



REPORT

Parasitism in reef fish communities: evaluating the roles of host traits, habitat use, and phylogeny on infection by *Scaphanocephalus* (Trematoda)

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Received: 12 November 2023 / Accepted: 26 January 2024 / Published online: 11 March 2024
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Abstract Parasites represent a critically understudied component of reef communities—a knowledge gap that has become more evident as infectious diseases emerge. Here, we test the roles of competing ecological and evolutionary factors in driving infections by an emerging infectious phenomenon: Black spot syndrome (BSS) in Caribbean reef fishes. BSS, a condition associated with localized hyperpigmentation in the dermis and fins of fishes, has recently been linked to infection by trematode parasites in the genus *Scaphanocephalus*. Using phylogenetic generalized linear mixed models, we evaluated the influence of host phylogeny, habitat preference, body size, and trophic position on infection abundance. Metacercariae of *Scaphanocephalus* were recorded in 29 of 41 fish species, including 21 new host species records, and within 306 fish (62.3% prevalence). Among species, infection load increased significantly with host body size and decreased with host trophic level, such that large-bodied herbivores tended to support the most infection. There was no significant effect of host phylogeny on infection load. These results suggest the parasite is a generalist in its use of fish intermediate hosts and emphasize the influence of local variation in parasite exposure risk. Overall, the count of visible spots per fish was a positive predictor of *Scaphanocephalus* abundance among species and individuals, although not all fish species exhibited spots, even when infection loads were high. Findings from this study indicate that *Scaphanocephalus* infections are far more prevalent

in reef fishes than previously recognized and highlight the importance of investigating infection patterns beyond the external symptoms of BSS.

Keywords Black-spot syndrome · Trematode · Host–parasite interaction · Emerging wildlife disease

Introduction

Coral reef ecosystems support some of the most spectacular displays of animal biomass and biodiversity worldwide (see Spalding et al. 2001; Hovland 2008; Duffy et al. 2016). This includes multi-faceted interactions between species, including those between predators and prey, corals and algal symbionts, and cleaner species and ectoparasitic infestations (Boaden and Kingsford 2015; LaJeunesse et al. 2018; Sikkell and Welicky 2019). Yet we know considerably less about the endoparasite communities within reef-dwelling species, in part because they are often hidden from view. In well-studied marine systems, such as temperate coastlines and estuaries, macroparasites can account for substantial biomass, a large fraction of food web links, and entail effects on host behavior, growth, and survival (Barber et al. 2000; Heins and Baker 2008; Lafferty et al. 2008). Within reef systems, however, both the diversity of endoparasites and their ecological roles remain open questions (see Dyer et al. 1985; Wood et al. 2015; Bray et al. 2016).

Digenetic trematodes are often among the most abundant parasites in intertidal and coastal environments (Lauckner 1984; Mouritsen and Poulin 2002; Kuris et al. 2008). These flatworm parasites typically use three different hosts in their life cycles: gastropods as first intermediate hosts, a range of (in)vertebrates as second intermediate hosts, and vertebrates as definitive hosts (Schell 1985; Esch et al.

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2002). Eggs are released with the feces of definitive hosts and become infective to the first intermediate host (often a snail). Within the first intermediate host, asexual reproduction leads to the release of large numbers of free-living cercariae that subsequently infect second intermediate hosts and form an encysted stage called a metacercaria. Infected second intermediate hosts are consumed by the definitive host, wherein parasites mature into the adult stage and reproduce sexually. Owing to the involvement of multiple hosts in their life cycles, digenean parasites can influence ecosystem dynamics across trophic levels (Mouritsen and Poulin 2010; Poulin et al. 2016). For example, high loads of trematode metacercariae can increase mortality of juvenile fish (Lemly 1984; Jacobson et al. 2008) or alter their behavior in ways that increase predation by definitive hosts (Shaw et al. 2009). In estuaries, the annual production of cercariae by infected snails was reported to exceed that of total bird biomass by threefold to tenfold (Kuris et al. 2008). These examples highlight the importance of understanding the roles of trematodes in marine environments, including coral reef ecosystems.

Over the last decade, multiple studies have reported conspicuous black spots on the fins or epidermis of Caribbean reef fish species (Bernal et al. 2016; Dennis et al. 2019; Eierman and Tanner 2019; Elmer et al. 2019; Kohl et al. 2019). Reports of this phenomenon, referred to as Black Spot Syndrome (BSS), often involve surgeonfishes and parrotfishes from areas such as Bonaire, Curaçao, St. Kitts, Belize, and Turks and Caicos. Kohl et al. (2019) linked BSS to infection by *Scaphanocephalus expansus*, a digenetic trematode that encysts in the fins and skin of tropical marine fishes. Immunological responses by the host coupled with pathology induced by the parasite lead to the characteristic black spots, which correlate directly with the number of encysted metacercariae (Kohl et al. 2019). Herbivorous fish species, which have been increasingly identified as important for the health of Caribbean reef ecosystems (Cheal et al. 2010; Dell et al. 2020), appear to be disproportionately affected by BSS (Elmer et al. 2019). Osprey (*Pandion haliaetus*), the definitive host, become infected with *Scaphanocephalus* spp. after consuming infected fish, while the first intermediate host is as of yet unknown. Examinations of archived museum samples of surgeonfishes and parrotfishes from Curaçao and Bonaire indicate that *Scaphanocephalus* infection load has increased by roughly 30-fold since 1905, raising questions about both the drivers and potential consequences of its emergence (Johnson et al. unpublished). There is also evidence that more than one species of the parasite occur sympatrically in the Caribbean (see Dennis et al. 2019), leading us hereafter to refer generically to the parasite as “*Scaphanocephalus*”.

To date, 17 species of reef fishes known to occur in the Caribbean have been reported with *Scaphanocephalus*

infection (Hutton 1964; Skinner 1982; Montoya-Mendoza et al. 2004; Bullard and Overstreet 2008; Overstreet and Hawkins 2017; Kohl et al. 2019; Roberts 2021). The host records include several species that are consumed by humans, either commercially or recreationally, such as: *Caranx ruber*, *Cephalopholis cruentata*, *Sparisoma aurofrenatum*, and *S. chrysopterum*. Because many such records are based on small sample sizes or from species conspicuously afflicted with BSS, little is known about how the prevalence and abundance of *Scaphanocephalus* varies among fish species in the broader community. Expanding on this knowledge may provide key insights into the factors that determine host-infection exposure as well as susceptibility (Valenzuela-Sánchez et al. 2021). Moreover, several reports have described black spots in Caribbean fish species that resemble BSS but have yet to be examined for *Scaphanocephalus*, such as *Halichoeres poeyi* and *Xyrichtys splendens* (de Graaf and Simal 2015; Bernal et al. 2016; Eierman and Tanner 2019). Thus, we suspect that knowledge of the second intermediate fish host community is incomplete, which represents an important knowledge gap for understanding the drivers of infection and their potential consequences for reef ecosystems.

The primary goals of this study were to determine how *Scaphanocephalus* infection varies among fish species within nearshore reef communities and to identify the combination of host-, environmental-, and evolutionary factors that contribute to infection patterns. We focused on the fish communities near coral reefs of Curaçao, an island in the southern Caribbean that has been identified as a hotspot for BSS (e.g., Elmer et al. 2019). By examining a large taxonomic range of species, including 41 species across 18 families and 12 orders, we compared the explanatory influence of host life history, habitat use, and host phylogeny on trematode parasite abundance. We included two reef locations known to vary considerably in BSS severity (de Wit and Johnson personal observations), thereby creating a likely gradient in parasite exposure. Among fish species, we tested competing hypotheses about the roles of host body size, trophic position, habitat use, and phylogeny on infection load. Such questions have rarely been explored in reef ecosystems (see Poulin et al. 2016). Across 11 islands in the Pacific Line Islands, for instance, Williams et al. (2022) reported that island area and island isolation both significantly predicted parasite abundance. However, these relationships depended critically on parasite type and life history (direct vs. complex life histories). Here, we focused specifically on the roles of host traits (both within- and among species) and habitat characteristics in determining variation in the abundance of a complex life cycle trematode. We additionally assessed the link between visibly external spots and infection by *Scaphanocephalus* across a wider range of fish species than considered previously.

Materials and methods

Study locations and fish collection

This study was conducted on the fringing reefs of Curaçao, an oceanic island in the southern Caribbean. Fish were collected at two different locations along the south coast: Piscadera Bay (12° 07' 14.8" N 68° 58' 11.4" W) and Rif St. Marie (12° 11' 49.6" N 69° 04' 45.5" W), between March and December of 2022. Piscadera Bay, which is situated between two limestone cliffs on the western side of Otrobanda, is moderately developed. Located nearby are several major hotels, restaurants, as well as the Caribbean Research and Management of Biodiversity Foundation (CARMABI) field station. Rif St. Marie is located farther west along the leeward shoreline and is comparatively less developed, surrounded by mud flats, shrubland and forests that collectively provide habitat to flamingos and other waterbirds (Cuppens and Vogels 2004). The location was designated as a conservation area in 1995 (Debrot et al. 1999). Based on previous, noninvasive surveys of BSS in *Acanthurus tractus* (ocean surgeonfish), these two sites were expected to encompass a broad range in infection values, with Piscadera Bay in the low to moderate range and Rif St. Marie standing out as one of the sites with the highest detected BSS values (de Wit and Johnson personal observations). By sampling a diversity of fish species at both sites, we sought to evaluate the relative influences of fish species identity as well as sample site in determining observed parasite load. We expected that differences between sites were associated with variation in parasite exposure, whereas variation in infection among species represents a combination of both parasite exposure and host susceptibility.

To understand the patterns of *Scaphanocephalus* infection and how they varied among shallow water reef fish, our target fish species were chosen to encompass broad variation in trophic level, phylogeny, body size, habitat use, and diet (see Table 1). Additionally, several fish species were chosen based on previous visual surveys of dermal parasites among reef fishes of Bonaire (de Graaf and Simal 2015). All collected species are relatively abundant in the shallow waters of Curaçao. Individual fish were collected haphazardly, rather than based on the presence of black spots or other infection symptoms. Fish were collected using a variety of approved methods, such as hand nets, seine nets, pole spears, and angling, and euthanized by hypothermic shock followed by carbon dioxide immersion. After collection, fishes were frozen until dissection. Fish taxonomy followed FishBase (Froese and Pauly 2023), although it should be noted that current evidence suggests the parrotfish belong in the family Labridae, rather than Scaridae as indicated by FishBase (see Westneat and Alfaro 2005). All protocols were in accordance with guidelines from the University of Colorado Boulder

Institutional Animal Care and Use Committee (approval number 2844).

Fish dissections and parasite identification

Based on the insights from preliminary dissections and previous research (e.g., Kohl et al. 2019), we developed a streamlined protocol to detect and quantify BSS and parasites from the fins and dorsal sections of the skin and muscle on one side of the fish (selected at random). We assumed similar numbers of parasites on each side of the fish, given that similar numbers of black spots occur on both sides (Elmer et al. 2019). For a subset of 152 fish, the number of externally visible black spots were recorded for one entire side of the fish prior to freezing. At necropsy, fish were thawed, measured (total length), and photographed. An incision was made in the epidermis (just under the scales) from the base of the caudal fin anteriorly to the base of the pectoral, then upwards toward the dorsal fin and along the dorsal ridge back to the caudal fin base, creating a 'dissection window' that scaled with fish length. The epidermis was carefully peeled off the dermis and muscle layer, and the dissection window (length and width) was measured using calipers or with the program ImageJ (Abràmoff et al. 2004). The removed dissection window epidermis was placed on a gridded Petri dish and examined using bottom illumination. The underlying muscle tissue on the fish was examined using top illumination and teased apart to detect any metacercariae. The dorsal, caudal, and one pectoral fin were removed and examined for parasites under a stereo dissecting microscope. Because transmitted light often did not completely penetrate the base of fins or, for some species, the entire fins, we also removed the outermost layer of epidermis from the fins to increase parasite detection.

All encysted metacercariae were removed from the host and identified. On a subset of cysts within each dissected fish (at least 5 per host, or all cysts for fish with infection loads of < 5), metacercariae were mechanically excysted and further examined using a compound microscope (40–200× magnification). Excysted parasites were identified using key morphological traits (see Schell 1985; Hoffman 1999; Bray et al. 2008). *Scaphanocephalus* was identified based on its distinctive, wing-shaped anterior expansions, a characteristic that is specific to the genus (Kohl et al. 2019; Fig. 2E). The quantity of metacercariae was recorded for each of five body locations (epidermal tissue of the dissection window, muscle tissue underlying the dissection window, dorsal fin, caudal fin, and pectoral fin).

Statistical analysis

To explore which factors influenced variation in *Scaphanocephalus* load among fish (number of metacercariae per

Table 1 Overview of fish species examined for *Scaphanocephalus* spp. infection and results

Species	Common name	Family	N sampled	Previously recorded	Prevalence	Abundance	Load range	Trophic level
<i>Acanthurus chirurgus</i>	Doctorfish	Acanthuridae	1	Yes ^{1,2,4}	1.00	1.00	1	2.1
<i>Acanthurus coeruleus</i>	Blue tang	Acanthuridae	14	Yes ^{1,2}	0.07	0.71 ± 0.07	0–1	2.2
<i>Acanthurus tractus</i>	Ocean surgeonfish	Acanthuridae	64	Yes ^{1,2,3,4}	0.80	21.34 ± 3.88	0–167	2.0
<i>Aulostomus maculatus</i> *	Atlantic trumpetfish	Aulostomidae	18	No	0.66	6.38 ± 2.58	0–46	4.3
<i>Platybelone argalus</i>	Keel-tail needlefish	Belonidae	1	No	0.00	0.00	0	4.5
<i>Bothus lunatus</i> *	Plate fish	Bothidae	1	No	1.00	1.00	1	4.5
<i>Caranx bartholomaei</i> *	Yellow jack	Carangidae	2	No	1.00	1.00 ± 0.00	1	4.5
<i>Caranx crysos</i> *	Blue runner	Carangidae	5	No	0.60	0.60 ± 0.24	0–1	4.1
<i>Caranx ruber</i>	Bar jack	Carangidae	6	Yes ^{1,3}	0.67	3.12 ± 1.74	0–10	4.3
<i>Trachinotus goodei</i>	Great pompano	Carangidae	1	No	0.00	0.00	0	4.3
<i>Chaetodon ocellatus</i> *	Spotfin butterflyfish	Chaetodontidae	1	No	1.00	60.00	0	3.7
<i>Cephalopholis cruentata</i>	Graysby	Epinephelidae	10	Yes ^{1,4}	0.10	0.50 ± 0.50	0–5	4.3
<i>Cephalopholis fulva</i> *	Coney	Epinephelidae	2	No	1.00	7.50 ± 0.50	7–8	4.1
<i>Gerres cinereus</i>	Yellowfin mojarra	Gerreidae	1	No	0.00	0.00	0	3.5
<i>Brachygenys chrysargyreum</i> *	Smallmouth grunt	Haemulidae	16	No	0.19	0.19 ± 0.101	0–1	3.5
<i>Haemulon flavolineatum</i>	French grunt	Haemulidae	18	No	0.00	0.00	0	3.5
<i>Holocentrus adscensionis</i>	Squirrelfish	Holocentridae	7	No	0.00	0.00	0	3.1
<i>Myripristis jacobus</i> *	Blackbar soldierfish	Holocentridae	39	No	0.77	8.54 ± 1.96	0–55	3.4
<i>Clepticus parrae</i> *	Creole wrasse	Labridae	18	No	0.44	1.61 ± 0.71	0–10	3.4
<i>Scarus iseri</i> *	Striped parrotfish	Labridae	17	No	0.71	11.35 ± 5.12	0–73	2.0
<i>Scarus taeniopterus</i> *	Princess parrotfish	Labridae	43	No	0.86	25.14 ± 7.61	0–240	2.0
<i>Sparisoma aurofrenatum</i>	Redband parrotfish	Labridae	53	Yes ^{1,3,4}	0.91	63.55 ± 14.37	0–564	2.0
<i>Sparisoma chrysopteron</i>	Redtail parrotfish	Labridae	21	Yes ¹	0.81	14.48 ± 4.25	0–64	2.0
<i>Sparisoma rubripinne</i> *	Redfin parrotfish	Labridae	2	No	1.00	31.00 ± 12.00	19–43	2.0
<i>Sparisoma viride</i> *	Stoplight parrotfish	Labridae	18	No	0.56	5.06 ± 3.32	0–60	2.0
<i>Halichoeres bivittatus</i>	Slippery dick	Labridae	1	No	0.00	0.00	0	3.8
<i>Halichoeres garnoti</i> *	Yellowhead wrasse	Labridae	15	No	0.87	3.33 ± 0.98	0–14	3.7
<i>Halichoeres pictus</i> *	Rainbow wrasse	Labridae	1	No	1.00	1.00	1	3.5
<i>Xyrichtys martincensis</i> *	Rosy razorfish	Labridae	1	No	1.00	2.00	2	3.5

Table 1 (continued)

Species	Common name	Family	N sampled	Previously recorded	Prevalence	Abundance	Load range	Trophic level
<i>Xyrichtys splendens</i> *	Green razorfish	Labridae	3	No	1.00	4.00 ± 1.15	2–6	3.2
<i>Lutjanus apodus</i>	Schoolmaster snapper	Lutjanidae	5	No	0.00	0.00	0	4.3
<i>Ocyurus chrysurus</i> *	Yellowtail snapper	Lutjanidae	1	No	1.00	1.00	1	3.9
<i>Cantherhines pullus</i>	Orangespotted filefish	Monacanthidae	2	Yes ¹	1.00	20.50 ± 1.50	19–22	4.0
<i>Pseudupeneus maculatus</i> *	Spotted goatfish	Mullidae	10	No	0.90	22.10 ± 6.98	0–56	2.6
<i>Abudefduf saxatilis</i> *	Sergeant major	Pomacentridae	29	No	0.79	12.24 ± 3.86	0–66	3.8
<i>Azurina multilineata</i> *	Brown chromis	Pomacentridae	18	No	0.33	1.00 ± 0.46	0–7	3.0
<i>Pterois volitans</i> †	Red lionfish	Scorpaenidae	13	No	0.00	0.00	0	4.4
<i>Scorpaena plumieri</i>	Spotted scorpionfish	Scorpaenidae	2	No	0.00	0.00	0	3.6
<i>Hypoplectrus puella</i>	Barred hamlet	Serranidae	1	No	0.00	0.00	0	3.5
<i>Synodus intermedius</i>	Sand diver	Synodontidae	1	No	0.00	0.00	0	4.2
<i>Canthigaster rostrata</i>	Sharpnose puffer	Tetraodontidae	9	No	0.00	0.00	0	3.3

Listed for each species is the number of dissected individuals, whether the species has previously been recorded as a host of *Scaphanocephalus*, the proportion of hosts infected (prevalence), the average infection load (± 1 SE), and the range in infection. Taxonomic information and trophic level data follow FishBase (Froese and Pauly 2023), with the exception of the placement of parrotfish within the family Labridae. Previous infection records: 1: Kohl et al. 2019, 2: Dennis et al. 2019, 3: Elmer et al. 2019, 4: Roberts 2021. *New *Scaphanocephalus* host species records. †Non-native species in the region (although we acknowledge these could be *P. miles* or a combination of species)

fish), we used generalized linear mixed models (GLMMs) with an overdispersed Poisson distribution. Preliminary explorations of the data indicated that these models offered a superior fit (lower AIC value) relative to alternative distributions (e.g., negative binomial, with or without zero inflation). Only fish species with at least five individuals dissected were included in this analysis, which resulted in a dataset of 459 fish belonging to 23 species (i.e., 18 species with fewer than five individuals dissected were not included in the analysis). As fixed effects, we included sampling location (Piscadera Bay vs. Rif St. Marie), fish total length (measured from the tip of the snout to the end of the caudal fin), and trophic level (a continuous value based on isotopic values from delta N15; see FishBase, Froese and Pauly 2023). Standard length was scaled prior to inclusion by subtracting the mean and dividing all values by the standard deviation. Trophic levels were derived from diet studies (Froese and Pauly 2023) and scaled in the same manner. We further incorporated variables on fish species' habitat preferences derived from the dataset Robertson and Tornabene (2021). Habitat preference variables were dichotomous and included water column position (benthic vs. pelagic), use of hard bottom substrate (yes vs.

no), use of soft bottom substrate (yes vs. no), and whether a species is considered demersal (yes vs. no). Additional terms were either collinear with these variables (correlation coefficient > 0.9) or exhibited a lack of variation. For instance, 'reef-associated' was excluded because all fish species within the current study belonged to this category.

Models included random intercept terms for observation (i.e., to help account for overdispersion), host species (to account for repeated individuals from each fish species), the identity of the researcher who did the dissection (to help address any observer variation), and taxonomic family (as an initial effort to incorporate phylogenetic relationships, see below for phylogenetically explicit models). Full models were fit using the `glmmTMB` function (Brooks et al. 2017) in R (R Core Team 2022) and we used the performance package (Lüdtke et al. 2021) to derive diagnostic information related to model fit (conditional and marginal R^2 values), collinearity (Variance Inflation Factors), and distributions of the residuals and random effects. After fitting the full model, we used likelihood ratio tests to progressively remove noninfluential terms and refit the model until any further removals resulted in $P > 0.1$.

Phylogenetic model

To explicitly test the influence of fish phylogeny on patterns of infection among fish species, we developed a phylogenetic generalized linear mixed model (PGLMM) using the function `pglmm` in the R package `phyr` (see Li et al. 2020). This allowed us to compare the influence of different predictor variables on infection, while accounting for the nonrandom relationships among fish host species (see Ives 2018; Pearse et al. 2022). We first used the package `FishPhyloMaker` (Nakamura et al. 2021) to develop a phylogenetic tree for the 23 species in our dataset with sufficient replication. This package uses an algorithmic approach based on rules of insertion for cladistics. The model structure followed the GLMM outlined above, only here we omitted the random effect of fish family and instead incorporated the assembled phylogeny as a covariance matrix. After running the model, we assessed the influence of the included random effects (observation-level random effect, non-phylogenetic effect of fish species, and fish phylogeny) using likelihood ratio tests within the `phyr` package.

Linking spot counts and parasite load

To explore the predictive value of externally visible dermal spots on infection load during dissection, we constructed an additional overdispersed Poisson GLMM using a subset of 152 fish from 17 species. For these fish, visible dermatopathies were counted by eye shortly after collection and before freezing. While often dark in color, spots in certain

fish species can appear white. Spot count per fish was used as a fixed predictor, while observation and fish species identity were incorporated as random intercept terms. Note that spot counts were based on one entire side of the fish (the dissected side), including all fins on that side, whereas parasite counts were based on the dissection window (muscle and skin tissue) as well as the dorsal-, caudal-, and pectoral fin.

Results

Overview

A total of 491 individual fish belonging to 41 species were dissected and examined for dermal parasites (Table 1). These included 267 fish from Rif St. Marie and 224 from Piscadera Bay. Overall, *Scaphanocephalus* metacercariae were detected in 29 out of 41 fish species. The infected hosts spanned 10 taxonomic orders (of the 12 orders in total) and 14 families (of 18). The 29 infected fish species included 21 new host records (Table 1). The abundance (average infection load per fish) across all species was 15.8 ± 1.99 SE ($n = 491$) and the intensity (load per infected individual) was 25.4 ± 3.07 ($n = 306$) (Fig. 1). In total, 7765 *Scaphanocephalus* metacercariae were identified in 306 individual fish hosts (prevalence = 63%). Only four fish species with at least five dissected individuals did not yield any infections: *Holocentrus adscensionis*, *Lutjanus apodus*, *Canthigaster rostrata*, and the non-native *Pterois volitans* (see Table 1).

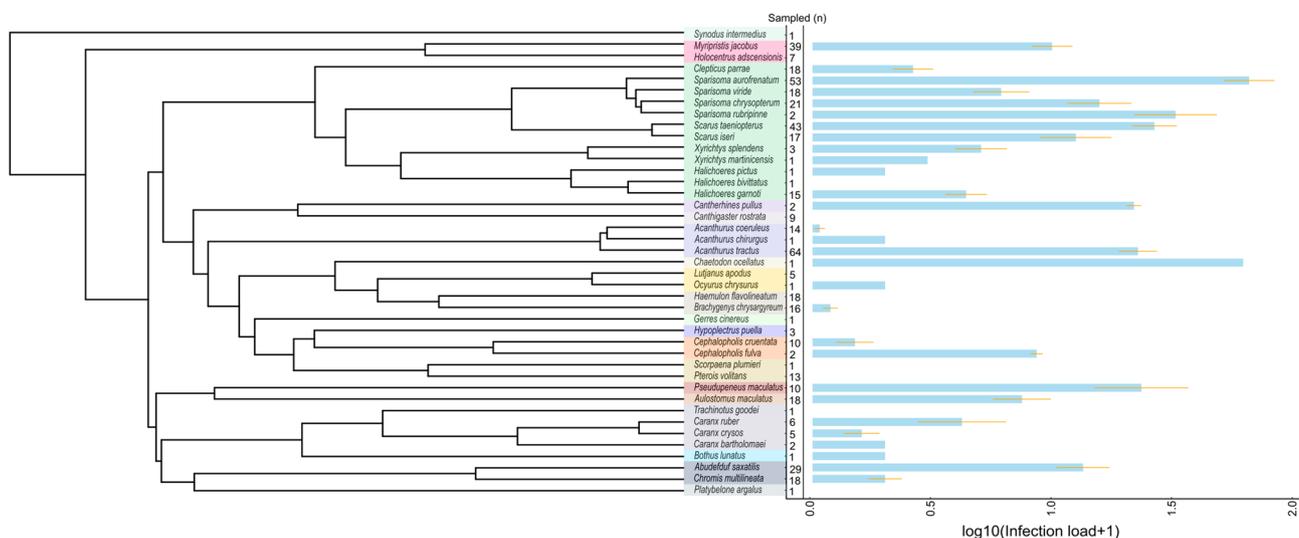


Fig. 1 Patterns of *Scaphanocephalus* infection among reef-dwelling fish species of Curaçao. **A** Phylogenetic tree of fish species examined, as generated by `FishPhyloMaker` (Nakamura et al. 2021) using taxonomy from FishBase (see Froese and Pauly 2023). Colors reflect taxonomic family affiliations. **B** Average number of *Scaphanocephalus*

metacercariae ± 1 SE for each fish species. Data values are $\log_{10} + 1$ transformed to facilitate visual comparisons. The sample sizes for each species are listed along the Y-axis of the plot. Note that statistical analyses were performed only for species with at least five individuals sampled

Encysted *Scaphanocephalus* were identified initially based on their large size, discoidal shape, and sturdy cyst wall (Fig. 2). The mean size of encysted *Scaphanocephalus* metacercariae was ($1053.2 \times 991.7 \mu\text{m}$; $n = 39$). (Fig. 2). Roughly half (49.4%) of metacercariae were found attached to the epidermis tissue, with the majority located between epidermis and dermal layers of the skin. Furthermore, 44.8% of metacercariae were present in the fins, with the dorsal, caudal and pectoral fins accounting for 14.9%, 18.5%, and 11.4%, respectively (Fig. 2). Lastly, 5.8% of metacercariae were located inside the muscle tissue (Fig. 2B). This within-host distribution of *Scaphanocephalus* was relatively consistent for members of the families Labridae, Mullidae, and Pomacentridae. However, we found considerable variance of within-host parasite distribution among several host taxonomic families. For example, Carangidae were much more likely to be infected in the skin (87.5% of metacercariae), which correlated to the location of black spots (Fig. 6E). Metacercariae in parrotfishes were present in the skin tissue and fins (Fig. 6F, H). In contrast, *Myripristis jacobus* and *Cantherhines pullus* (Fig. 6D) are examples of species that developed black spots mainly on the fins, which also corresponded with the location of most metacercariae.

In addition to *Scaphanocephalus*, metacercariae of three other trematode taxa were discovered in 46 host individuals belonging to eight different fish species. In no cases were these metacercariae closely associated with the symptoms of BSS, although they sometimes co-occurred with *Scaphanocephalus* in the same fish. These cysts included metacercariae of *Stephanostomum* spp. (prevalence = 2.2%), which has anterior trunk spines and collar spines around the oral sucker, *Bucephalus* spp. (prevalence = 28.3%), and an unidentified metacercaria (prevalence = 69.6%). Each of these taxa were easily differentiated from *Scaphanocephalus* based on morphology, including the absence of the wing-shaped anterior end (Fig. 2), as well as differences in the size and sturdiness of the surrounding cyst. The unknown metacercariae cysts ($334.3 \times 273.81 \mu\text{m}$; $n = 21$) were found within

the fin rays and were much smaller than encysted *Scaphanocephalus* ($1053.2 \times 991.7 \mu\text{m}$; $n = 39$). After excystment, tissues were too degraded to identify morphologically.

Influence of host taxonomy, trophic level, and habitat use on infection

On average, fish from Piscadera Bay supported significantly lower *Scaphanocephalus* infection loads compared to those from Rif St. Marie (overdispersed Poisson GLMM: location[Piscadera Bay] = -1.757 ± 0.257 , $z = -6.84$, $P < 0.000001$; $n = 459$) (Fig. 3). *Scaphanocephalus* infection load also increased with host size and decreased with trophic level (scaled[total length] = 1.478 ± 0.182 , $z = 8.13$, $P < 0.000001$; Trophic level = -1.941 ± 0.496 , $z = -3.91$, $P = 0.00009$; $n = 459$) (Fig. 4). Thus, even while controlling for fish species identity, larger hosts from lower trophic levels tended to support the highest infection loads. Examples include *Sparisoma aurofrenatum* and *Scarus taeniopterus*, both of which are large-bodied herbivores that exhibited higher infection loads relative to second order carnivores, such as *Cephalopholis cruentata* and *Caranx ruber*. Interestingly, several fish species with high infection loads deviated from this pattern. For example, *Abudefduf saxatilis* and *M. jacobus* both supported moderate infection abundances (8.5 and 12.2, respectively), yet are relatively small-bodied (~12.5 cm) and of higher trophic level (3.4–3.8) compared to parrotfishes (genera *Sparisoma* and *Scarus*) (2.0). Other moderately infected species, such as *Aulostomus maculatus* and *Pseudupeneus maculatus*, were also of higher trophic level but tended to have larger body sizes (Table 1). There were no significant effects of the dichotomous habitat variables (benthic, hard bottom, soft bottom, and demersal) on infection load (all $P > 0.14$). The marginal and conditional R^2 values were 0.69 and 0.38, respectively, and all VIFs were < 2.5 .

The phylogenetic model yielded comparable coefficient estimates. For this model, we included a

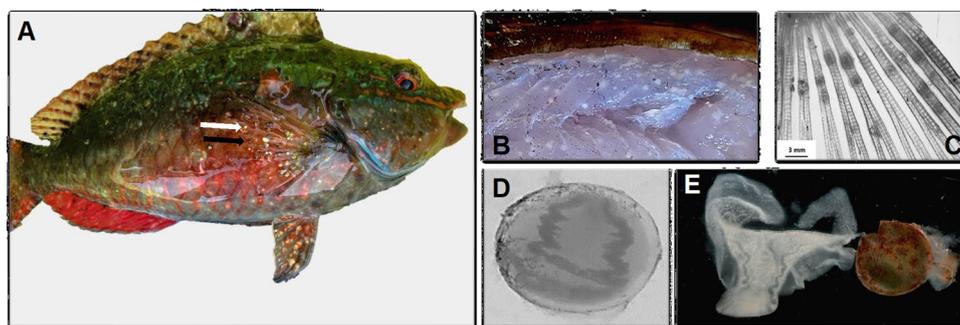


Fig. 2 Infections by *Scaphanocephalus*. **A** An infected redband parrotfish (*Sparisoma aurofrenatum*) illustrating metacercariae cysts that can appear either white (see white arrow) or black (see black arrow)

in color. **B** Metacercariae encysted in the muscle tissue; **C** Metacercariae encysted along the fin rays; **D** An isolated metacercariae still encysted; **E** excysted metacercariae

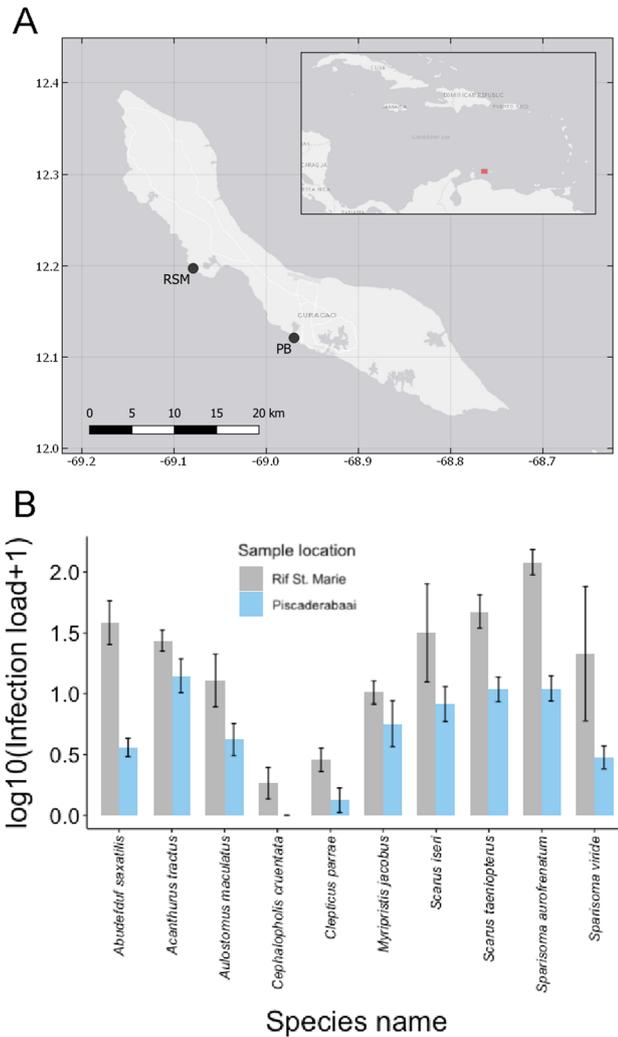


Fig. 3 Differences in *Scaphanocephalus* infections among fish species between sites. Among fish species with at least three individuals examined at both reef locations ($n=6$ or more in total), fish from Rif St. Marie (Coral Estate) supported consistently higher average infection loads relative to those from Piscadera Bay, highlighting the influence of local heterogeneity in parasite exposure

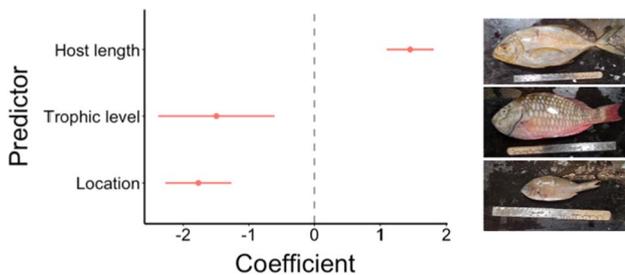


Fig. 4 Coefficient plot illustrating the influence of fixed effects from the best-fitting model in explaining *Scaphanocephalus* infection load among fish species (i.e., the average number of metacercariae per host species). Results derived from the non-phylogenetic GLMM. Presented are the scaled coefficient values for each fixed effect ± 1 SE. The dashed vertical line at 0 is a reference to indicate a lack of effect

phylogenetic covariance structure while removing the random intercept term for family, which yielded significant fixed effects of site, fish total length, and trophic position (overdispersed Poisson PGLMM: location[Piscadera Bay] = -1.616 ± 0.229 , $z = -7.06$, $P < 0.000001$; scaled[total length] = 1.249 ± 0.161 , $z = 7.74$, $P < 0.000001$; scaled[trophic level] = -1.314 ± 0.461 , $z = -2.85$, $P = 0.0062$; $n = 459$). Based on likelihood ratio tests, there was no significant influence of the phylogenetic random effect of species (LR = 0.362; $P = 0.197$), whereas the remaining random intercept terms were all significant (fish individual, LR = 2664, $P = 0$; non-phylogenetic species effect, LR = 20.9, $P < 0.000001$; identity of researcher doing the dissection, LR = 2.58, $P = 0.0116$). We did not include categorical terms related to habitat within this model.

Linking spot counts and parasite load

The black spot count per fish was a strong, positive predictor of the *Scaphanocephalus* infection load across all fish species (overdispersed Poisson GLMM, spot count per fish = 0.202 ± 0.034 , $z = 6.01$, $P < 0.00001$; $n = 152$; Fig. 5). Thus, visible spots on the fins and epidermis of shallow water Caribbean reef fish offer a good indicator for determining whether a fish is infected by *Scaphanocephalus*, at least among the subset of fish individuals and species for which we collected these data. In almost all cases, the number of parasites exceeded the number of spots. However, while spot count offered a proxy for comparing relative infection load between fish individuals of the same species, it is less reliable as an indicator of variation in infection load between fish individuals of different species; thus, approximately half of infected fish did not exhibit visible spots, including some of the most infected individuals. This fact was attributed to

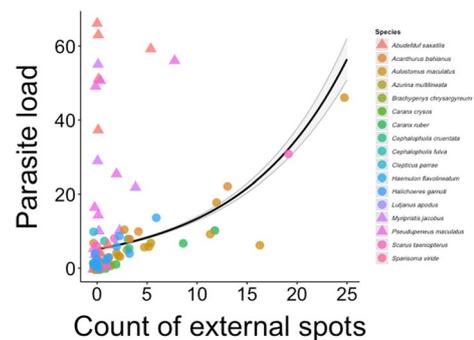
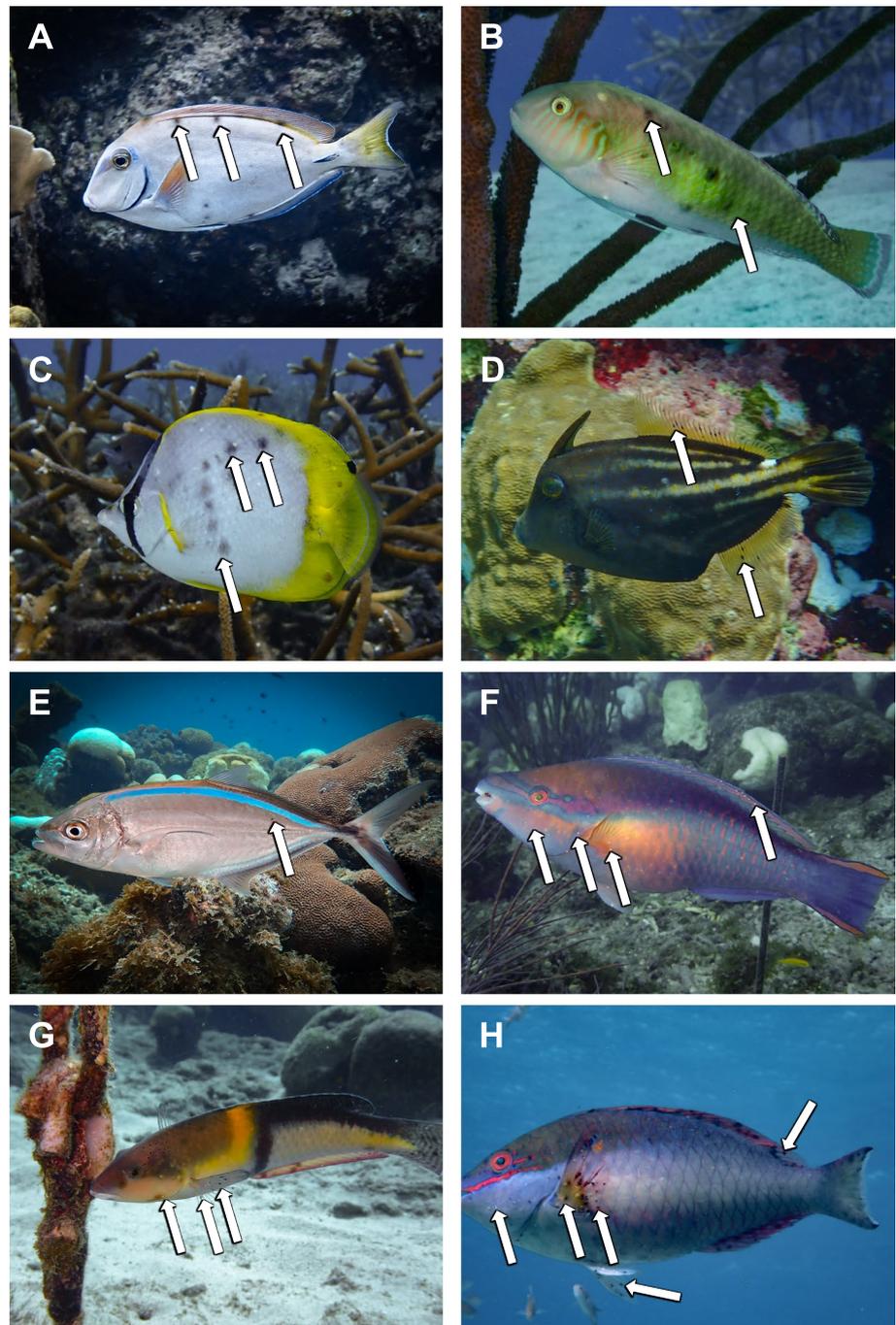


Fig. 5 Relationship between the number of external visible dermatophies prior to dissection and the count of encysted *Scaphanocephalus* metacercariae. The best-fit line from an overdispersed GLMM is also presented. While the number of spots positively predicted parasite load overall, three species (depicted with triangles) were relative outliers. These species exhibited few external signs of infection even when the metacercariae count was relatively high

Fig. 6 Examples of *Scaphanocephalus*-induced dermatopathies in reef fishes. In some species, conspicuous black spots were evident on the fins and body, such as for ocean surgeonfish (*Acanthurus tractus*) (A), the green razorfish (*Xyrichtys splendens*) (B), and the spotfin butterflyfish (*Chaetodon ocellatus*) (C). In orangespotted filefish (*Cantherhines pullus*) (D), spots were especially noticeable on the fins while in bar jacks (*Caranx ruber*) (E), they tended to occur only on the body. Princess parrotfish (*Scarus taeniopterus*) (F) exhibited white spots on the fins and body, while some species exhibited a combination of white and black spots when infected with *Scaphanocephalus* (yellowhead wrasse (*Halichoeres garnoti*) (G) and redband parrotfish (*Sparisoma aurofrenatum*) (H)). Arrows used to indicate representative infections



interspecific variation in the likelihood of an infected host developing conspicuous spots. For example, all five infected *Clepticus parrae*, as well as eight out of ten *A. saxatilis* individuals examined, did not develop visible spots, despite the latter species possessing a moderate average infection load (12.24 metacercariae per host) (Fig. 5). On the other hand, 11 out of 12 infected *A. maculatus* and three of four infected *A. tractus* exhibited clearly visible spots. These examples illustrate the extremes, but a large portion of infected host species possessed a more intermediate prevalence of black

spots, ranging between 25 and 75%. The cause of interspecific variation in the prevalence of black spots among infected hosts is, as of yet, unclear, as species of various families, sizes, colors, and trophic levels occur on both ends of the prevalence spectrum.

The location, size, and color of spots were also species-specific (Fig. 6). For example, the genera *Acanthurus*, *Xyrichtys*, and *Chaetodon* tended to develop conspicuous, relatively large black spots on the fins and epidermis (Fig. 6A–C, respectively). Other fish species developed

black spots typically not larger than the encysted metacercariae itself. Examples include *Cantherhines pullus*, for which spots were only detected in the fins (Fig. 6D), and species of jack (Carangidae), such as *C. ruber*, for which spots were only present on the epidermis (Fig. 6E). For *Pseudupeneus maculatus* and *M. jacobus*, the connective tissue around the cysts was a similar color to the fish, making it almost impossible to notice the spots prior to dissection. Some species, such as *S. taeniopterus*, exhibited white rather than black cysts covering on the fins and epidermis (Fig. 6F), while *Halichoeres garnoti* and *S. aurofrenatum* developed both black and white cysts often concentrated on the fins and, to a lesser extent, in their epidermis (Fig. 6G, H). *Aulostomus maculatus* have natural, darkly pigmented spots on the scales and fins, which can make distinguishing between natural coloration and infection associated spots challenging. However, the connective tissue around the cysts in *A. maculatus* was often dark reddish—a difference in color that is particularly conspicuous when observed under magnification.

Discussion

By sampling a wide taxonomic range of shallow water reef fish species, this research revealed that infections by *Scaphanocephalus* are more abundant and widespread than previously recognized. In the majority of individual fish (306 of 491 total, 62.3%) and fish species (29 of 41 total, 70.7%), *Scaphanocephalus* was detected at loads from 1 to 564 metacercariae per fish (based on streamlined dissections of one side only). These represent the highest infection loads of *Scaphanocephalus* metacercariae reported to date in any fish species or location. Infected fish included individuals from 14 different taxonomic families, with standard lengths ranging from 9.8 to 60.7 cm, and with trophic levels ranging from 2.0 (herbivores such as *A. tractus*) to 4.5 (second order carnivores such as *Caranx bartholomaei*). The abundance of *Scaphanocephalus* on one side of *A. tractus* in our study (21.3 ± 3.9 , $n = 64$) was roughly 2 × greater than previous findings from Bonaire by (Kohl et al. 2019) (average infection on both sides: 19.4 ± 9.4 , $n = 31$). By selecting fish species based on habitat (abundant, nearshore, shallow water reef fish), rather than the presence of obvious pathology, our approach identified 21 new host records and indicated that *Scaphanocephalus* is a relative generalist in its second intermediate host use. Given that only a small subset of the ~357 known reef-associated fish species on Curaçao (Froese and Pauly 2023) have been examined, it is likely that many more host species are yet to be identified.

Influence of host taxonomy, trophic level, and habitat use on infection

Based on findings from the PGLMM, infection increased with fish length, decreased with trophic level, and was significantly higher at Rif St. Marie relative to Piscadera Bay across all fish species. The influence of these terms was broadly unaffected by host phylogeny; coefficient estimates for each variable were similar between the phylogenetic and non-phylogenetic models, and a likelihood ratio test indicated that the phylogenetic effect of host species was non-significant. Previous studies from other systems have similarly identified fish body size as a positive predictor of infection load (Poulin 2000; Maceda-Veiga et al. 2016; Calhoun et al. 2018; Timi and Poulin 2020), which likely reflects increased exposure opportunities. Larger hosts offer a more substantial physical target in the water column for short-lived cercariae; their bigger size may also reflect a greater host age, thereby offering more temporal opportunities for parasite exposure (Sweeting 1974; Harrod and Griffiths 2005; Galaktionov et al. 2015). In a study of reef fishes across the Pacific Line Islands, for example, Williams et al. (2022) reported that larger fish supported higher loads of all helminth parasites.

The inverse relationship between *Scaphanocephalus* infection and host trophic level reflects the result that many of the most heavily infected fish were grazing herbivores, particularly surgeonfishes (Acanthuridae) and parrotfishes (Labridae). Second order carnivores, such as species in the families Carangidae and Serranidae, exhibited infection but typically at lower average loads, even after controlling for body size. Because *Scaphanocephalus* is transmitted to fish by free-swimming cercariae, rather than through host diet, the observed link to trophic level likely reflects differences in host habitat use or swimming speed. Although the first intermediate host of *Scaphanocephalus* remains unidentified, it is likely an intertidal or shallow water snail that occurs close enough to shore to come into contact with osprey feces. Previous work has shown that BSS levels are greatest in shallow waters close to the coast (< 5 m depth; see Elmer et al. 2019), which is also where many surgeonfish and parrotfish graze on algae-covered substrate (Cheal et al. 2010; Dell et al. 2020) and could encounter infective cercariae.

Given the expectation that habitat use affects proximity to parasite infective stages, it is somewhat surprising that none of the habitat-related variables included in the models accounted for additional variation in *Scaphanocephalus* infection. This may be explained by the broad, categorical nature of these terms (e.g., benthic vs. pelagic, demersal vs. not-demersal, etc.; Robertson and Tornabene 2021), which likely failed to capture fine-scale variation in factors such as depth preference and proximity to shore. We nonetheless expect that habitat-mediated differences in exposure

are important for several reasons. Species closely associated with sandy bottoms generally had a high prevalence of *Scaphanocephalus* infection, including *P. maculatus*, *Bothus lunatus*, *X. martinicensis*, and *X. splendens*. In contrast, species associated with live corals, such as *Brachygenys chrysargyreum* and *H. flavolineatum*, had lower infection loads and prevalence (~0–20%; Table 1). Such habitat effects could reflect proximity to infected snails or the added influence of nonhost species; for instance, reef-associated taxa such as corals, bivalves, anemones, and crustaceans can consume infective parasites or interfere with transmission, and thereby reduce infection loads in nearby fish hosts (Hopper et al. 2008; Artim and Sikkil 2013; Welsh et al. 2017). An alternative variable that could influence patterns of fish exposure is ontogenetic migration, particularly for species that use bays, mangroves, or estuaries as nursery habitats before migrating to reef habitats as adults (Nagelkerken et al. 2002). However, we consider this unlikely to explain significant variation in the observed data for several reasons. First, many of the most infected species reported here, such as *A. tractus*, *C. ocellatus*, and *P. maculatus*, settle directly to coastal reef habitats, rather than migrating from nursery habitats (Nagelkerken et al. 2000). Second, the high prevalence of *Scaphanocephalus* among numerous different fish species—including consistently higher infections at Rif St. Marie relative to Piscadera Bay—suggest exposure is occurring locally. High infections among species such as razorfish (*Xyrichtys* spp.), which exhibit strong and very localized site fidelity, further supports this hypothesis (e.g., Victor 1987).

The importance of local habitat effects is also reflected by the average differences in infection between the two reef locations we sampled, which tended to be greater than differences observed within a site among species. On average, fish from Rif St. Marie supported > threefold more metacercariae relative to those from Piscadera Bay—a pattern that was consistent among species (Fig. 4). Such differences could stem from variation in activity of the definitive (osprey) or first intermediate hosts (unidentified mollusk), or conditions for transmission among hosts (e.g., calmer, more protected waters). This result is also consistent with the findings from visual surveys conducted by de Wit and Johnson (personal observations), who observed the highest number of black spots per *A. tractus* (6.6) at Rif St. Marie from across 32 locations along the southern coast of Curaçao. Because *A. tractus* develop conspicuous black spots, visual surveys of BSS in this species likely offer an informative measure for comparing infection load among different locations, even for species less likely to develop external symptoms.

Similar suggestions have been made by Shimose et al. (2020) during a survey of 30 species of parrotfish from Japanese fish markets. Based on visual examinations of harvested fish, all but one species hosted *Scaphanocephalus*

metacercariae, but prevalence varied considerably among species (ranging from 0.1 to 38.5%). Based on host feeding habits, the authors suggested that such variation was primarily caused by differences in exposure to cercariae, rather than taxonomic affiliation or use of nocturnal cocoons (which has been shown to reduce certain ectoparasites (Grutter et al. 2011)). Specifically, parrotfish species that feed on epilithic algae associated with sand included those with the highest prevalence (22.5–38.5%), whereas those that fed on algae associated with live coral were rarely infected (prevalence 0.4–2.2%). Prevalence values often varied highly even between species in the same genus, leading the authors to discount the role of phylogeny. These results, in combination with our own, support the hypotheses that *Scaphanocephalus* has low second intermediate host specificity and that differences in infection among fish species is driven primarily by variation in exposure, rather than by evolutionary differences in susceptibility.

The link between infection and external symptoms in fish

Results of the current study indicated that the presence of externally visible dermatopathies (i.e., BSS) was consistently associated with infection by *Scaphanocephalus* metacercariae. Although other trematode metacercariae were detected, they were comparatively rare, found in locations other than the fins and skin, and were not linked to the symptoms of BSS (also see Kohl et al. 2019). For the subset of fish in which we had pre-dissection counts of visible spots, spot count per fish was a strong, positive predictor of *Scaphanocephalus* infection load, as reported previously for *A. tractus* alone (Kohl et al. 2019). Thus, dermal spots on the fins and epidermis of shallow water Caribbean reef fish generally offer a good indicator for determining whether a fish is infected by *Scaphanocephalus*. Interestingly, both the likelihood of observing spots and the form in which they manifested varied among fish species. For example, species that were likely to develop spots when infected included *C. ruber*, *A. tractus*, *A. maculatus*, and *X. splendens* (75 to 100%), whereas species such as *C. parrae*, *A. saxatilis*, and *M. jacobus* rarely developed spots even when moderately infected. Furthermore, the name “Black Spot Syndrome” can be misleading, as some host species develop spots that match their natural pigmentation (e.g., *P. maculatus*) or even white spots (e.g., *S. taeniopterus*). Future research with larger sample sizes might be able to establish whether there is a species-specific relationship between the quantity of black spots and the corresponding infection load, which so far has been examined only for *A. tractus* (Kohl et al. 2019). Similarly verified relationships from other reef fish species would offer noninvasive opportunities to characterize infection patterns across reef fish communities, including

within other regions of the world where *Scaphanocephalus* infection has been linked to conspicuous dermatopathies (e.g., Shimose et al. 2020; Al-Salem et al. 2021; Cohen-Sánchez et al. 2023).

Ecological implications of *Scaphanocephalus* infection

Results from the current study, which broadly sampled fish species from nearshore reef communities, indicated that *Scaphanocephalus* infection loads are highest among large-bodied herbivores, particularly parrotfishes and surgeonfishes—often cited as keystone grazers in reef ecosystems (Dell et al. 2020). Infections occurred in the majority of adequately sampled species, even those without externally obvious signs of BSS, emphasizing that *Scaphanocephalus* is a relative generalist that is more widespread in fish communities than previously realized. The lack of phylogenetic signal—coupled with strongly consistent differences in infection load between sites—suggests that local variation in cercariae exposure likely accounts for infection patterns, rather than sharp differences in host species susceptibility. Rather than being specialized to fish species known to be consumed by osprey definitive hosts, metacercariae of *Scaphanocephalus* occur in a wide range of fish sizes, species, and taxonomic families. One study of osprey diets conducted in Belize identified *Mulloidichthys* (genus of goatfishes), *Ocyurus chrysurus* (yellowtail snapper), and *Acanthurus* (genus of surgeonfishes) to be the main prey items (Wiley et al. 2014). While goatfish and surgeonfish both supported high infection loads in the current study, high infection prevalence was also present in many species unlikely to be consumed by osprey due to smaller body sizes or depth preferences, such as razorfishes (100%) and damselfishes (80.9%). The relevance of *Scaphanocephalus* infections for fish harvests, market sales, and human illness is also an open question. Shimose et al. (2019) reported that infections reduced the market value of infected parrotfish by 200–300 yen kg⁻¹; in our own examinations of fish from local grocery stores in Curaçao, we detected *Scaphanocephalus* metacercariae in species such as *C. fulva*.

Looking forward, it will be important to determine the effects of *Scaphanocephalus* infections on fish behavior, survival rates, feeding activity, and reproduction. Ecologically similar parasites are known to have adverse effects on fish when infection loads are high. In freshwater fish, for example, black spots induced by trematodes can cause infected hosts to be more vulnerable to predators (Tobler and Schlupp 2008) or avoided during mate selection (Tobler et al. 2006). In temperate marine environments of North America and Europe, the trematode *Cryptocotyle lingua*—which is closely related to *Scaphanocephalus* (Kohl et al. 2019)—can increase mortality among young fish and reduce reproductive success in species that exhibit high counts of

parasite-induced spots (Lauckner 1984; Rosenqvist and Johansson 1995; Mazzi 2004). Investigation into such questions for *Scaphanocephalus* will require a more detailed examination of the behavioral effects associated with infection alongside identification of the elusive first intermediate host, which is necessary both for conducting experimental exposure studies and for more closely understanding the habitats in which fish become exposed.

Acknowledgements We would like to thank Cheyenna de Wit, Jeroen Schneider, and Nicole Brackenborough for their support and assistance in fish collection, and Aydan Roth, Evelyn Esparza, Kavari Kapur, Mackenzie Campbell, Sydney Watson, and Phoebe Oehmig for their assistance with fish dissections. We would also like to express our gratitude to the CARMABI staff and in particular to Dr. Mark Vermeij for providing support and historical knowledge essential to this project. L. Valentine and O. Osbourne offered advice and inspiration on study design. Finally, we gratefully acknowledge financial support from the David and Lucile Packard Foundation, the Eppley Foundation, and undergraduate research grants from the Biological Sciences Initiative and the Undergraduate Research Opportunity Program.

Author contributions RJM and PTJJ designed the study; RJM, LJVtH, and JP collected field data; RJM, PTJJ, JP and DMC conducted fish necropsies; RJM and PTJJ performed statistical analyses and visualizations; RJM and PTJJ drafted the manuscript and all authors contributed to revisions.

Data availability Data used in this study are available through figshare (<https://doi.org/10.6084/m9.figshare.25335541>).

Declarations

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

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