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High prevalence of dermal parasites among coral reef fishes of Curaçao

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Abstract During expeditions to Curaçao in August and October of 2013, a large number of fish infected with dermal parasites was observed. Infected individuals presented black spots and white blemishes on their skin and fins that were easily observed by divers, and which have been associated with infections by trematodes, turbellarians, and protozoans (*Cryptocaryon*). In order to compare rates of infection across localities in the Caribbean, we conducted visual censuses of reef fish communities along 40 m^2 belt transects in Belize (n=35), Curaçao (n=82), and Mexico (n=80) over a 4-week period. Three affected individuals were recorded in Belize, 75 in Curaçao, and none in Mexico. Approximately 68 % of the infected individuals in Curaçao were surgeonfishes (Acanthuridae). There was no correlation between incidence of infection and species abundance (r^2=0.03), or with functional traits (diet, mobility, schooling behavior, or position in the water column). The causes of the strikingly high incidence of dermal parasites in Curaçao and its consequences remain unknown. However, considering that parasites with complex life cycles have several hosts throughout their lives, and that past disease outbreaks have had severe consequences on communities of the Caribbean, we caution that coral reef ecosystems of Curaçao should be closely monitored.

Keywords Tropical Western Atlantic · Caribbean · Infectious diseases · Metacercaria · Turbellaria · Marine fishes

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Introduction

Parasites are a major component of marine ecosystems (Kuris et al. 2008), affecting the survival (Finley and Forrester 2003), fecundity (Rosenqvist and Johansson 1995), and behavior (Barber et al. 2000; Poulin et al. 2005) of their hosts. They can also influence biodiversity and community structure by altering the outcome of competitive interactions between host species (Price et al. 1986; Poulin and Fitzgerald 1987) and can occupy vital links in local food webs (Grutter 1995; Cheney and Cote 2003). Thus, documenting and quantifying parasite–host interactions and occurrences is essential for improving our understanding of the dynamics of marine ecosystems. Yet, despite their importance, marine parasites have received little attention compared to their host organisms (i.e., fishes and corals), in part because they are often inconspicuous, specimen preparation requires expertise, and many groups are poorly resolved taxonomically (Justine 2010).

Studies on parasite abundance and diversity have typically focused on global patterns (Grutter 1998). These studies reveal that parasite diversity in aquatic systems varies predictably, with more species found in shallow waters (Rohde and Heap 1998) and near the equator (Rohde 1999; Luque and Poulin 2008). Taking this into account, shallow water habitats of tropical coral reefs offer a great opportunity to advance our understanding of the dynamics of host–parasite interactions in marine environments. A growing body of work in coral reef fishes has demonstrated dramatic changes in parasite density and diversity at small spatial scales. At a regional scale, a comparison between a pristine and a highly fished atoll revealed higher diversity and abundance of parasites in the former (Lafferty 2008). Within the same locality, Grutter (1998) found stark differences in the number of parasitic isopods between individuals inhabiting reef flats and reef slopes in the blackeye thicklip wrasse, *Hemigymnus melapterus*, at a scale of hundreds of meters. Other studies have revealed temporal differences in parasite density in the same area (Grutter 1994; Grutter and Hendrikz 1999). Due to these variations across spatial and temporal scales, parasites hold great promise as natural tags of coral reef fishes (Williams et al. 1992; Hutson et al. 2011), as well as indicators of ecological impacts on coastal communities (Lafferty 2008). However, most published studies have focused on the fish faunas of the Indo-Pacific, with fewer examples from the Caribbean.

With more than 815 species of coral reef fishes, the Caribbean is the biodiversity hotspot of the Western Atlantic (Floeter et al. 2008). Because parasite diversity can be at least 20 times higher than that of their fish hosts (Justine et al. 2012), there is great potential for variation in the interactions between parasites and their hosts in the Caribbean. During surveys in Curaçao, we noticed a remarkably high incidence of dermal parasites on coral reef fishes. Infections presented themselves as dark or white blemishes on the epidermal tissues, which are usually associated with the presence of digenean metacercaria, turbellarians, and/or protozoan infections (Fig. 2, Fig. S1). These observations prompted additional visual surveys to assess the prevalence of parasites in Curaçao and to compare rates of infection of this island with two other locations in the Caribbean. With the exception of one individual of *Acanthurus tractus* (Fig. S1), no detailed histological work was done to identify the parasites causing the blemishes. As such, this study focused on comparing rates of infection of reef fishes with dermal parasites from three localities in the Caribbean (Belize, Curaçao, and Mexico) to determine which groups of fishes were most prone to infection and to test for correlation between functional traits (diet, mobility, schooling behavior, and position in the water column) and parasite load.

Materials and methods

Study sites

Visual counts of reef fishes were made between October and November 2013 in Belize, Curaçao and Mexico (Fig. 1). In Belize, visual surveys were conducted along 35 transects at depths of 3–12 m, comprising the reef slope (10–12 m), patch reefs, and shallow reef crest (3–6 m). The surveys were conducted October 7–10 at six sites around the Smithsonian Institution's field station at Carrie Bow Cay. These reefs are part of the Meso-American Barrier Reef system, forming a semicontinuous barrier reef parallel to the coast (Arias-Gonzalez et al. 2008). Surveyed reefs were relatively flat, with some sites dominated by octocorals (e.g., gorgonians), while others were characterized by higher complexity due to coral boulders (e.g., *Porites*). Some areas demonstrated low complexity and algal overgrowth, most likely due to human impacts.

In Curaçao, visual surveys were conducted October 26–31 along 82 transects at eight different sites on the southwestern edge of the island (Fig. 1b). All sites were located on the shallow plateau that begins at the waterline and gradually slopes down to 10 m (usually 50 to 100 m from the high watermark), from where it drops off quickly (Bak 1975; Van den Hoek et al. 1975). Due to the abrupt drop-off as well as the direct influences of the Caribbean Current (Fratantoni 2001), this island has a very distinct assemblage of coral reef fishes compared to other sites in the Caribbean. Approximately 50 % of the fish biomass consists of planktivores, and herbivores comprise 43 % (Sandin et al. 2008). There is a noticeable absence of large-bodied fishes, and apex predators represent only 7 % of the total biomass (Sandin et al. 2008). The slope and reef crest harbored most of the living coral cover, having great structural complexity. In these areas,

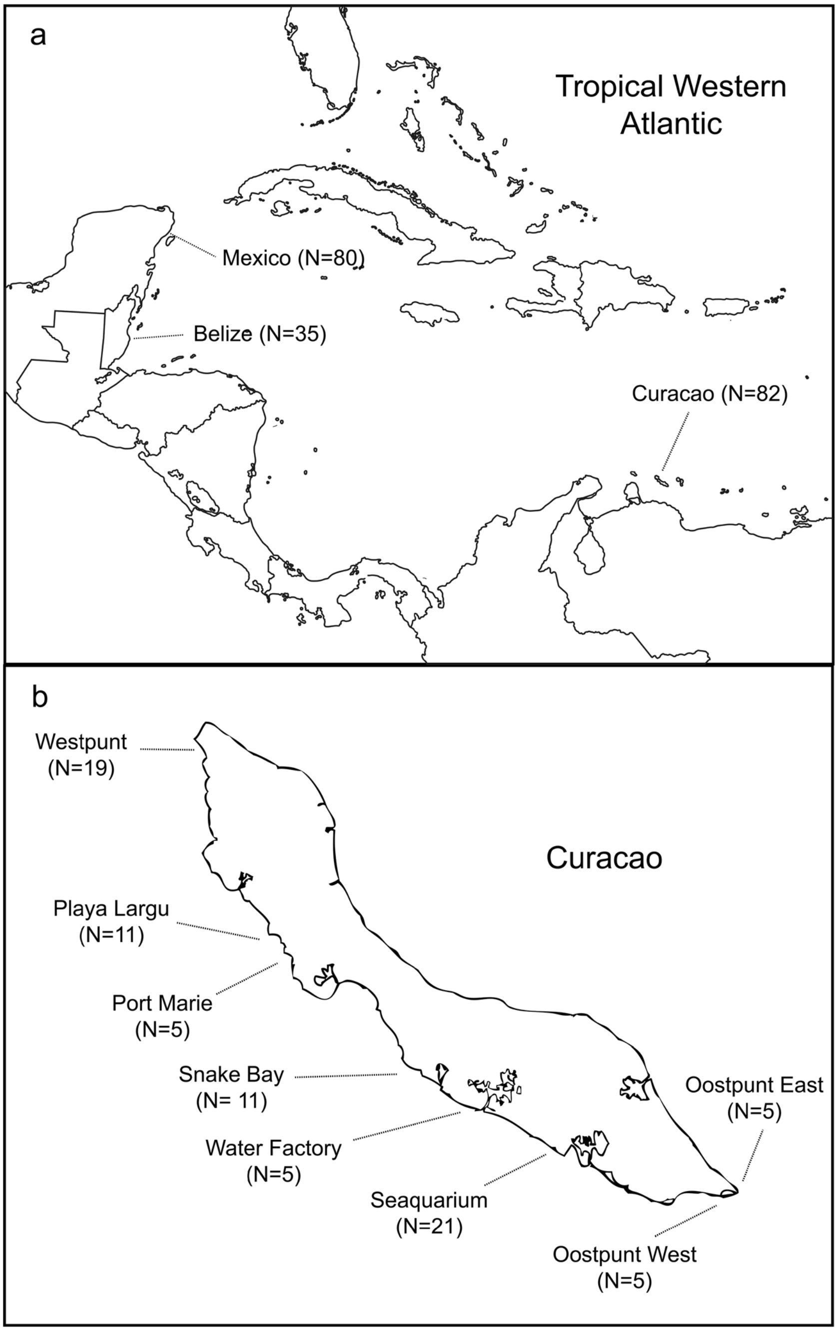


Fig. 1 Map of the greater Caribbean with (**a**) the three locations where the surveys were made, as well as (**b**) the eight sites surveyed in Curaçao

scleractinian coral colonies were interspersed with large octocorals (e.g., gorgonians) and sponges. At most sites, the plateau comprised sandy substrate with scattered patch reefs and abundant coral rubble (mainly *Acropora cervicornis*). At two survey sites, the plateau was covered with large colonies of the coral *Acropora palmata*, the fire coral *Millepora complanata*, and gorgonians.

In Mexico, visual surveys were conducted November 13–15 along 80 transects in the Quintana Roo region at five sites along the reefs of Playa del Carmen and at two sites on Cozumel. Surveys were at depths of 6–12 m in the coastal back reefs of Playa del Carmen and patch reefs of Cozumel. Like the reefs surveyed in Belize, these reefs are part of the Meso-American Barrier Reef system. The reefs along Playa del Carmen form large plateaus, which were dominated by octocorals (e.g., gorgonians), sponges, and algal turfs, interspersed with areas of low coral cover. The sites in Cozumel were characterized by extensive coral cover and high topographic complexity. All sites in Mexico are influenced by moderate to strong ocean currents, are in close proximity to large tourist facilities, and are heavily used by the diving industry.

Underwater visual census

For each of the localities, replicated visual censuses were conducted by scuba divers using belt transects. Each transect was 20 × 2 m, allowing for the observation of camouflaged or cryptic species (Floeter et al. 2007) as well as the clear observation of individuals with dermal infections. While laying out the transect tape, divers counted, identified, and estimated the size (total length in cm) of all fishes observed within the water column above the reef, whereas benthic, small, and cryptic species were recorded while rolling up the transect line on the return swim. Fishes that showed dark blemishes and/or white spots in the skin and fins were reported as infected (Fig. 2). Large parasites such as isopods were not considered in the analysis. Observations in the three locations were conducted by the same group of divers (SRF, RM, GOL, and CELF).

In addition, 1,200 underwater photographs of fishes from Curaçao were examined (photos taken by LAR and SRF). These photographs made it possible to determine whether species that were not observed in the transects are also affected by dermal parasites.

Data analysis

A Fisher's exact test was used to determine whether the number of infected fish differed among locations. For this analysis, host species that showed infections in Curaçao were considered 'species prone to infection'. For each of these species, the

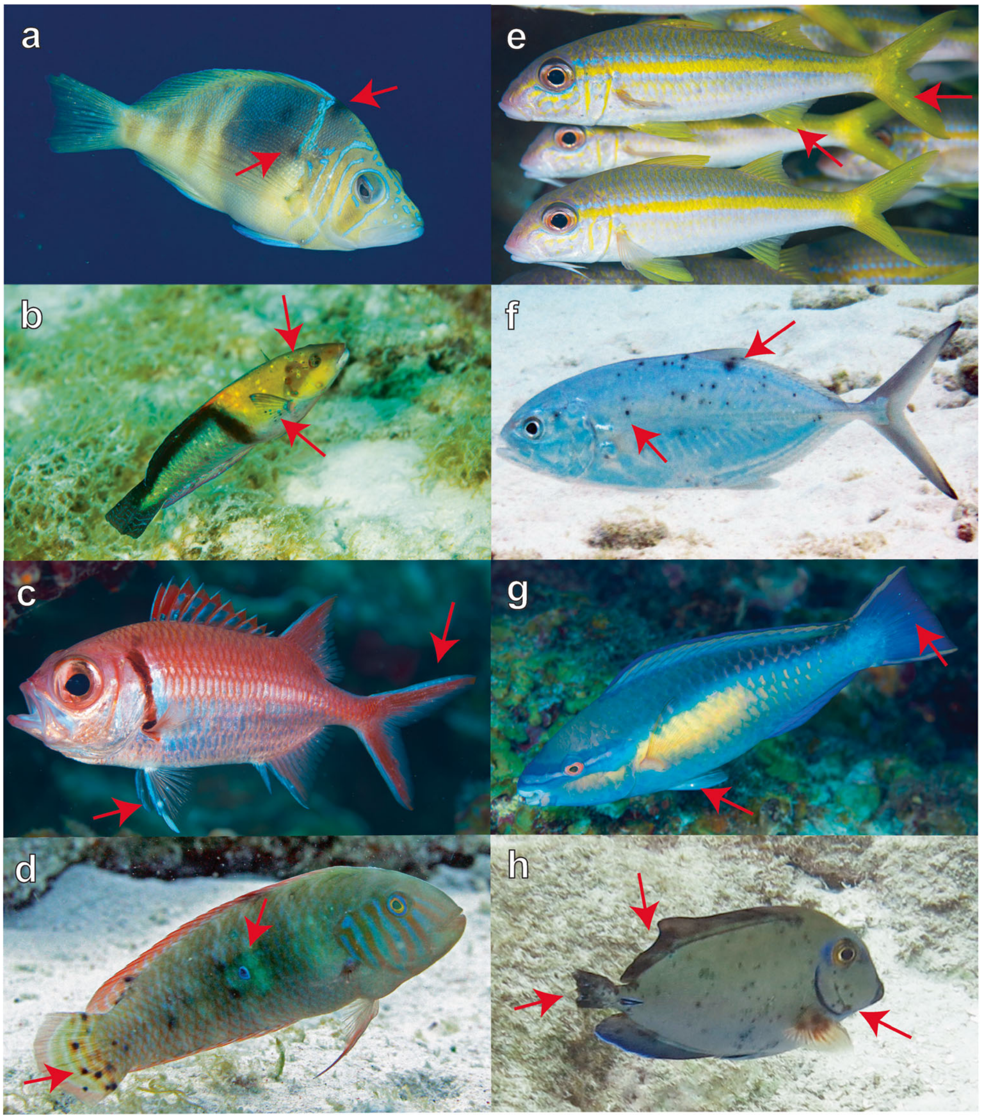


Fig. 2 Fishes infected with dermal parasites in Curaçao. Infected species include: **a** *Hypoplectrus puella*, **b** *Halichoeres poeyi*, **c** *Myripristis jacobus*, **d** *Xyrichtys splendens*, **e** *Mulloidichthys martinicus*, **f** *Caranx crysos*, **g** *Scarus taeniopterus*, **h** *Acanthurus tractus*. Photos **a**, **b**, **c**, **e**, **g** by LAR, **d**, **h** by SRF, and **f** by MJAV

total number of individuals observed (abundance) and the proportion infected at each of the three localities were calculated. A linear regression was used to determine whether host species abundance correlated with the number of infected individuals. A generalized linear mixed model (GLMM) with binomial distribution and taxonomic family as a random intercept was used to determine whether functional traits had a significant effect on the rate of infection. The random intercept was added to diminish taxonomic pseudo-replication, since some families were represented by more than one species. Following the procedure described by Mouillot et al. (2014), the traits considered as independent class variables were: diet (piscivores, herbivores-detritivores, macro-algal herbivores, sessile invertebrate feeders, mobile invertebrates feeders, omnivores, and planktivores), mobility (sedentary, mobile within a reef, highly mobile), schooling behavior (solitary; small group, 3–20 individuals; medium group, 21–50; large group 51 and higher), and position in the water column (bottom, above the bottom, pelagic). The response variable was the combination of the number of infected ("successes") and healthy ("failures") individuals for each species. All statistical analyses were performed in R (R Core Team 2013).

Results

During the visual censuses, we recorded 3,364 reef fishes of 79 species in Belize (96.11 individuals per transect), 33,890 of 96 species in Curaçao (413.29 individuals per transect), and 8,200 of 110 species in Mexico (102.50 individuals per transect) (Table 1). The larger number of fishes observed on Curaçao was due, in part, to the abundance of planktivorous species, mostly *Chromis* spp. (7,712 individuals) and *Coryphopterus* spp. (13,957 individuals). Of the fishes observed, 75 individuals belonging to 14 species were affected by dermal parasites in Curaçao (Table 2). In contrast, only three infected individuals of one species, *Acanthurus tractus*, were observed in Belize, and no infected individuals were observed in Mexico. The 14 species prone to infection in Curaçao totaled 1,951 individuals, of which 3.80 % were infected. In Belize, we found 736 individuals of species prone to infection, and 0.40 % was infected. Thus Curaçao had higher total counts as well as a higher proportion of infected individuals compared to the other two localities (Fisher's exact test, $p<0.0001$).

In Curaçao, the species with the highest infection rates were *A. tractus*, with 19.7 %, followed by *Cantherhines pullus* (18.2 %), *Caranx ruber* (17.7 %), and *A. chirurgus* (11.5 %) (Table 2). The rate of infection was not related to host species abundance (linear regression; $r^2=0.03$, $p=0.54$, Fig. S2), and none of the functional traits considered had a significant influence on the probability of infection (Table S1).

In an examination of the 1,200 photographs taken in Curaçao, infections were detected in 22 additional species not recorded during the visual surveys (Table S2). Parrotfishes and wrasses (Labridae) had the highest number of infected species—seven and six, respectively (Fig. 3)—when visual census data and photographs were combined. For the other groups, there was at least one infected individual for every species of the family. This was the case for the boxfishes (Ostraciidae; three species), surgeonfishes (Acanthuridae; three species), soldierfishes (Holocentridae; two species), tilefishes (Malacanthidae; one species), and triggerfishes (Balistidae; one species). Other groups that were well represented in our surveys, such as gobies (Gobiidae; seven species) and angelfishes (Pomacanthidae; five species), showed no signs of infection (Fig. 3).

Discussion

The rate of parasite infections in coral reef fishes is known to vary in both space and time, yet the scale at which these variations can occur has been relatively unexplored in the Caribbean. Here we report a dramatically higher rate of infection (tenfold) by dermal parasites on reef fishes of Curaçao compared to Belize, where infection rates were very low, and Mexico, where no infected individuals were observed. Affected fishes showed black blemishes and white spots across the body that were easily detected visually and that have been associated with digeneans, turbellarians, and/or protozoan infections (Fig. 2).

Several studies have offered general explanations as to why dermal parasites can become more prevalent in certain locations, yet it is still unclear why Curaçao has such dramatic rates of infection. First, the abundance of mutualistic cleaners, such as shrimps and fishes, can affect the number and size of

Table 1 Total area surveyed, number of fishes counted, and number of infected fish by location

Location	Number of transects	Total area (m^2)	Number of fish species	Number of individuals	Individuals per transect	Infected	Infected per transect
Belize	35	1,400	79	3,364	96.11	3	0.08
Curaçao	82	3,280	96	33,890	413.29	76	0.93
Mexico	80	3,200	110	8,200	102.50	0	–

Table 2 Fish species infected and total number of infected individuals observed in visual censuses in Curaçao

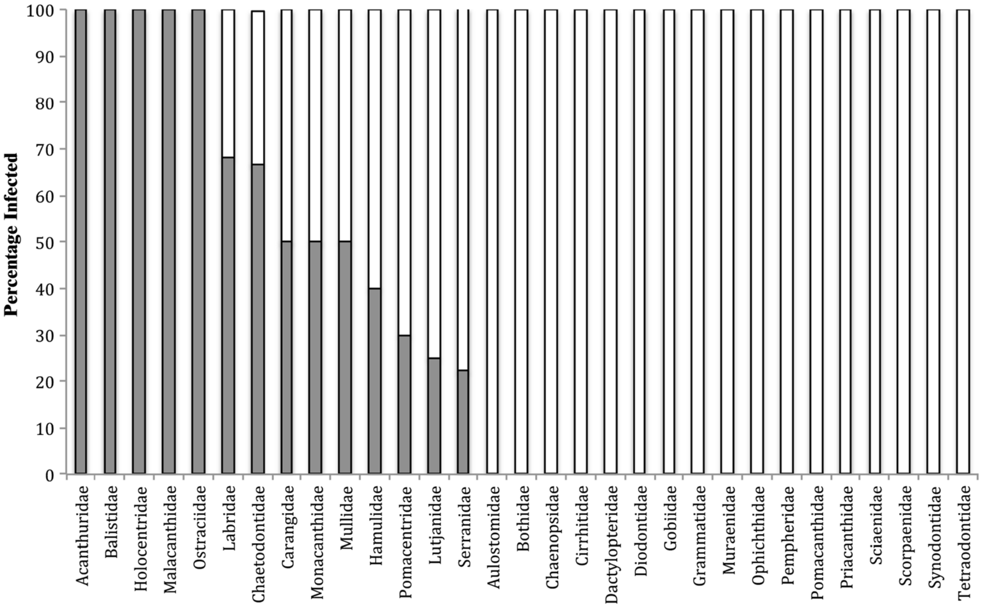
Species	Total	Infected	Percentage infected
Acanthurus chirurgus	52	6	11.54
Acanthurus coeruleus	241	17	7.05
Acanthurus tractus	147	29	19.73
Cantherhines pullus	11	2	18.18
Canthigaster rostrata	277	2	0.72
Caranx ruber	17	3	17.65
Haemulon chrysargyreum	151	2	1.32
Halichoeres garnoti	266	2	0.75
Lactophrys triqueter	20	1	5.00
Lutjanus apodus	36	1	2.78
Mulloidichthys martinicus	275	6	2.18
Scarus iseri	224	2	0.89
Sparisoma rubripinne	13	1	7.69
Sparisoma viride	221	1	0.45

parasites per infected fish (Grutter 1995; McCammon et al. 2010; but see Kent and Olson 1986). However, during surveys in Curaçao, we observed a great number of shrimps actively cleaning fishes. Further, there was no scarcity of cleaner fishes in Curaçao, including *Thalassoma bifasciatum* (1,953 individuals; 23.82 per transect), *Elacatinus evelynae* (58 individuals; 0.71 per transect), and *Bodianus rufus* (28 individuals; 0.34 per transect). These numbers are comparable to or higher than observed abundance in Mexico (*T. bifasciatum*=1,293, 16.16 per transect; *E. evelynae*=5, 0.06 per transect; *B. rufus*=20, 0.25 per transect), and Belize (*T. bifasciatum*=144, 4.11 per transect; *E. evelynae*=1, 0.03 per transect; *B. rufus*=2, 0.01 per transect). Thus, it appears unlikely that the high rates of infection in Curaçao is due to a scarcity of cleaners.

Habitat preference of the host is another factor known to influence parasite abundance. On Heron Island, Australia, the number of monogeneans found on the blackedge thicklip wrasse, *Hemigymnus melapterus*, was much higher in individuals inhabiting reef flats than in those found on the reef slope (Grutter 1998). In this particular location, monogenean eggs were more abundant on reef flats, suggesting that individuals inhabiting shallower reef flats come into contact with the parasites more often than the individuals on reef slopes (Grutter 1998). However, this was not likely the case in our study, as Curaçao has narrow ledges surrounded by steep slopes, while Mexico and Belize have very broad continental shelves.

An important difference among the three studied locations was the remarkably low abundance of large-bodied piscivores in Curaçao (Sandin et al. 2008). Previous studies have suggested that removal of predators can lead to an increase in parasite abundance (Packer et al. 2003). This is especially important for parasites with direct transmission, where the absence of predators can lead to increased population size, which in turn increases the chance of contact between infected and healthy individuals. Furthermore, in the absence of top predators, heavily infected fish are not effectively removed from the ecosystem by top-down control (e.g., Lafferty and Morris 1996). For example, many surgeonfish individuals in Curaçao presented black blemishes that covered most of their body and fins, and showed compromised swimming ability compared to mildly infected or healthy fish (Fig. 2h). In some cases, these individuals moved so slowly that it seemed that they could be caught with bare hands. This compromised swimming ability makes it unlikely that fish with high parasite

Fig. 3 Fish species infected with dermal parasites in Curaçao, by family. Gray bars represent the percentage of infected species per family



loads would be able to survive in communities with high numbers of predators.

On the other hand, studies have suggested that a high incidence of parasites reflects a healthy, well-structured ecosystem (Hudson et al. 2006). This is especially relevant for groups of parasites with complex life cycles, such as trematodes, for which coral reef fishes are intermediate hosts (Bray et al. 2005). The first hosts are usually mollusks, and their definitive hosts, in which they reproduce, are large predatory fish or birds (Poulin and Cribb 2002). Thus, parasites with complex life cycles are expected to be in low abundance if one or more of their required hosts is rare or missing (Hechinger and Lafferty 2005). For example, a study that compared the abundance and diversity of parasites in five fish species between the pristine Palmyra Atoll and the heavily fished Kirimati Atoll showed a richer parasite community in the former compared to the latter (Lafferty 2008). The authors suggested that overfishing in Kirimati could have reduced the number of hosts necessary for the proper development of groups with complex life cycles, which in turn led to lower parasite diversity (Lafferty 2008). In this context, it is possible that many more species of hosts required for the development of parasites with complex life cycles are present in Curaçao than in the other localities. Although Curaçao has more coral cover and biomass of grazers than other locations included in the surveys, (Jackson et al. 2014), this hypothesis has not been tested.

Our results indicate that surgeonfishes were disproportionally affected by dermal parasites. Previous studies have reported high rates of infection by monogeneans, turbellarians, and parasitic copepods in Acanthuridae in both the Caribbean (Sikkel et al. 2009; McCammon et al. 2010) and the Indo-Pacific (Lewis 1964; Work and Aeby 2014). The elevated rates of infection could be related, at least in part, to their behavior. Surgeonfishes roam the reef in large feeding schools, which may increase the chance of parasite transmission between individuals (Grutter 1998; Sikkel et al. 2009). Also, acanthurids are frequently found at the bottom, where they can come into contact with eggs and larvae of parasites (Grutter 1998; Marcogliese 2002). Even though these traits (association with the benthos and schooling) have been found to correlate with elevated infection rates, our analysis for fishes of Curaçao detected no correlation between any of the functional traits surveyed and the probability of infection (Table S1).

At this time, the reason for the high rates of parasite infection in Curaçao, and the full impact it may have on the health of local ecosystems, remain unknown. Several factors, including oceanographic conditions, lack of predators, and high biodiversity, could all contribute to the observed patterns. In light of the devastating effects that infections have previously had in communities of the Caribbean (e.g., *Diadema* mass mortality, Lessios 2005; white band disease in corals, Pantos and Bythell 2006), and that multiple parasites have complex life cycles that include several hosts, we recommend further studies to gain an understanding of the causes and effects of high rates of infection in Curaçao. Lastly, the marine ecosystems of Curaçao offer a great opportunity to study parasite–host interactions in Caribbean coral reef fishes, and to improve our understanding of the ecological consequences of parasites on the wider reef community at various spatial scales.

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