may lack the needed details for a finer-scale analysis. Furthermore, the practicality of this type of analysis for marine ecology will only grow as reliable underwater camera systems become more commonplace and affordable.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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