Black Spot Syndrome in ocean surgeonfish: using video-based surveillance to quantify disease severity and test environmental drivers on Curacao reefs

Cheyenna D. G. de Wit
University of Amsterdam: Universiteit van Amsterdam
Pieter Johnson
pieter.johnson@colorado.edu
University of Colorado Boulder https://orcid.org/0000-0002-7997-5390

Research Article

Keywords: host-parasite interaction, coral reef ecosystem, disease ecology, global change, 40 emerging disease, non-invasive disease surveillance, fish disease

Posted Date: February 21st, 2024

DOI: https://doi.org/10.21203/rs.3.rs-3623539/v1

Black Spot Syndrome in ocean surgeonfish: using video-based surveillance to quantify disease severity and test environmental drivers on Curacao reefs

Cheyenna D. G. de Wit[1] and Pieter T. J. Johnson[2*]

[1]Freshwater and Marine Biology, University of Amsterdam, Amsterdam, NH, The Netherlands (cheyenna.dewit@gmail.com)

[2]Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA (pieter.johnson@colorado.edu)

**Corresponding author* (pieter.johnson@colorado.edu); Ph: 303.492.5623; Fax: 303.492.8988

Running page head: Spatial distribution of BSS

Type of article: Original paper

Author contributions: PTJJ and CDGW designed the study; CDGW and PTJJ collected field; PTJJ and CDGW performed statistical analyses and visualizations; CDGW and PTJJ jointly wrote and edited the manuscript.

Abstract

Observations of Black Spot Syndrome (BSS), a pigmented dermatopathy in marine fishes, have been increasingly reported in important grazers such as surgeonfish and parrotfish in the Caribbean. This condition has been linked to infection by the trematode parasite, *Scaphanocephalus* spp., although relatively little is known about the environmental drivers of infection and how they vary spatially. This study introduces a non-invasive, video-based method to survey BSS presence and severity in ocean surgeonfish (*Acanthurus tractus*). We then apply the approach across 35 coastal sites in Curaçao to evaluate the influence of environmental factors on BSS, including longitude, herbivorous fish density, wave energy, depth, nutrient pollution, and inhabited surface area. Of the 5,123 fish surveyed, 70% exhibited visible signs of BSS, and the average number of spots per fish increased by ~5-fold from eastern to western sites along the leeward coastline. Within a site, estimates of BSS severity were broadly consistent between different divers, reviewers of video footage, and date of sampling, emphasizing robustness of the surveillance approach. Analyses of environmental factors indicated that BSS decreased with wave intensity while increasing in association with higher nutrient runoff and fishing pressure. This study provides insight into environmental correlates of BSS severity while highlighting the use of video-based surveillance as a non-invasive survey method. The precise mechanisms linking environmental factors with BSS remain unknown, emphasizing the need for long-term and experimental studies in this system.

Keywords: host-parasite interaction, coral reef ecosystem, disease ecology, global change, emerging disease, non-invasive disease surveillance, fish disease

Introduction

Despite reported increases in disease syndromes affecting multiple marine taxa (Harvell et al. 2004, Groner et al. 2016, Tracy et al. 2019), parasites remain relatively understudied in marine systems. In most cases, the environmental drivers that contribute to emerging infections are broadly unknown. Some of the most important barriers to studying marine parasites are the inherent logistical and financial challenges to surveying patterns of infection at larger spatial scales, particularly when involving parasites that may be difficult to census owing to their cryptic nature. This emphasizes the need for innovative methodologies to detect and monitor infections, including the use of less-invasive techniques that do not require sacrifice or injury to hosts. Particularly promising approaches include the use of environmental DNA (eDNA) to detect evidence of pathogens from water or sediment, and analysis of imagery for disease systems with externally visible pathologies. For example, increased use of eDNA and eRNA in aquatic environments has offered new opportunities to identify pathogens with relevance for harmful algal blooms, wildlife conservation, and human health (Amarasiri et al. 2021, Ríos-Castro et al. 2021). Similarly, the use of repeated, multi-year surveys involving archivable images or video has facilitated a greater understanding of pathogens in invertebrate and vertebrate hosts (Dalton & and Smith 2006, Lamb et al. 2018, Burns et al. 2020). For instance, Lamb et al. (2018) described a multi-species outbreak of ulcerative skin disease in Galapagos fishes, for which bi-annual video monitoring helped link the outbreak to the 2015-2016 El Niño event. Importantly, these techniques can reduce sources of observation bias, the amount of time required underwater, and the taxonomic expertise or skill required of observers (see Cappo et al. 2003, Houk Van Woesik 2006, Mallet & Pelletier 2014, Burns et al. 2020; Castañeda et al. 2020).

In the Caribbean, increasing observations of Black Spot Syndrome (BSS) have been reported in many important fish grazers, such as surgeonfish and parrotfish (Bernal et al. 2015, Elmer et al. 2019). This condition presents as black spots (or pigmented dermatopathies) on the epidermal tissue of the body or fins (Fig. 1) (Dennis et al. 2019). The spots are often well-defined and distinguishable from trauma to the body such as cuts and scrapes (Happel 2019). Kohl et al. (2019) recently linked cases of BSS in the Caribbean to infection by the parasite, *Scaphanocephalus* spp., a group of trematodes with distinctive, wing-like expansions of the anterior region. Importantly, the number of spots visible on affected surgeonfish correlates directly with the number of encysted *Scaphanocephalus* (Kohl et al. 2019), suggesting that non-invasive survey methods – including video-based transects – could provide an effective tool for censusing infection. In locations where BSS has been reported, ocean surgeonfish (*Acanthurus tractus*) often exhibit among the highest frequencies of externally visible infections (Bernal et al. 2015, Dennis et al. 2019, Elmer et al. 2019, Kohl et al. 2019).

Like other digenetic trematodes, *Scaphanocephalus* spp. have a complex life cycle involving multiple host species across different trophic levels (Kohl et al. 2019). The first intermediate host is a marine mollusc, likely a snail, although the specific identity of this host has not yet been established. In the snail, parasites reproduce asexually and release free-swimming cercariae that penetrate the skin of fishes as the second intermediate host. In fish, the parasites develop into metacercariae cysts and are eventually eaten by piscivorous birds, for which most records to date involve osprey (*Pandion haliaetus*) (Kohl et al. 2019). Adult parasites reproduce sexually in the gut of the bird, after which the eggs are released with feces of the bird and re-enter the marine snail (Kohl et al. 2019). Numerous species of tropical or subtropical marine fish from the Indo-Pacific, Atlantic, and Caribbean have been reported to support infection by metacercariae of *Scaphanocephalus* spp., including damselfishes, hogfishes, trumpetfishes, goatfishes, wrasse, parrotfishes and pufferfishes (Tubangui 1933, Hutton 1964, Skinner 1978, Inohuye Rivera 1995, Iwata 1997, Bullard & Overstreet 2008). Likely there are multiple species of *Scaphanocephalus* that have yet to be fully described either morphologically or genetically.

Although *S. expansus* has been recorded in numerous fish species, little is known about how infection varies among locations or in response to environmental variables. Elmer et al. (2019) reported that BSS on the island of Bonaire decreased with depth (higher between 2 and 5 meters than between 12 and 18 meters), and tended to be highest at coastal sites near the urban center of Kralendijk (see also De Graaf & Simal 2015). These patterns likely emerge from a combination of biological and physical characteristics of the environment and their influence on parasite transmission. Previous research on marine trematodes suggests that infection in second intermediate hosts will be a function of the density of infective stages in the environment, the success of those stages in finding a suitable host, and the susceptibility of hosts to becoming and maintaining infection through time (e.g., Combes et al. 2001). The density of infective stages will generally be dictated by the abundance of first intermediate hosts (i.e., snails) and the proportion that are infected (i.e., based on inputs from definitive hosts, such as birds; Fredensborg et al. 2006, Byers et al. 2008). Nutrient runoff and localized eutrophication, which can promote algal growth and snail biomass, lead in some cases to greater production of trematode infective stages and therefore increased infection risk to downstream hosts (see Johnson et al. 2007, Johnson and Carpenter 2008, Budria 2017). The success of parasites in finding and establishing within suitable hosts is hypothesized to be greater in calm, protected conditions, and can decrease in the presence of predators or ‘decoy hosts’ that reduce infective stage contacts with susceptible hosts (Johnson & Thieltges 2010, Welsh et al. 2017, Koprivnikar et al. 2023). Additional human activities, such as fishing pressure, can have direct and indirect effects on parasite transmission (Lafferty et al. 2008, Wood et al. 2014). Direct harvest of larger-bodied individuals, which tend to be the most heavily infected, can reduce average infection load in a population; however, top-down losses of predators through overharvesting may lead to increased infections among fish from lower trophic levels owing to greater survival, particularly when those species are not directly fished themselves (Packer et al. 2003, Wood & Lafferty 2014). In summary, spatial variation in parasite prevalence can be driven by environmental variables acting over a hierarchy of scales. Identifying the role of such drivers is essential to better understanding patterns of infection, their potential emergence, and opportunities for management.

In the current study, we set out to optimize a non-invasive, video-based transect method for quantifying the presence and severity of BSS in ocean surgeonfish (*Acanthurus tractus*) between depths and across locations. Our goal was to develop an approach that was easy to implement, generated archivable imagery, and was robust to observer variation. We then used this approach to survey reef sites across the leeward coast of Curaçao and assess whether infection patterns varied in response to specific environmental gradients. We focused on ocean surgeonfish because of their high abundance, established susceptibility to infection by *Scaphanocephalus* spp., and the previously demonstrated link between infection and the presence of visibly conspicuous dermatopathies (see Kohl et al. 2019). Surgeonfish are also ecologically important due to their role as grazers on algae that can otherwise adversely affect coral growth (Bellwood et al. 2004, Côté et al. 2013). Building from previous research on marine trematodes, we evaluated the roles of physical and biological variables with the potential to influence exposure and transmission, including wave energy, the amount of coral cover, fish biomass, nitrogen concentrations (as an indicator for sewage runoff), fishing pressure, and the density of nearby houses. These variables, which vary broadly in value across selected sites, also reflect ongoing threats to coral reef ecosystems on the island of Curaçao, such as overfishing, pollution, and losses in coral cover (Jackson et al. 2014, Waitt Institute 2017). How such changes interact to influence emerging infections in marine ecosystems represents an important research frontier.

Methods

Study area

Fieldwork for this study was conducted between February 2022 and January 2023 along the leeward coast of Curaçao (12.1696°N, 68.9900°W) (Fig. 2). Curaçao is an oceanic island in the southern Caribbean Sea located approximately 65 km north of Venezuela. The prevailing currents come from the east/northeast, such that the northern (windward) shore of the island experiences strong wave energy (Van den Hoek et al. 1975). The more protected, southwestern coast is bordered by a fringing coral reef that starts with a plateau that slopes down to about 10 meters, after which it drops off steeply. Compared to other islands in the Caribbean, Curaçao has relatively high coral cover and fish biomass (Sandin et al. 2008). Nonetheless, factors such as coral cover, fish abundance, and water quality vary considerably among sites along the leeward coastline (Sandin et al. 2022), with generally greater coral cover, higher fish abundance, and less pollution toward the far east side of the island (Waitt Institute 2017). Impacts associated with human development are particularly concentrated around the urban center of Willemstad and the major commercial harbor of St. Annabaai, which collectively represent important sources of runoff for nutrients and other pollutants (e.g., Gast et al. 1999, Klaus et al. 2007).

Study sites and species

Study sites were selected to encompass a wide range of environmental conditions and attributes along the southwestern coast of Curaçao. We identified 35 dive site locations distributed along ~70 km of coastline that captured broad variation in physical and biological characteristics (see Appendix I for a list of sites and locations). At each site, we conducted multiple, replicate transects at both 2- and 5-meter depths on the shallow plateau. These depths were selected based on previous research on Bonaire in which the majority of BSS occurred at shallow depths, with a decrease in infection beyond 5 m (Elmer et al. 2019). Surveys focused on the ocean surgeonfish (*Acanthurus tractus*), which is a ray-finned fish in the family Acanthuridae that occurs commonly throughout the Caribbean. It is one of the most abundant herbivorous fish species in the shallow reef habitats around Curaçao (Robertson et al. 2005), and is considered ecologically important in preventing the overgrowth of algae on coral reefs and helping to cycle nutrients (McManus 2000, Burkepile & Hay 2006, Côté et al. 2013, Bloch et al. 2021). Visual counts of BSS were performed on ocean surgeonfish with the use of the video footage collected during transects (see below). This species was chosen because of its high abundance and because its pale, uniform coloring facilitates detection of BSS compared with species exhibiting natural spots or complex color patterns. Previous research has established that *A. tractus* is one of the most externally affected by BSS among studied species (Bernal et al. 2015, Dennis et al. 2019, Elmer et al. 2019, Kohl et al. 2019).

SCUBA transects to assess the severity of Black Spot Syndrome

We used a video-based method to assess BSS presence and severity in *A. tractus* across 35 sites and 2 depths. At each site, SCUBA divers collected video footage using a GoPro® Hero

5 to 8 series attached to a 1-m extension rod, which allowed divers to get closer to individual fish. Three transects were conducted at 2 meters and three transects at 5 meters. The video resolution was set to 1080 p at 60 frames per second on the linear angle setting (see Appendix I for additional details on the sampling and processing protocols). Pairs of divers conducted transects in parallel, with one individual at 2 m depth and the other at 5 m, swimming within eyesight but far enough away to avoid recording the same fish. The divers swam along the depth contour at a speed of approximately 1.5 m per s to locate and record at least 20 haphazardly selected *A. tractus*. Individual fish were approached slowly to obtain footage close enough (~0.5 to 1 m) for subsequent inspection during video analysis. Only adult surgeonfish (estimated at >15 cm) were recorded. Transects continued for 10 minutes or until at least 20 ocean surgeonfish had been adequately recorded. Thus, unlike transects focused on quantifying fish abundance (e.g., protocols from the Atlantic and Gulf Rapid Reef Assessment following a static transect line), here divers sought to film as many surgeonfish as possible to provide robust estimates of infection while swimming along a specific depth isobath. After both divers completed a transect at a given depth, they switched depths and conducted another video transect. This switch was conducted to help minimize observer bias (i.e., each depth was surveyed by multiple divers for each site).

Video processing

Videos were processed using VLC Media Player, a freely available program equipped with viewing tools. During analysis, the video was paused whenever an *A. tractus* was clearly visible and within range for observation. All spots on one side of the fish were counted, with the assumption that sides were not significantly different in infection severity. For each fish, an observer recorded the estimated number of spots (Fig. 1) and the time point in the video from which the count was derived. This approach differs from past studies by counting the specific number of spots rather than classifying BSS as present/absent or into ordinal classes (e.g., de Graaf & Simal 2015, Dennis et al. 2019, Eiermann & Tanner 2019, Elmer et al. 2019). When multiple fish were evident in the same frame, we described where each fish occurred spatially (right, left, top, bottom, etc.). If circumstances made it difficult to count the spots accurately (e.g., the fish was too distant, too dark, incompletely in the frame, or at a bad angle), the count was left blank with an explanation as to why no count was made. For a subset of transects, videos were processed by two independent observers; the first observer recorded the time (minutes and seconds) each fish was detected and estimated the number of spots. The second reviewer used the times recorded by the first reviewer but made an independent assessment of spot count (i.e., they were not provided with reviewer 1's counts). This approach allowed us to test the congruence of reviewer counts while helping to reduce potential confusion over the identity of the individual fish assessed.

Environmental factors

Data for the site-level environmental factors were derived from existing information for Curaçao collected during an intensive, island-wide survey in 2015 (see Waitt Insitute 2017, Sandin et al. 2022). This marine scientific assessment included detailed information on the physical and biological environments at 122 sites along the leeward shore, for which the island was divided into eight zones based on a combination of biological, physical, and anthropogenic characteristics. As part of this survey, Sandin et al. (2022) published an extensive dataset on fish biomass, coral cover, benthic assemblages, fishing pressure, pollution, and site-specific physical features, which was used here to develop potential predictor variables. Previous research on marine parasites has highlighted the influence of both the biotic community and habitat-related differences on infection abundance, including fish abundance, fishing pressure, coral cover, pollution, and water movement (Grutter 1998, Byers et al. 2008, Lacerda et al. 2017, Williams et al. 2022). Building from this foundation, we included the following variables in the analysis as potential predictors of BSS severity (average number of spots detected per fish on one side of the body):

Wave energy: Trematode infective stages emerging from snails (i.e., cercariae) are short-lived with limited swimming ability (Pietrock & Marcogliese 2003), such that their success in contacting suitable second intermediate hosts may be greatest in relatively calm, protected waters (Upatham 1974, Sousa & Grosholz 1991, Galaktionov & Bustnes 1995, Byers et al. 2008). We used an ordinal measurement of shoreline wave intensity that was ranked through visual assessment and divided into five levels based on wave height: Level 1 (2 to 3.5 m), Level 2 (1.5 to 2.0 m), Level 3 (1 to 1.5 m), Level 4 (0.5 to 1 m), Level 5 (0.3 to 0.5 m), and Level 6 (0 to 0.3 m) (derived from van Duyl (1985)). These values were inverted to make them positively related to wave height (i.e., by multiplying by -1) (Sandin et al. 2022).

Coral cover: the amount of coral cover in shoreline reefs has the potential to inhibit the success of cercariae in contacting fish second intermediate hosts via active predation (i.e., consumption by coral polyps) and through mechanical interference (i.e., structural complexity leads to greater cercariae losses) (Paula et al. 2021, Welsh et al. 2023). While corals can function as second intermediate hosts for some trematode parasites (Aeby 2003), this is not the case for *Scaphanocephalus* spp. Coral cover also has the potential to indirectly alter trematode transmission through its effects on the identity and abundance of species in the community, including those directly involved in the parasite's life cycle (e.g., snails and fish) or those that disrupt it (e.g., predators of cercariae or decoy hosts that interrupt transmission). This variable was incorporated as the average percentage of reef-building corals measured using benthic imagery along transects (n = 122, depths of 8 to 12 m, see Sandin et al. 2022), followed with a $\log_{10}$-transformation (+1).

Nitrogen concentration: nutrient runoff can amplify trematode infection through at least two mechanisms. Increased algal growth can promote faster growth and reproduction of aquatic snails, which are the typical first intermediate hosts for trematode parasites (note that the specific first intermediate host of *Scaphanocephalus* remains unknown). In addition, infected snails from eutrophic environments can produce more infective cercariae per day, thereby increasing the exposure risk for local fish populations (e.g., see Johnson et al. 2007, Sasal et al. 2007, Budria 2017). Common sources of elevated nitrogen in the nearshore waters of Curaçao include sewage pollution, stormwater inputs, and construction runoff, which have likely contributed to increases in benthic algae and losses of coral (see Gast et al. 1999, Lapointe & Malin 2011). We used the delta-15-N levels in macroalgae (n = 122) (with a $\log_{10}$-transformation (+1)) as an indicator of anthropogenic nutrient inputs (see Lapointe & Malin 2011, Sandin et al. 2022).

Fishing pressure: The intensity of fishing pressure can affect parasite transmission both directly, i.e., by removing large-bodied fish that are often disproportionately infected, and indirectly by reducing predation pressure on unfished species at lower trophic levels (Sasal et al. 2007, Lafferty et al. 2008, Wood et al. 2014). Because surgeonfish are rarely caught for human consumption or as baitfish in Curaçao, higher fishing pressure is more likely to influence infection indirectly, i.e., by increasing the overall abundance of herbivorous fishes due to reduced predation by piscivorous species or by increasing the abundance of heavily infected fish specifically (which might otherwise by easier prey for predators) (Packer et al. 2003, Wood & Lafferty 2014). The data used for fishing pressure were based on interviews of local anglers (n = 118) and subjected to a $\log_{10}$-transformation (+1) (see Waitt 2017, Sandin et al. 2022).

Inhabited surface area: human population density can also influence patterns of parasite infection through the collective effects of disturbance, pollution, and shoreline modification. For instance, human-mediated alterations can inhibit activity by bird definitive hosts, thereby reducing trematode inputs to snails (Smith 2001, Fredensborg et al. 2006, Byers et al. 2008). Alternatively, pollutants can weaken immune defenses or the body condition of fish hosts, leading in some cases to elevated infection levels (Sures & Nachev 2022). As a proxy for overall human activity and density, we used inhabited surface area, which reflects the proportion of the local watershed covered by buildings, commercial areas, and roads (see Sandin et al. 2022).

Fish biomass: host density or biomass is often a key variable dictating parasite transmission. For trematode cercariae, a higher density of hosts is expected to dilute the number of encysted metacercariae detected per fish (Stumbo et al. 2012, Buck & Lutterschmidt 2017). Over longer time periods, however, higher fish density could promote overall parasite transmission and lead to increases in infection pressure (Johnson et al. 2013, Buck et al. 2017). For this measure, we used site-specific estimates of herbivorous fish biomass as derived from transects conducted along the forereef (n = 122, 8 to 12 m depth, 300 m^2 of survey area; see Sandin et al. 2022). This choice was made based on the observation that *Scaphanocephalus* appears to infect a wide range of herbivorous fish (e.g., parrotfish, surgeonfish, damselfish).

Statistical analysis

To assess consistency between independent reviewers of video footage, we calculated the concordance correlation coefficient between their spot counts for fish scored by both reviewers. Corcordance analysis measures agreement between alternative methods (or reviewers) to evaluate consistency (e.g., Lin 1989). Because the count of spots per fish involved discrete data that were overdispersed (i.e., the variance was much larger than the mean), we used the R package iccCounts to estimate the intraclass correlation coefficient between reviewers (Carrasco 2010, Carrasco 2022). This package applies generalized linear mixed models to model the within-subjects variance using alternative discrete distributions (e.g., Poisson and negative binomial) and varying forms of zero-inflation. After identifying the model distribution with the lowest AIC, we tested its validity by comparing randomized quantile residuals from the fitted model with those obtained by simulation (Carrasco 2022).

For subsequent analyses aimed at evaluating patterns of BSS severity among locations, we focused on the scores from reviewer 1 (i.e., only a subset of videos were reviewed by two independent reviewers). Once again, we used Generalized Linear Mixed Models (GLMMs) for which we could vary the distribution (Poisson and negative binomial) and incorporate zero-inflation. Models were constructed using the glmmTMB package (Brooks et al. 2017) in the R statistical environment (R Core Team 2023 version 4.3.1). In all models, site identity and the individual transect were included as random intercept terms. As additional assessments of whether the transect method was robust, we tested how diver identity and date of sampling influenced estimates of BSS severity by including them as categorical fixed effects. These terms were assessed using a likelihood-ratio test and subsequently removed after being found to have no significant influence.

To evaluate how potential drivers of trematode infection affected BSS, we incorporated transect depth (2 m versus 5 m), wave energy, hard coral cover, herbivorous fish biomass, nitrogen concentration, fishing pressure, and inhabited surface area as fixed effects. Prior to inclusion, numeric predictor variables were centered and scaled using the scale function and tested for collinearity to ensure that all pairwise correlations coefficients were less than 0.6. After initial explorations indicated that a zero-inflated model with a negative binomial distribution ('nbinom1') had the lowest AIC score, we used a backward elimination approach to identify terms influential in predicting spots per fish. Beginning from the full model, likelihood ratio tests were applied to sequentially compare against a reduced model with the least significant term removed. Model reduction continued until any further removals resulted in a *P*-value of <0.1. As diagnostics on the final model, we used the performance package (Lüdecke et al. 2021) to calculate the marginal and conditional R^2 values (i.e., the coefficient of determination considering only the fixed effects [marginal R^2] or both fixed and random effects together [conditional R^2]), variance inflation factors (VIFs, an indicator of collinearity between predictors), overdispersion, and any influential outliers. We also examined whether residuals showed evidence of spatial autocorrelation by calculating their correlation with longitude.

Results

Overview and validity of video transect approach

In total, we examined 5,968 ocean surgeonfish on 35 sites along the southern coast of Curaçao. This included 214 transects (105 at 2 m and 109 at 5 m), with an average of 5.2 transects per site. Spot counts could not be reliably quantified on 845 fish (14.2%) that were out of frame, too far away, too dark, or at a poor angle. Of the 5,123 fish with reliable counts, 3,580

(70%) showed visible signs of BSS (one spot or more; range: 1 to 55 spots on one side of the body) (Fig. 1). Spatially among sampled sites, there was a significant effect of longitude on BSS severity, such that the average number of spots per fish increased substantially from east to west along the leeward shore (negative binomial GLMM: scale(longitude) = -0.435 ± 0.068; z = -6.32, $P < 0.00001$) (Fig. 2). The lowest values were from East Point (Secrets; $\bar{x} = 0.2$ spots per fish), while the greatest infection was at Coral Habitat ($\bar{x} = 6.5$ spots per fish), with multiple sites toward West Point exceeding 5 spots per fish (see Fig. 2). There was no effect of depth (2 vs. 5 m) on spot count (scale(depth) = -0.030 ± 0.021; z = -1.40, $P = 0.16$; Fig. 2), and the addition of diver identity (as a fixed effect) was not significant (likelihood ratio test comparing model with and without diver identity; $\chi^2 = 25.7$, df = 19, $P = 0.14$).

Based on the concordance analysis, the estimated intraclass correlation coefficient between spot counts for different reviewers was 0.915 (95% CI = 0.905 to 0.924). This indicates that, among the subset of fish with multiple assessments, ratings of the two independent reviewers were broadly consistent (see Fig. 3). The best-fitting model used a Poisson distribution and yielded a mean spot count of 4.54 per fish with a variance among subjects (i.e., individual fish) of 1.65 and a variance between methods (i.e., reviewers) of 0.032. Exponentiation of the fixed effect of reviewer (0.2528) from the GLMM yielded a value of 1.28; thus, for every 1 unit increase in spots reported by reviewer 1, the spot count for reviewer 2 increased by 1.28. This indicates that reviewer 2 consistently counted more spots than reviewer 1. Fitting the data with a negative binomial model yielded nearly identical results, albeit with a slightly higher AIC value (+2). Incorporation of zero-inflation led to failures in model convergence. Because of the high concordance between reviewers, we subsequently focused on ratings from reviewer 1 only, which provided a larger total sample size (628 fish lacked ratings from reviewer 2).

Effect of environmental factors on the spatial distribution of infection around Curaçao

Based on AIC comparisons of alternative response variable distributions, a model with a zero-inflated negative binomial distribution (nbinom1, or the 'alternative formulation' in glmmTMB had a delta AIC of 5 to 10,628 units lower relative to alternative responses involving Poisson, overdispersed Poisson, or nbinom2). We did not include longitude in this model because it was collinear with several of our hypothesized predictors (Pearson $r > 0.7$), and because the goal was to better understand what factors mechanistically contributed to the observed spatial pattern among sites. Following a backward selection approach, the final reduced model included significant effects for wave energy, fishing pressure, and nitrogen concentration (Fig. 4). Wave intensity negatively predicted spot count per fish (negative binomial GLMM, scale(wave intensity) = -0.367 ± 0.079; z = -4.65, $P < 0.00001$), while nitrogen (scale(15N) = 0.312 ± 0.0.088; z = 3.57, $P = 0.00036$) and fishing pressure (scale(logfishing) = 0.225 ± 0.09; z = 2.48, $P = 0.013$) both had positive effects. For instance, wave intensity at East Point sites where infection was lowest averaged -3.3 compared with average values of -5.7 at the west end where infection was higher (Fig. 4). There was no effect of transect depth. The conditional R^2 (fixed and random effect influence) of the final model was 0.25 while the marginal R^2 (fixed effects only) was 0.13. Model diagnostics did not detect evidence of overdispersion ($P = 0.33$) or collinearity (all VIFs < 1.7). Residuals from the final model were weakly correlated to longitude ($r = -0.03$), suggesting incorporated predictor variables broadly accounted for the observed spatial pattern.

Discussion

Despite evidence of Black Spot Syndrome (BSS) from archival imagery of *A. tractus* as far back as 1985 (Elmer et al. 2019), we know relatively little about how BSS varies spatially among reef locations and its potential links to environmental factors. A key prerequisite to this inquiry is the development of consistent and repeatable survey methodologies. While many parasitic infections of fish require dissection or molecular-based sampling to detect and quantify, infection by the trematode *Scaphanocephalus* spp. – the primary etiological agent associated with BSS – can be counted via the conspicuous black spots formed on the otherwise pale bodies of ocean surgeonfish (Kohl et al. 2019). Building from this foundation, here we optimized the use of non-invasive and low-cost video transects conducted during SCUBA dives to quantify variation in BSS at specific depths along the leeward coast of Curaçao. Individual transects were relatively short in duration (~10 min) and could be performed by divers swimming in parallel yet sufficiently spaced to avoid filming the same individual fish (although note that this may depend on water clarity and safety concerns). Perhaps most importantly, video footage provides a permanent record that can be analysed by multiple, independent observers and archived for additional comparisons in the future, thereby helping to minimize methodological differences and measurement error among studies or observers. When analysing footage, for instance, reviewers can pause or replay the video to carefully examine individual fish, which will often be more consistent than attempting to classify spots while diving (including opportunities for post-processing of videos). Concordance analysis of our video transects showed high agreement between two independent reviewers, with an estimated intraclass correlation coefficient of 0.92. By including replicate transects at each depth and site, we were also able to show that the identity of the diver who conducted the transect did not affect estimates of BSS severity. These results highlight opportunities to extend and apply such video-based transects to evaluate patterns of BSS among islands and geographic regions, with application potential for management and conservation organizations. Community-based science by volunteer networks, including the recreational diving industry, offer additional avenues for obtaining video or photographic material and crowd-sourcing spot counts (e.g., Barve 2014, Daume 2016, Elmer et al. 2019).

Spatial distribution of BSS around Curaçao and insights into potential drivers

Across sites and transects, we detected a high overall prevalence of BSS (~70%) with considerable spatial variation in the average number of spots per surgeonfish around Curaçao. Prevalence and intensity of BSS were lowest in the southeast and highest toward the west end of the island. Longitude was therefore a strongly influential predictor in initial statistical models. On the east end of Curaçao, which is privately owned and associated with less urban and industrial development, BSS was present but the average number of spots per fish was often <2. Infection values increased from east to west along the island, with several western sites exhibiting average spot counts of 6 or higher (maximum count per fish: 55). Similar patterns in BSS distribution were reported on the neighbouring island of Bonaire (see Elmer et al. 2019). Using an ordinal classification system (range: 0 to 4), they found that BSS was lowest along the southern shores and increased around the city of Kralendijk and the northwestern portion of the island. The southeastern shores of both Curaçao and Bonaire are characterized by low anthropogenic development and strong offshore tradewinds, which could drive variation in BSS severity either directly or indirectly. The Bonaire study also reported a significant decrease in BSS with transect depth, which was not detected here. However, this is likely because we included only two depths – 2 and 5 m – whereas Elmer et al. (2019) surveyed at 2, 5, 12 and 18

m. They noted a substantial decrease in average infection among the deepest depths (12 and 18 m), which is consistent with the expectation that trematode exposure of fish is associated with nearshore sources. We selected only the two shallowest depths based on this finding as a way to optimize our survey time.

To better understand why BSS severity varied along Curaçao's leeward shoreline, we tested the influence of variables hypothesized to affect trematode infection or transmission. Surprisingly few studies have evaluated potential drivers of heterogeneity in trematode loads among fish on tropical reefs (Cribb et al. 2001, Williams et al. 2022). Based on a model selection approach, we found that the number of spots per surgeonfish was negatively associated with wave intensity and positively associated with nitrogen concentration and fishing pressure. No statistically significant effects were detected for hard coral cover, nearshore housing cover, herbivorous fish biomass or transect depth. Wave energy, which is generally greatest toward the eastern portion of the island subjected to tradewinds and the open ocean (van Duyl 1985), has the potential to adversely affect transmission between infective cercariae and suitable fish hosts. Although cercariae have tails and are free-swimming, they are generally short-lived (<24 hour) and unable to overcome significant water movement, such that calm, protected waters are advantageous for successful contact between cercariae and aquatic hosts (Combes et al. 2001). For instance, higher water velocity can damage trematode cercariae and inhibit infection of subsequent hosts (see Upatham 1974, Sousa & Grosholz 1991), as also found for some monogenean, fungal, and myxosporean parasites in aquatic systems (Barker & Cone 2000, Bodensteiner et al. 2000, Hallett & Bartholomew 2008). This same pattern is likely evident on Bonaire. A comparison of wave intensity scores for sites on the island by van Duyl (1985) suggests an inverse relationship with the BSS scores presented by Elmer et al. (2019), similar to that reported here. Wave energy is also very high on the north shore of Curaçao, which unfortunately precluded us from collecting data at such sites in the current study. Future surveys of the north shore conducted during calmer times of the year would provide a valuable comparison.

Nutrient pollution had a positive influence on the observed severity of BSS. As an indicator of sewage and domestic runoff, isotopically heavy nitrogen (delta-15-N) within algal tissue tends to be highest in the waters near the main city of Willemstad and lowest on less-populated eastern and western ends of the island (Klaus et al. 2004, Lapointe & Malin 2011, Sandin et al. 2022). Runoff of nutrients and other pollutants can enhance parasite infection through multiple mechanisms. Contaminant exposure can reduce immunological defenses and increase host susceptibility to trematode infection (Sures & Nachey 2022). Eutrophication associated with coastal runoff of N and P from wastewater elevates algal growth and can increase biomass of the herbivorous snails that serve as trematode intermediate hosts. Although the specific intermediate host for *Scaphanocephalus* spp. is not yet known, it is likely to be a snail found in coastal or shallow nearshore environments. In an experimental study, Johnson et al. (2007) showed that eutrophication caused both an increase in snail density and greater per-snail production of infective cercariae, which collectively elevated infections among second intermediate amphibian hosts by ~5-fold relative to non-eutrophic (ambient) conditions. Other studies have similarly linked nutrient runoff with increased helminth infections in both freshwater and marine ecosystems (Sasal et al. 2007, Johnson & Carpenter 2008, Johnson et al. 2010, Budria 2017).

Finally, higher fishing pressure also correlated positively with the average spot count per surgeonfish. Previous, comparative work in marine environments has found that fishing can be associated positively or negatively with parasite abundance, depending on transmission strategy (e.g., direct vs. multi-host life cycles) and the specific identity of the parasite. Wood et al. (2014) reported that while the abundance of many multi-host parasites decreased with higher fishing pressure, responses of trematodes were highly variable among species. For metacercariae of one trematode species that covaried positively with fishing pressure (i.e., *Stephanostomum* sp.), the authors hypothesized that harvest of predatory fish may release intermediate snail hosts from predation, thereby increasing the density of snails able to transmit trematode infective stages. How fishing affects trematode infections is likely to depend strongly on the hosts in the life cycle: for trematodes that use predatory fish as definitive hosts, high fishing pressure – which often targets higher trophic levels – is likely to lower host availability and reduce infection abundance. But for trematodes that use fish from lower trophic levels as second intermediate hosts and mature in fish-eating birds, as in the case for *Scaphanocephalus* spp., human-associated harvesting may increase host availability (i.e., by decreasing predation pressure on fish lower in the food web). Further comparisons both among islands and across locations with different fishing practices will help to understand the mechanistic links underlying this relationship. In a study from the Mediterranean, for instance, Cohen-Sanchez et al. (2023) reported higher average loads of *Scaphanocephalus* spp. metacercariae from razorfish (*Xyrichtys novacula*) outside of a marine protected area than within its borders, which the authors suggested could stem from differences in either parasite exposure or stress-mediated changes in host susceptibility.

This study characterized spatial variation in BSS severity among ocean surgeonfish from Curaçao and identified environmental factors that may help explain such patterns. Given that these relationships are correlational, it is important to recognize that other variables might additionally or alternatively be involved. For instance, if the distribution of fish-eating osprey – which are the only known definitive hosts of *Scaphanocephalus* in the Caribbean – mirrors that of human fishing pressure, observed spatial variation may emerge from differences in bird activity and its role in spreading parasite propagules, rather than any influence of human harvest (e.g., Fredensborg et al. 2006, Byers et al 2008). The additional movement of birds, fish, and water among sites all have the potential to alter the observed spatial pattern in ways that could alter or obscure the underlying mechanisms. These challenges are exacerbated by ongoing uncertainty about the identity of the first intermediate host for *Scaphanocephalus*, which so far has precluded additional comparisons between fish and infection within this source host. The high overall prevalence of BSS among surgeonfish reported in this study raises additional questions about the consequences of infection for individual fish hosts and how these might 'scale up' to affect the coral reef ecosystem. Future research to examine these questions – along with investigations into seasonal changes in the abundance of migratory osprey – would greatly help to advance this field. We highlight the utility of non-invasive, video-based transect methods for studying marine disease phenomena and hope to encourage other research groups, student courses, and community scientists to apply such tools in developing a larger-scale understanding of BSS in affected regions, including the Caribbean, the western Mediterranean, the Arabian Gulf, and Japan (Al-Salem et al. 2020, Shimose et al. 2020, Cohen-Sanchez et al. 2023).

Compliance with Ethical Standards

The authors declare no conflicts of interest. All applicable international, national, and institutional guidelines for the sampling, care, and use of organisms were followed, including necessary approvals.

Data availability

The data used as part of this study will be archived on Dryad (forthcoming).

Acknowledgments

For assistance in collecting transect data, we thank Rémon Malawauw, Lars ter Horst, Mike Lenstra, Julia Piaskowy, Nicole Brackenborough, Phaedra Hernández, and students of 2022-2023 *Coral Reef Ecology and Conservation* course at the University of Colorado. For help with processing video footage, we gratefully acknowledge the assistance of Kiara Gelbman and Phoebe Oehmig. Mark Vermeij generously provided feedback about the study design and logistical support through CARMABI. We thank the authors of Sandin et al. (2022) for providing the environmental data used in our analyses. Dana Calhoun, Petra Visser, and Zachary Kohl engaged in discussions helpful in shaping the manuscript. Funding for this project was provided, in part, by the David and Lucile Packard Foundation.

References

Aeby GS (2003) Corals in the genus Porites are susceptible to infection by a larval trematode. Coral Reefs 22:216. https://doi.org/10.1007/s00338-003-0310-9

Al-Salem AAM, Baghdadi HB, Mahmoud MA, Ibrahim M, Bayoumy EM (2020) Morphomolecular and pathological study of *Scaphanocephalus* sp. in new host *Siganus argenteus* in the Arabian Gulf. Dis Aquat Org 144: 221-230. https://doi.org/10.3354/dao03586

Amarasiri M, Furukawa T, Nakajima F, Sei K (2021) Pathogens and disease vectors/hosts monitoring in aquatic environments: potential of using eDNA/eRNA based approach. Sci Total Environ 796:148810. https://doi.org/10.1016/j.scitotenv.2021.148810

Barker E, Cone DK (2000) Occurrence of *Ergasilus celestis* (Copepoda) and *Pseudodactylogryrus anguillae* (Monogenea) among wild eels (*Anguilla rostrata*) in relation to stream flow, pH and temperature and recommendations for controlling their transmission among captive eels. Aquaculture 187:261-274. https://doi.org/10.1016/S0044-8486(00)00324-0

Barve V (2014) Discovering and developing primary biodiversity data from social networking sites: a novel approach. Ecol Inform 24:194-199. https://doi.org/10.1016/j.ecoinf.2014.08.008

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827-833. https://doi.org/10.1038/nature02691

Bernal MA, Floeter SR, Gaither MR, Longo GO, Morais R, Ferreira CEL, Vermeij MJ, Rocha LA (2015) High prevalence of dermal parasites among coral reef fishes of Curaçao. Mar Biodivers 46:67-74. https://doi.org/10.1007/s12526-015-0322-z

Bloch A, Al-Shaer L, Baumann B, Draud M, Itzkowitz M (2021) Composition changes and movements in mixed-species groups of algae grazing fish in Jamaica and Grand Cayman Island. Part II. Open J Mar Sci 11:41-54. https://doi.org/10.4236/ojms.2021.111003

Bodensteiner LR, Sheehan RJ, Wills PS, Brandenburg AM, Lewis WM (2000) Flowing water: an effective treatment for ichthyophthiriasis. J Aquat Anim Health 12:209-219. https://doi.org/10.1577/1548-8667(2000)012<0209:FWAETF>2.0.CO;2

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, ... Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9: 378-400. https://doi.org/10.32614/RJ-2017-066

Buck JC, Lutterschmidt WI (2017) Parasite abundance decreases with host density: evidence of the encounter-dilution effect for a parasite with a complex life cycle. Hydrobiologia 784:201-210. https://doi.org/10.1007/s10750-016-2874-8

Buck JC, Hechinger RF, Wood AC, Stewart TE, Kuris AM, Lafferty KD (2017) Host density increases parasite recruitment but decreases host risk in a snail-trematode system. Ecology 98: 2029-2038. https://doi.org/10.1002/ecy.1905

Burns JHR, Weyenberg G, Mandel T, Ferreira SB, Gotshalk D, Kinoshita CK, Marshall MJ, Del Moral NAV, Murphy SJ, Pascoe KH, Runyan A, Spengler AJ, Wells BD, Wilde DK, Pelayo R (2020) A comparison of the diagnostic accuracy of in-situ and digital image-based assessments of coral health and disease. Front Mar Sci 7: 304. https://doi.org/10.3389/fmars.2020.00304

Budria A (2017) Beyond troubled waters: the influence of eutrophication on host-parasite interactions. Funct Ecol 31:1348-1358. https://doi.org/10.1111/1365-2435.12880

Bullard SA, Overstreet RM (2008) Digeneans as enemies of fishes. Fish diseases 2: 817-976

Burkepile DE, Hay M E (2006) Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology 87:3128-3139. https://doi.org/10.1890/0012-9658(2006)87[3128:HVNCOM]2.0.CO;2

Byers JE, Blakeslee AMH, Linder E, Cooper AB, Maguire TJ (2008) Controls of spatial variation in the prevalence of trematode parasites infecting a marine snail. Ecology 89:439-451. https://doi.org/10.1890/06-1036.1

Cappo M, Harvey E, Malcolm H, Speare P (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In: Beumer JP, Grant A, Smith DC (eds) Aquatic protected areas: What works best and how do we know? Vol 1 (Cairns edn). University of Queensland, p 455−464.

Carrasco JL (2010) A generalized concordance correlation coefficient based on the variance components generalized linear mixed models for overdispersed count data. Biometrics 66: 897-904. https://doi.org/10.1111/j.1541-0420.2009.01335.x

Carrasco JL (2022) iccCounts: An R package to estimate the intraclass correlation coefficient for assessing agreement with count data. R J 14: 229-243. https://doi.org/10.32614/RJ-2022-034

Castañeda RA, Van Nynatten A, Crookes S, Ellender BR, Heath DD, MacIsaac HJ, Mandrak NE, Weyl OL (2020) Detecting native freshwater fishes using novel non-invasive methods. Front Environ Sci 29:8. https://doi.org/10.3389/fenvs.2020.00029

Cohen-Sánchez A, Valencia JM, Box A, Solomando A, Tejada S, Pinya S, Catanese G, Sureda A (2023) Black spot disease related to a trematode ectoparasite causes oxidative stress in *Xyrichtys novacula*. J Exp Mar Biol Ecol 560:151854. https://doi.org/10.1016/j.jembe.2022.151854

Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. University of Chicago Press, Chicago 60637

Côté IM, Green S, Hixon MA (2013) Predatory Fish Invaders: Insights from Indo-Pacific lionfish in the Western Atlantic and Caribbean. Biol Conserv 164:50-61. https://doi.org/10.1016/j.biocon.2013.04.014

Cribb T, Bray R, Littlewood D (2001) The nature and evolution of the association among digeneans, molluscs and fishes. Int J Parasitol 31:997-1011. https://doi.org/10.1016/S0020-7519(01)00204-1

Dalton SJ, Smith SD (2006) Coral disease dynamics at a subtropical location, Solitary Islands Marine Park, eastern Australia. Coral Reefs 25:37-45. https://doi.org/10.1007/s00338-005-0039-8

Daume S (2016) Mining Twitter to monitor invasive alien species-An analytical framework and sample information topologies. Ecol Inform 31:70-82. https://doi.org/10.1016/j.ecoinf.2015.11.014

De Graaf M, Simal F (2015) Quick scan to assess the prevalence of dermal parasites among coral reef fishes of Bonaire. IMARES Report C055/15, pp. 13

Dennis M, Izquierdo A, Conan A, Johnson K, Giardi S, Frye P, Freeman M (2019) *Scaphanocephalus*-associated dermatitis as the basis for black spot disease in Acanthuridae of St. Kitts, West Indies. Dis Aquat Org 137:53-63. https://doi.org/10.3354/dao03419

Eierman LE, Tanner CE (2019) Prevalence and severity of cutaneous pigmented lesions on ocean surgeonfish, *Acanthurus bahianus*, at Turneffe Atoll and Glover's Reef of Belize. Caribbean Naturalist 62: 1-11.

Elmer F, Kohl ZF, Johnson PTJ, Peachey RBJ (2019) Black spot syndrome in reef fishes: using archival imagery and field surveys to characterize spatial and temporal distribution in the Caribbean. Coral Reefs 38:1303-1315. https://doi.org/10.1007/s00338-019-01843-3

Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail-from small to large scale. Mar Biol 149:275-283. https://doi.org/10.1007/s00227-005-0184-1

Galaktionov K, Bustnes JO (1995) Species composition and prevalence of seabird trematode larvae in periwinkles at two littoral sites in North-Norway. Sarsia 80:187-191. https://doi.org/10.1080/00364827.1995.10413590

Gast GJ, Jonkers PJ, Van Duyl FC, Bak R P M (1999) Bacteria, flagellates and nutrients in island fringing coral reef waters: influence of the ocean, the reef and eutrophication. Bull Mar Sci 65:523-538.

Groner ML, Maynard J, Breyta R, Carnegie RB, Dobson A, Friedman CS, Froelich B, Garren M, Gulland FMD, Heron SF, Noble RT, Revie CW, Shields JD, Vanderstichel R, Weil E, Wyllie-Echeverria S, Harvell CD (2016) Managing marine disease emergencies in an era of rapid change. Philos Trans R Soc Lond B Biol Sci 371:20150364. https://doi.org/10.1098/rstb.2015.0364

Grutter AS (1998) Habitat-related differences in the abundance of parasites from a coral reef fish: an indication of the movement patterns of *Hemigymnus melapterus*. J Fish Biol 53:49-57. https://doi.org/10.1111/j.1095-8649.1998.tb00108.x

Hallett SL, Bartholomew JL (2008) Effects of water flow on the infection dynamics of *Myxobolus cerebralis*. Parasitology 135:371-384. https://doi.org/10.1017/S0031182007003976

Happel A (2019) A volunteer-populated online database provides evidence for a geographic pattern in symptoms of black spot infections. Int J Parasitol 10:156-163. https://doi.org/10.1016/j.ijppaw.2019.08.003

Harvell D, Aronson R, Baron N, Connell J, Dobson A, Ellner S, Gerber L, Kim K, Kuris A, McCallum H, Lafferty K, McKay B, Porter J, Pascual M, Smith G, Sutherland K, Ward J (2004) The rising tide of ocean diseases: unsolved problems and research priorities. Front

Ecol Environ 2:375-382. https://doi.org/10.1890/1540-9295(2004)002[0375:TRTOOD]2.0.CO;2
Houk P, Van Woesik R (2006) Coral reef benthic video surveys facilitate long-term monitoring in the Commonwealth of the Northern Mariana Islands: toward an optimal sampling strategy. Pac Sci 60:177-189. https://doi.org/10.1353/psc.2006.0005
Hutton RF (1964) A second list of parasites from marine and coastal animals of Florida. Trans Am Microsc Soc 83:439. https://doi.org/10.2307/3224765
Inohuye Rivera RB (1995) Helmintofauna de cuatro especies de cabrillas del género *Epinephelus* Bloch, 1793 (Osteichthyes: Serranidae) en la costa sudoriental de Baja California Sur, México. Doctoral dissertation, Instituto Politécnico Nacional. Centro Interdisciplinario de Ciencias Marinas.
Iwata K (1997) *Scaphanocephalus* larva from marine fishes of Iromote Island. Bull Inst Oceanic Res Devel Tokai Univ 18:43-50.
Jackson JBC, Donovan MK, Cramer KL, Lam VV (editors). (2014) Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
Johnson PTJ, Thieltges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. J Exp Biol 213:961-970. https://doi.org/10.1242/jeb.037721
Johnson PTJ, Chase JM, Dosch KL, Hartson RB, Gross JA, Larson DJ, Sutherland DR, Carpenter S R (2007) Aquatic eutrophication promotes pathogenic infection in amphibians. Proc Natl Acad Sci USA 104:15781-15786. https://doi.org/10.1073/pnas.0707763104
Johnson PTJ, Carpenter S R (2008) Influence of eutrophication on disease in aquatic ecosystems: patterns, processes, and predictions. Chapter 4 (pp. 71-99) in Ostfeld R S, Keesing F, Eviner

V T, Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems. Princeton University Press, Princeton, NJ. https://doi.org/10.1515/9781400837885.71

Johnson PTJ, Preston DL, Hoverman JT, Richgels KL (2013) Biodiversity decreases disease through predictable changes in host community competence. Nature 494:230-233. https://doi.org/10.1038/nature11883

Klaus JS, Frias-Lopez J, Bonheyo GT, Heikoop JM, Fouke BW (2005) Bacterial communities inhabiting the healthy tissues of two Caribbean reef corals: interspecific and spatial variation. Coral Reefs 24:129-137. https://doi.org/10.1007/s00338-004-0447-1

Klaus JS, Janse I, Heikoop JM, Sanford RA, Fouke BW (2007) Coral microbial communities, zooxanthellae and mucus along gradients of seawater depth and coastal pollution. Environ Microbiol 9:1291-1305. https://doi.org/10.1111/j.1462-2920.2007.01249.x

Kohl ZF, Calhoun DM, Elmer F, Peachey RBJ, Leslie KL, Tkach V, Kinsella JM, Johnson PTJ (2019) Black-spot syndrome in Caribbean fishes linked to trematode parasite infection (*Scaphanocephalus expansus*). Coral Reefs 38:917-930. https://doi.org/10.1007/s00338-019-01819-3

Koprivnikar J, Thieltges DW, Johnson PTJ (2023) Consumption of trematode parasite infectious stages: from conceptual synthesis to future research agenda. J Helminthol 97: E33. https://doi.org/10.1017/S0022149X23000111

Lacerda A, Roumbedakis K, Bereta Junior J, Nuñer A, Petrucio M, Martins M (2017) Fish parasites as indicators of organic pollution in southern Brazil. J Helminthol 92:322-331. https://doi.org/10.1017/S0022149X17000414

Lafferty KD (2008) Ecosystem consequences of fish parasites. J Fish Biol 73:2083-2093. https://doi.org/10.1111/j.1095-8649.2008.02059.x

Lafferty KD, Harvell CD (2014) The role of infectious diseases in marine communities. Chapter 5 in: Marine Community Ecology and Conservation (eds. Bertness, MD, Bruno, JF, Silliman, BR & Stachowicz, JJ). Sinauer Associates Sunderland Massachusetts, pp. 85-108.

Lamb JB, Willis BL, Fiorenza EA, Couch CS, Howard R, Rader DN, True JD, Kelly LA, Ahmad A, Jompa J, Harvell CD (2018) Plastic waste associated with disease on coral reefs. Science 359:460-462. https://doi.org/10.1126/science.aar3320

Lapointe BE, Mallin MA (2011) Nutrient enrichment and eutrophication on fringing coral reefs of Bonaire and Curaçao, Netherlands Antilles. Report to the United Nations Environment Programme for the NACRI Coral Reef Monitoring Program, Harbor Branch Oceanographic Institute, Ft Pierce Fl, 42.

Lin LIK (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 45: 255-268. https://doi.org/10.2307/2532051

Lüdecke D, Patil I, Ben-Shachar MS, Wiernik BM, Waggoner P, Makowski D (2021) performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6:3139-3149. https://doi.org/10.21105/joss.03139

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952-2012). Fish Res 154:44-62. https://doi.org/10.1016/j.fishres.2014.01.019

McManus J (2000) Coral reef fishing and coral-algal phase shifts: implications for global reef status. ICES J Mar Sci 57:572-578. https://doi.org/10.1006/jmsc.2000.0720

Packer C, Holt RD, Hudson PJ, Lafferty KD, Dobson AP (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecol Lett 6:797-802. https://doi.org/10.1046/j.1461-0248.2003.00500.x

Paula JR, Sun D, Pissarra V, Narvaez P, Rosa R, Grutter AS, Sikkel PC (2021) The role of corals on the abundance of a fish ectoparasite in the Great Barrier Reef. Coral Reefs 40:535-542 https://doi.org/10.1007/s00338-021-02051-8

Pietrock M, Marcogliese DJ (2003) Free-living endohelminth stages: at the mercy of environmental conditions. Trends Parasitol 19:293-299. https://doi.org/10.1016/S1471-4922(03)00117-X

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Ríos-Castro R, Romero A, Aranguren R, Pallavicini A, Banchi E, Novoa B, Figueras A (2021) High-throughput sequencing of environmental DNA as a tool for monitoring eukaryotic communities and potential pathogens in a coastal upwelling ecosystem. Front Vet Sci 8:765606. https://doi.org/10.3389/fvets.2021.765606

Robertson D, Ackerman J, Choat J, Posada J, Pitt J (2005) *Acanthurus tractus*. I. The geography of demography. Mar Ecol Prog Ser 295:229-244. https://doi.org/10.3354/meps295229

Sandin SA, Alcantar E, Clark R, de León R, Dilrosun F, Edwards CB, ... Vermeij MJ (2022) Benthic assemblages are more predictable than fish assemblages at an island scale. Coral Reefs 41:1031-1043. https://doi.org/10.1007/s00338-022-02272-5

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS ONE 3:e1548. https://doi.org/10.1371/journal.pone.0001548

Sasal P, Mouillot D, Fichez R, Chifflet S, Kulbicki M (2007) The use of fish parasites as biological indicators of anthropogenic influences in coral-reef lagoons: a case study of Apogonidae parasites in New Caledonia. Mar Pollut Bull 54:1697-1706. https://doi.org/10.1016/j.marpolbul.2007.06.014

Shimose T, Katahira H, Kanaiwa M (2020) Interspecific variation of prevalence by *Scaphanocephalus* (Platyhelminthes: Trematoda: Heterophyidae) metacercariae in parrotfishes (Labridae: Scarini) from an Okinawan coral reef. Int J Parasitol 12:99-104.https://doi.org/10.1016/j.ijppaw.2020.05.007

Skinner RH (1978) Some external parasites of Florida fishes. Bull Mar Sci 28:590−595

Smith NF (2001) Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts. Oecologia 127:115-122.https://doi.org/10.1007/s004420000560

Sousa WP, Grosholz ED (1991) The influence of habitat structure on the transmission of parasites. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat Structure. Population and Community Biology Series, vol 8. Springer, Dordrecht. https://doi.org/10.1007/978-94-011-3076-9_15

Stumbo AD, James CT, Goater CP, Wisenden BD (2012) Shoaling as an antiparasite defence in minnows (*Pimephales promelas*) exposed to trematode cercariae. J Anim Ecol 81:1319-1326. https://doi.org/10.1111/j.1365-2656.2012.02012.x

Sures B, Nachev M (2022) Effects of multiple stressors in fish: how parasites and contaminants interact. Parasitology 149:1822-1828. https://doi.org/10.1017/S0031182022001172

Tracy AM, Pielmeier ML, Yoshioka RM, Heron SF, Harvell CD (2019) Increases and decreases in marine disease reports in an era of global change. Proc R Soc B 286:20191718. https://doi.org/10.1098/rspb.2019.1718

Tubangui MA (1933) Trematode parasites of Philippine vertebrates, VI. Descriptions of new species and classification. Philipp J Sci 52:167-197.

Upatham ES (1974) Dispersion of St. Lucian *Schistosoma mansoni* cercariae in natural standing and running waters determined by cercaria counts and mouse exposure. Ann. Parasitol. 68:343-352. https://doi.org/10.1017/S0031182000045698

Van den Hoek C, Cortel-Breeman A, Wanders J (1975) Algal zonation in the fringing coral reef of curaçao, Netherlands Antilles, in relation to zonation of corals and gorgonians. Aquat Bot 1:269-308. https://doi.org/10.1016/0304-3770(75)90028-5

Van Duyl F C (1985) Atlas of the Living Reefs of Curaçao and Bonaire (Netherlands Antilles). Foundation for Scientific Research in Surinam and the Netherlands Antilles, Vol. 117, Utrecht.

Waitt Institute (2017). Marine Scientific Assessment: The State of Curaçao's Coral Reefs. The Waitt Institute.

Welsh JE, Liddell C, Van der Meer J, Thieltges DW (2017) Parasites as prey: the effect of cercarial density and alternative prey on consumption of cercariae by four non-host species. Parasitology 144:1775-1782 https://doi.org/10.1017/S0031182017001056

Williams MA, Faiad S, Claar DC, French B, Leslie KL, Oven E, Guerra SA, Micheli F, Zglinczynski BJ, Haupt AJ, Sandin SA, Wood CL (2022) Life history mediates the association between parasite abundance and geographic features. J Anim Ecol 91:996-1009. https://doi.org/10.1111/1365-2656.13693

Wood CL, Sandin SA, Zgliczynski B, Guerra AS, Micheli F (2014) Fishing drives declines in fish parasite diversity and has variable effects on parasite abundance. Ecology 95:1929-1946. https://doi.org/10.1890/13-1270.1

Fig. 1

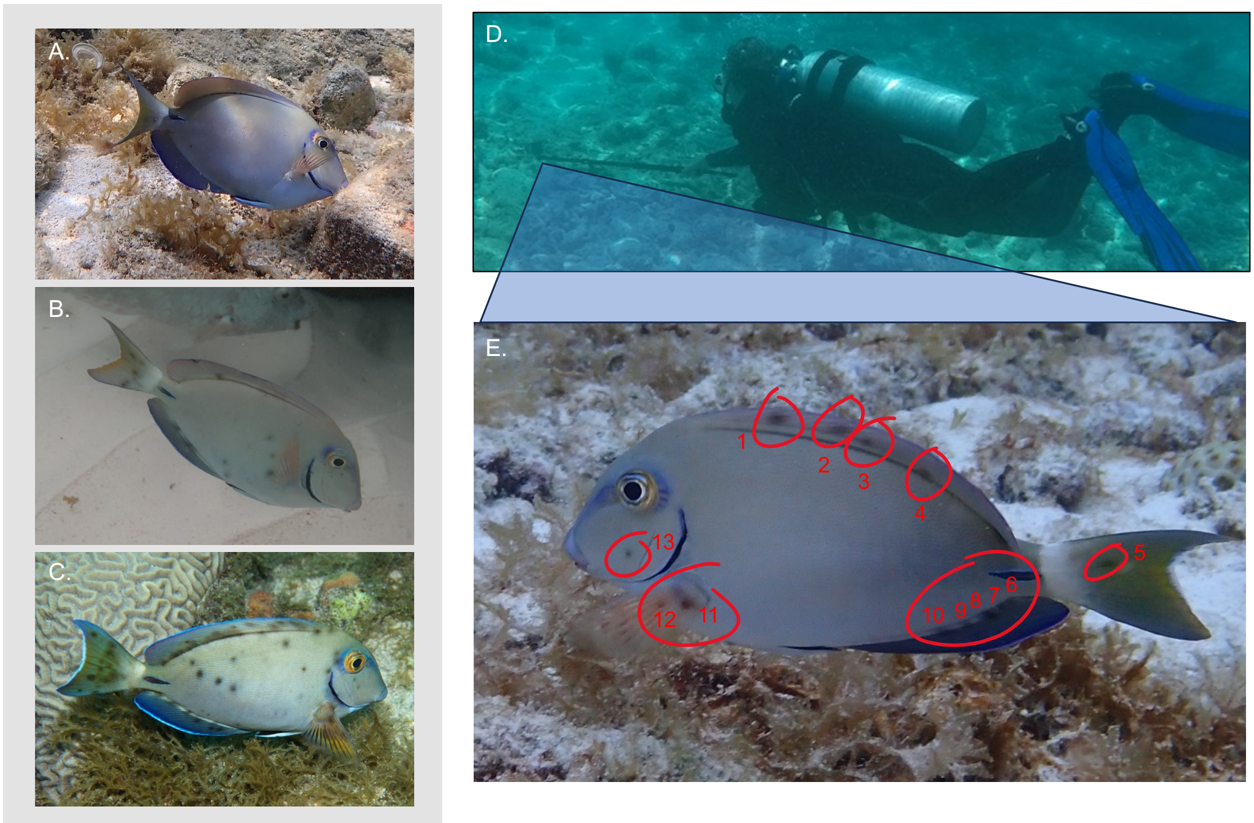

Figure 1. Black Spot Syndrome in ocean surgeonfish (*Acanthurus tractus*) from Curaçao. The number of spots per fish varies in severity among fish (see panels A [3 spots], B [18 spots], and C [58 spots]). After divers collect video footage during depth-specific transects (D), reviewers of the footage quantify the number of spots per fish on one side of each fish (see E). Red circles on in the last panel shown to illustrate counting process. Images by C. de Wit and P. Johnson

Fig. 2

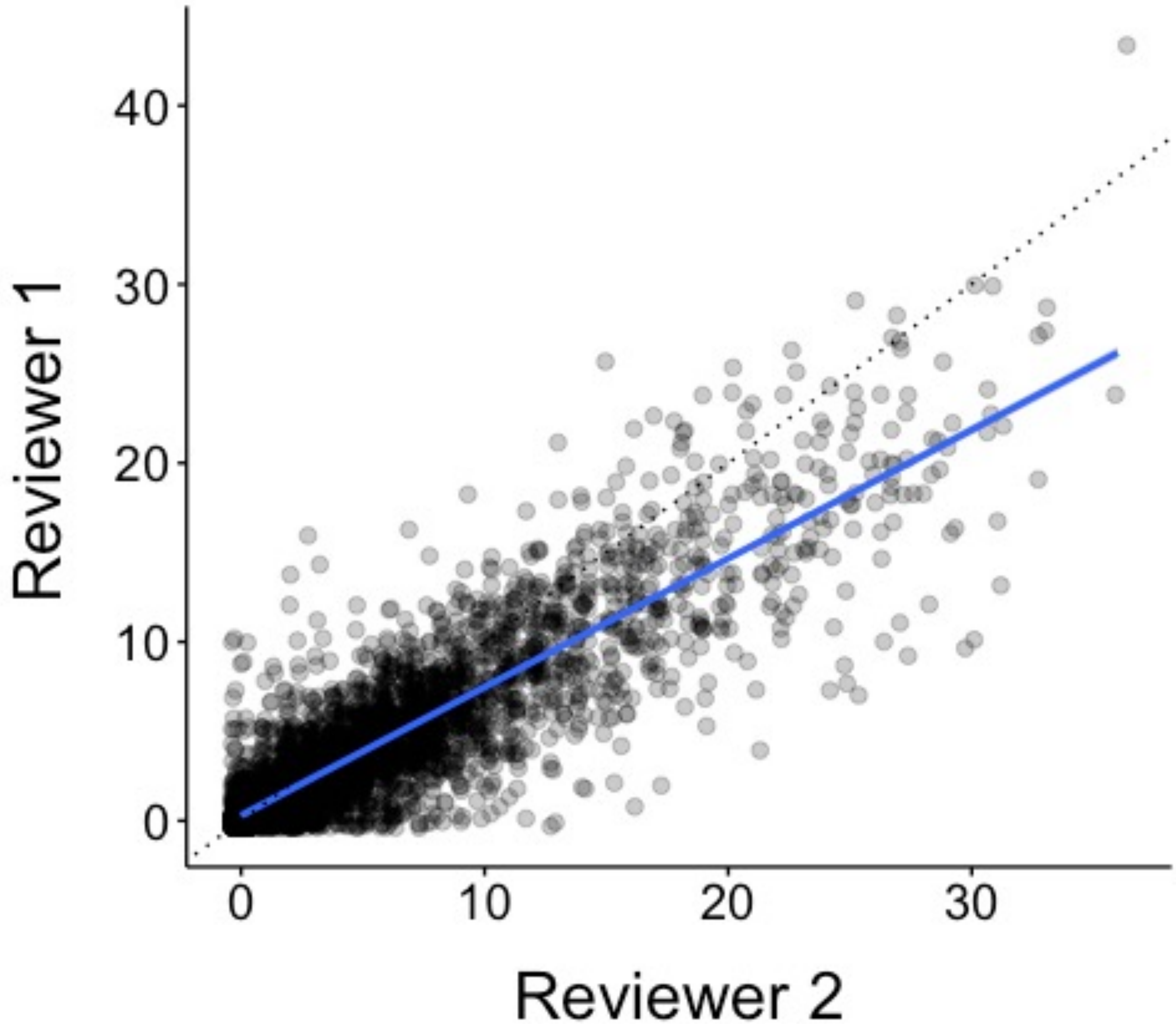

Figure 2. Concordance between reviewers in quantifying spots per fish among surgeonfish from video transects. For most individual fish (*n* = 4,495), two independent reviewers reviewed the footage and estimated the presence and number of spots. The dashed line represents the 1:1 line, while the solid blue line illustrates a linear fit between observations. The concordance coefficient between reviewers was estimated as 0.915 (95% CI = 0.905 to 0.924)

Fig. 3

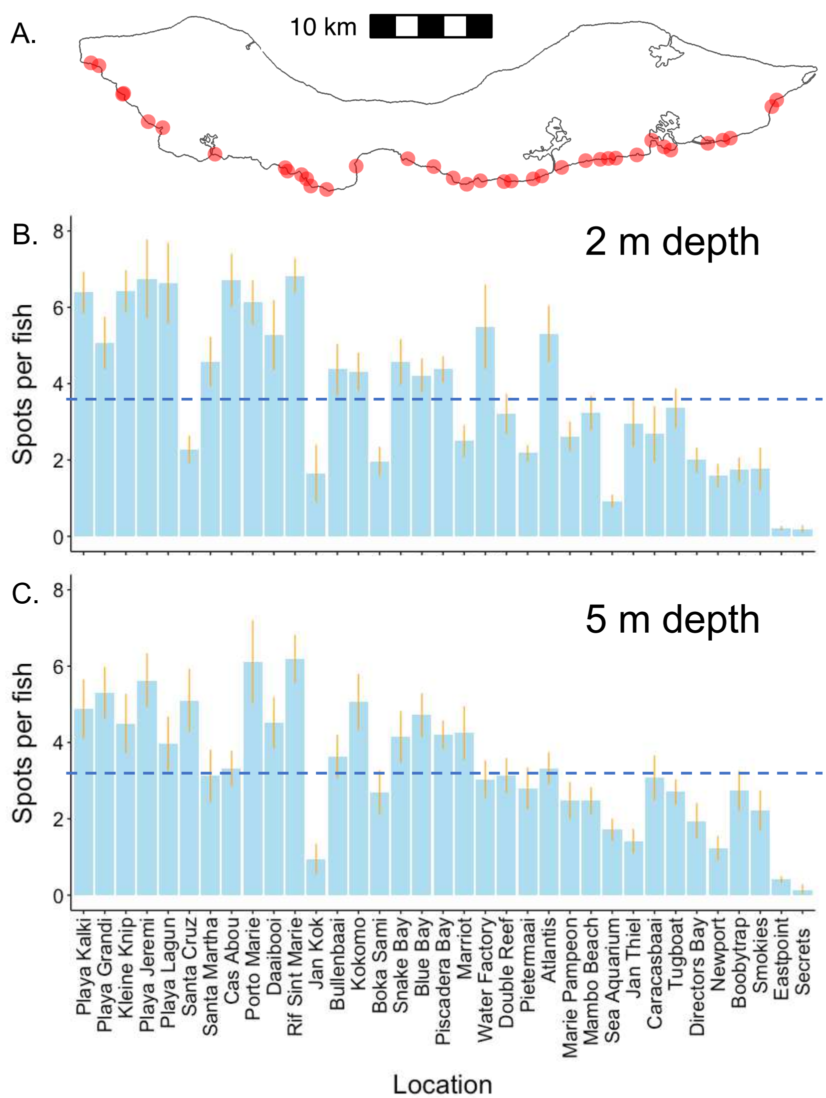

Figure 3. Variation in Black Spot Syndrome in ocean surgeonfish across sites and depths in Curaçao. Among the 35 sites sampled along the southern coastline (see red circles in map panel A), BSS severity (average spots per fish ± 1 SE) varied from <1 near the eastern edge of the island to upwards of 7 farther to the west. No overall difference was detected between transects conducted at 2 m depth (B) versus those at 5 m (C). Dashed horizontal lines represent the average counts per fish for each depth.

Fig. 4

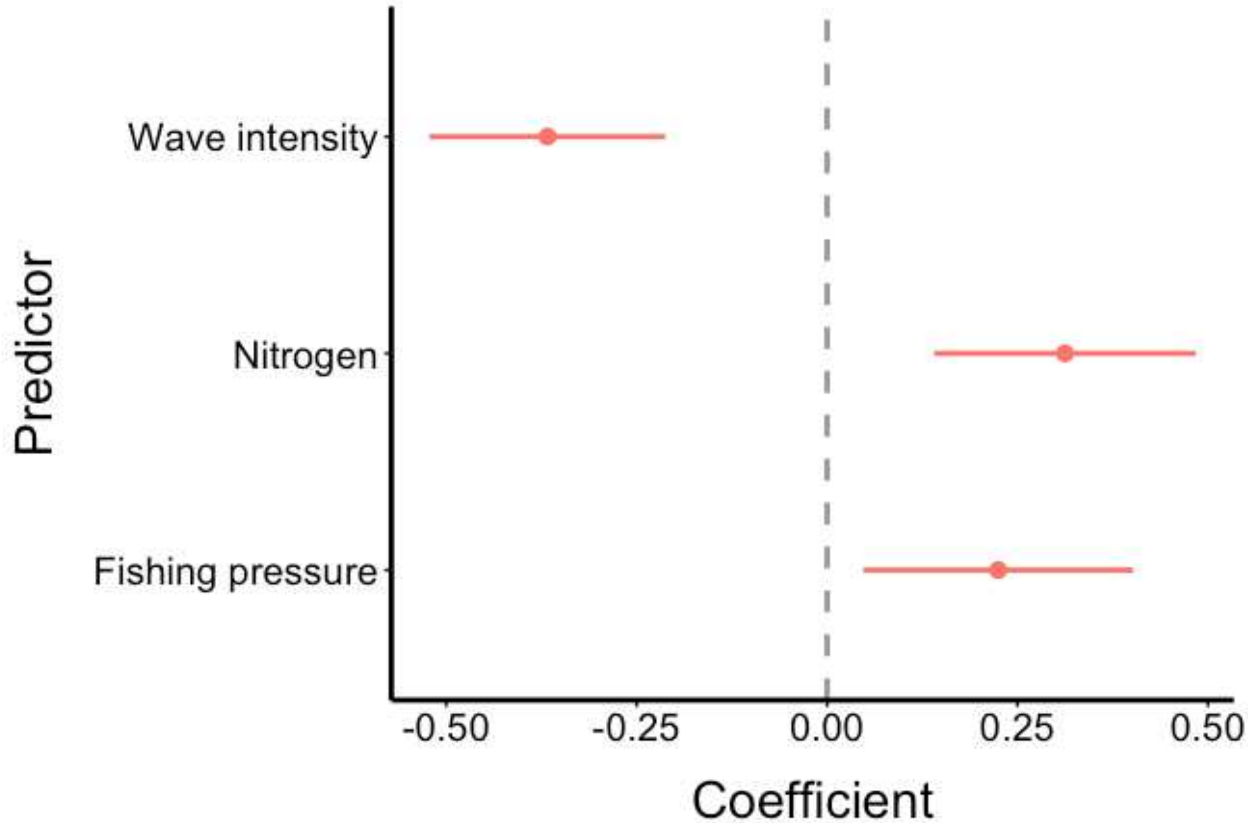

Figure 4. Influence of environmental variables on BSS severity among sites. Depicted is a coefficient plot illustrating the effect ± 1 SE of terms retained in the best-fitting model predicting BSS counts per fish across all transects and sites. Predictor terms were centered and scaled prior to inclusion to facilitate comparison of effect sizes. The vertical dashed line at zero indicates a lack of any effect

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- AppendixSOPBSS.docx