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REPORT

Long-term cleaning patterns of the sharknose goby (*Elacatinus evelynae*)

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Abstract Cleaning interactions, which involve a cleaner removing ectoparasites and other material from the body of a heterospecific (client), are iconic symbiotic interactions observed on coral reefs worldwide. These small cleaners play a disproportionately large role in the structuring and function of coral reefs, influencing species interaction networks, client health and biodiversity. Cleaning patterns, however, are likely to be context-dependent and highly heterogeneous, and although we have some understanding about their spatial variation, longer-term temporal changes in cleaning interactions have remained understudied. Given that coral reefs are globally threatened and are currently experiencing large shifts in their biodiversity, it is vital that we determine which clients are consistently most important for maintaining cleaning. Using a long-term, 8-yr data set (2010–17) on the cleaning behaviour of the predominant Caribbean cleaner, the sharknose goby (*Elacatinus evelynae*), we investigated whether cleaner fish from the same reef show consistent patterns in their interactions with client species over time. Here we conclusively show that cleaning behaviour is highly plastic, as no single species or family was cleaned consistently more than others, in terms of cleaning frequency and duration, across all years. Only 40% of the species were cleaned more than others, and we also observed ca. one-third of species experience inconsistent cleaning patterns across years. Our study thus quantifies how dynamic cleaner–client relationships are on the same reef across years and highlights the importance of long-term data.

Keywords Caribbean · Cleaner fish · Coral reef · Gobiidae · Mutualism · Time-series

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Introduction

Symbiotic cleaning interactions are ubiquitous on coral reefs (White et al. 2007) and involve a cleaner species removing ectoparasites and other material from the body of a heterospecific (client) host (Feder 1966). During these interactions, cleaners gain a source of food (Vaughan et al. 2017) whilst clients benefit from tactile contact and parasite removal (Grutter 1999; Clague et al. 2011; Soares et al. 2011). Despite being small in size and not highly abundant on reefs themselves (Grutter et al. 2003; Sazima et al. 2010), cleaners play a pivotal role in the structuring and functioning of coral reefs, as they interact with a wide range of fish species on a daily basis (Floeter et al. 2007; Sazima et al. 2010; Quimbayo et al. 2018). Different reef species, however, differ in their propensity to engage in cleaning interactions (Côté et al. 1998) and the nutritional material that they host, in terms of their ectoparasite assemblages and mucus composition (Eckes et al. 2015). Thus, differing clients provide asymmetric benefits to the interaction, but it is still not clear how these asymmetries in client identity and their engagement influences cleaner–client relationships. With rapid environmental degradation

threatening coral reef communities, identifying key client species and finding consistent cleaning patterns will help further knowledge on the evolution and conservation of interacting species (Toby et al. 2010).

Many studies have attempted to capture and describe cleaner–client interaction patterns (e.g. Arnal et al. 2000; Sikkel et al. 2000; Grutter et al. 2005; Soares et al. 2008b), but cleaning patterns across studies are inconsistent. For a given cleaner species, cleaning behaviour can vary with time of day (Sazima et al. 2000), cleaning station (Whiteman and Côté 2002b) and among reefs (Cheney and Côté 2005). All these previous studies are, however, short term ($\sim$ 1 yr), and as yet, there are no studies describing the variation in long-term cleaning patterns from the same reef. Both abiotic and biotic contexts, which will likely influence general interaction dynamics (Bronstein 2015), are more variable across rather than within locations over time. Thus, investigating consistent patterns over time within the same location and same season should minimise some sources of this variation (e.g. seasonal and location differences in ectoparasite assemblages, Grutter (1994); general client species diversity, i.e. some species are consistently found on one reef but not another, Malcolm et al. 2007). Long-term studies are fundamental for understanding true species interaction patterns (Brown et al. 2001) and have already advanced our knowledge on coral reef communities in terms of coral decline (De'ath et al. 2012), community assemblage (Nash et al. 2016), species space use (Heupel and Simpfendorfer 2015) and species interactions (Vergés et al. 2016). Even among cleaning studies, long-term removal experiments have demonstrated the impact of cleaner presence on the health and diversity of client fish (Clague et al. 2011; Waldie et al. 2011): a result not apparent from short-term studies (Grutter 1996). Long-term studies on cleaner–client interactions are thus urgently required to elucidate key drivers maintaining cleaner–client interactions.

Dedicated cleaners, which are thought to rely solely on client-gleaned material for nutrition (as opposed to the opportunistic facultative cleaners, Vaughan et al. 2017), are highly connected within reef interaction networks (Quimbayo et al. 2018). The bluestreak cleaner wrasse (*Labroides dimidiatus*) and cleaning gobies (*Elacatinus* spp. formally *Gobiosoma* spp.) are the most ubiquitous and widely studied dedicated cleaner fish (Côté and Soares 2011) and can interact with a large diversity of client species daily (e.g. *Elacatinus figaro* 27 client species, Sazima et al. 2000, *L. dimidiatus* 132 client species, Grutter and Poulin 1998). Gobies are the predominant cleaner fish in the Caribbean and provide an ideal model system for investigating which client species are consistently the most important for cleaning: unlike the bluestreak wrasse, the cleaning strategy of gobies does not knowingly involve tactics to manipulate client behaviour (Soares et al. 2008a; Côté and Soares 2011). Both cleaning gobies and bluestreak wrasse wait at their cleaning stations (defined by topological reef features; Potts 1973) for clients, which chose which cleaners to visit (Bshary and Schaffer 2002). Not all client visitors get cleaned, however (Côté et al. 1998; Arnal et al. 2001), because cleaners have a choice about which of the locally available clients to interact with and for how long. Bluestreak wrasse often adopt their cleaning behaviour to clean different clients more favourably to encourage their return (Grutter and Bshary 2003). This behaviour is not observed in gobies, and clients do not punish reluctance of cleaning (Soares et al. 2008a). Patterns of goby cleaning will hence reflect true decisions to clean certain clients by the cleaner, rather than manipulative behaviours towards different clients. In addition, Caribbean reefs, as opposed to Indo-Pacific reefs, are particularly vulnerable to loss of functional diversity (Bellwood et al. 2004) and thus understanding how their diversity is shaped is of high importance.

No study has yet quantified how consistent cleaning patterns are across time and so here we provide the first long-term data describing cleaning interactions of sharknose gobies (*Elacatinus evelynae*) recorded from the same coral reef over 8 yr. We specifically investigate whether gobies clean different client species consistently each year, to quantify how plastic cleaning interactions really are (in terms of cleaning frequencies and mean cleaning durations). This knowledge will help to explain why we still do not fully understand the true interaction dynamics of this well studied mutualism. In addition, although cleaners interact with a number of different species, if we can identify the key client species that are consistently important for facilitating the occurrence of cleaning interactions, irrespective of the fluctuating abiotic and biotic context, this will further our knowledge on how this important mutualism is likely to persist under future environmental conditions.

Methods

Cleaning interactions were observed over 8 yr on Booby Reef situated in the Man O' War Bay, Tobago (11°19.344′N 060°33.484′W). This relatively degraded fringing reef begins at the shoreline and extends to Booby Island, located 85–90 m northeast from the shore (Ramsaroop 1982). Our nearshore study area (1–2 m deep covering an area of 70 m $\times$ 60 m) is primarily composed of algae-covered dead coral, living brain corals (Faviidae) and an encrusting zooxanthid (*Palythoa caribaeorum*), which provides a suitable habitat for sharknose gobies (*E. evelynae*) (Soares et al. 2008b). Across 8 yr we did not observe

any significant changes in the coral structures or reef health. Tobago is situated outside of the Caribbean hurricane belt and so during this time period was unaffected by yearly reef structure damage (Gardner et al. 2005). Sharknose gobies show site fidelity to their coral cleaning stations (Whiteman and Côté 2002b), which were marked each year and matched between years using photographs (total number stations matched across 8 yr = 82). Individual stations were located at least 1 m apart from one another. Within each year, not all marked stations were occupied by sharknose gobies; the number of occupied versus marked stations ranged from 79.7 in 2015 to 95.3% in 2016. Individual sharknose gobies have high turnover rates on their cleaning stations (mean age < 50 d documented in White et al. 2007) and thus different individuals will have been observed at the same cleaning stations across years. In addition, the number of gobies occupying each station, within years, ranged from one to nine (mean ± S.E. number individuals per station across years = 1.53 ± 0.01). There is no means to naturally identify individual gobies in situ, and thus the cleaning behaviour of different individuals will have also been observed at the same station within each year. Therefore, this study represents the selective pressures of clients in seeking out cleaning over the years, irrespective of which cleaning goby individuals are occupying the station.

Cleaning interactions were observed using snorkelling over a 2 week (2010–2015; June) or 6 week (2016–2017; May/June/July) period between the hours of 07:30 to 17:00. Focal sharknose gobies were randomly selected from marked stations for each observation and were observed for 10 min (2010 n = 130 observations, 2011 n = 374, 2012 n = 281, 2013 n = 143, 2014 n = 175, 2015 n = 262, 2016 n = 307, 2017 n = 304). Observations were carried out randomly across all the marked occupied cleaning stations within each year (mean ± S.E. number of observations per station; 2010 = 3.73 ± 0.54, 2011 = 8.34 ± 0.68, 2012 = 7.13 ± 0.65, 2013 = 5.56 ± 0.48, 2014 = 5.8 ± 0.77, 2015 = 6.12 ± 0.68, 2016 = 4.94 ± 0.41 2017 = 4.54 ± 0.36). During each observation, we recorded the cleaning duration and frequency of different client species. These measures were used to calculate two probabilities of cleaning for each species in a given year using total cleaning frequencies/durations across all species and the number of species cleaned with each year. This created a standardised cleaning measures for each species, making them comparable within and across years. Five damselfish species, the dusky (*Stegastes adustus*), longfin (*S. diencaeus*), beaugregory (*S. leucostictus*), threespot (*S. planifrons*) and cocoa (*S. variabilis*) are morphologically similar and hence difficult to quickly identify in the field. We thus combined cleaning observations and species counts on the reef for these five species (hereafter termed *Stegastes* spp.). Frequency data for *Stegastes* spp. were subsequently divided by five to give comparable, yet conservative, values (duration data were considered in terms of the mean time per clean and thus were not adjusted). The number of different fish species within the study area was recorded each year at the start of June using 50-min random swim surveys (n = 19 yr^{-1}) and combined with sightings of species at cleaning stations for a total species count of potential clients.

Data analysis

To investigate patterns of cleaning, we calculated two measures of cleaning probability for each client within each year; cleaning frequency and mean time per clean (hereafter referred to as cleaning duration). To determine whether any client species was consistently cleaned the most across years, we only considered clients species which were cleaned in three or more years. These probability values were subsequently log10 transformed to increase the data resolution, which meant we could distinguish between very small probabilities. As a measure of how frequently/long clients were cleaned across years, we calculated mean cleaning probabilities on the log10 transformed values across years for each client species and cleaning type (for frequency and duration). As a measure of consistency in cleaning behaviour across years, we calculated the relative standard error (RSE) across transformed cleaning probabilities for each client species and cleaning type (frequency and duration). The RSE (expressed as a %) is similar to the coefficient of variation (CV) but provides a measure of variability whilst accounting for the mean and sample size (some clients were cleaned in 3 yr whilst others were cleaned in all 8 yr).

Data were analysed using *R* version 3.4.3 (R Core Team 2017). *Z*-scores were calculated for each client and for each cleaning type (frequency and duration) and for both probability and consistency measures (log10 means and RSEs) from bootstrapped (100,000 resampling) means and standard deviations. The log10 mean cleaning probabilities express whether certain clients are cleaned more than others, and clients with z-scores greater than 1.64 (based on a one-sided 95% CI) are considered to be key clients to the cleaner. The RSEs reflect whether there was significant temporal variation in cleaning activity of a client species across the years, and also here, z-scores greater than 1.64 are considered to indicate a significant inconsistency. It was not possible to use a two-tailed test to determine whether some clients were 'highly non-important to the interaction', as we do not know whether low cleaning probabilities represent a true choice to not clean by the gobies or simply a rare occurrence of the interaction between cleaner and client. *P*-values were computed from

these z-scores, and goodness-of-fit tests were subsequently used to determine whether the distribution of key clients versus non-key clients differed from a random distribution. In addition, we also applied this method to determine whether any client families were consistently cleaned more than others. Family cleaning frequencies and summed clean durations were divided by the number of species within each family, and families were only included if they were cleaned in three or more years. Finally, Spearman's rank correlation tests were performed to determine whether there were significant relationships between the mean log10 probability values and RSEs. We also compared whether cleaners differed in their variability in cleaning frequencies and durations using two-tailed 95% confidence intervals estimated through bootstrap resampling. Bootstrapped z-scores were also used to determine whether the proportion of clients cleaned versus those on the reef differed across years (significant if z-scores were greater than 1.96, based on two-tailed 95% CI).

Results

Across our 8-yr study in Tobago, we recorded 47 client fish species, from 17 families, being cleaned by sharknose gobies, *E. evelynae* (17–33 species cleaned within each year; Table 1). The number of potential client species occupying the study area ranged from 45–78 across years; thus only 32 to 64% of fish species on the reef were cleaned within any given year (Fig. 1). These proportions of reef species cleaned differed significantly across years, as the percentage of clients cleaned was significantly higher in 2011 ($z = 6.08$, $p < 0.001$), but lower in 2013 ($z = -3.75$, $p < 0.001$) and 2016 ($z = -2.95$, $p = 0.002$) compared to other years. Eight fish species were recorded as clients in each of the 8 yr, whilst nine species were only recorded as clients in 1 yr, despite these species being present on the reef. For 23 fish species, they were present on the reef every year but were not always cleaned within each year (Table 1).

Our 8-yr study included 312 h, 23 min and 22 s of observations at cleaning stations, within which we observed 3154 cleaning interactions totalling 9 h, 7 min and 57 s. On cumulative values across all years, Queen parrotfish (*Scarus vetula*) were the most frequently cleaned clients, whilst five species were only observed being cleaned once. Despite being cleaned more frequently, *S. vetula* did not receive the longest cleaning duration, instead graysbys (*Cephalopholis cruentata*) were cleaned for the longest, whilst slippery dicks (*Halichoeres bivittatus*) received the shortest cleaning durations (Table 1). On cumulative values across 8 yr, there was no significant relationship between cleaning frequencies and durations (rho = 0.08).

Cleaners interacted with some client species significantly more than others, both in terms of their cleaning frequencies ($\chi^2_1 = 106.04$, $p < 0.001$) and cleaning durations ($\chi^2_1 = 112.32$, $p < 0.001$) within each year. However, across years, no single client species was consistently cleaned the most frequently, with the exception of the redband parrotfish (*Sparisoma aurofrenatum*; most frequently cleaned client in 2015 and 2016). Fourteen client species were cleaned significantly more frequently than the other species (Fig. 2; species names highlighted in bold; from $z = 2.23$, $p = 0.013$ to $z = 9.27$, $p < 0.001$). The cleaning frequency of nine client species was significantly inconsistent across years (Fig. 2; from $z = 2.35$, $p = 0.008$ to $z = 12.00$, $p < 0.001$). Interestingly, clients that show significantly inconsistent cleaning activity were most frequently cleaned across years, as evidenced by the positive correlation between mean log10 p value and RSEs (rho = 0.90, $p < 0.001$).

The client species with the highest cleaning duration differed between years (Fig. 2). Eleven species (from $z = 2.20$, $p = 0.014$ to $z = 7.44$, $p < 0.001$) were cleaned for significantly longer than the remaining 17 clients (Fig. 2; species names highlighted in bold). Eleven species were cleaned for significantly different durations over the 8 yr (Fig. 2; from $z = 2.43$, $p = 0.007$ to $z = 10.71$, $p < 0.001$), and again, clients that showed significantly inconsistent cleaning activity were cleaned for longer (rho = 0.59, $p < 0.001$). Clients which were cleaned for longer were not cleaned at a higher frequency (rho = 0.18).

Cleaners also interacted more with some client families over others, in terms of their cleaning frequencies ($\chi^2_1 = 35.56$, $p < 0.001$) and cleaning durations ($\chi^2_1 = 25.81$, $p < 0.001$) within each year. In seven out the 8 yr, Pomacentridae clients were the most frequently cleaned. In 2014, they dropped to 5th however, and Acanthuridae clients were cleaned most frequently. Four families, the Acanthuridae ($z = 4.65$, $p < 0.001$), Mullidae ($z = 2.61$, $p = 0.005$), Pomacentridae ($z = 4.70$, $p < 0.001$) and Scaridae ($z = 5.09$, $p < 0.001$) were cleaned significantly more frequently than the other nine families (Fig. 3). Clients from three of these four families (Mullidae $z = 1.82$, $p = 0.033$, Pomacentridae $z = 5.45$, $p < 0.001$ and Scaridae $z = 8.17$, $p < 0.001$), however, were not consistently cleaned at a high frequency across all years (Fig. 3).

For cleaning durations, no single family was consistently cleaned for longer across years, although Monacanthidae were cleaned for the longest durations in 2012 and 2015. Four families, the Acanthuridae ($z = 4.92$, $p < 0.001$), Haemulidae ($z = 2.70$, $p = 0.003$), Scaridae

Table 1 Client species cleaned by sharknose gobies (*E. evelynae*) over 8 yr on Booby Reef Man O' War Bay Tobago. Total clean frequencies and durations represent cumulative sums over 8 yr. Time per clean represents total clean duration/total clean frequency (top 10 highlighted in bold, lowest value in italics). Ranges show minimum and maximum ranks for different species across years with one being the most important client species. Rank changes highlight how fluid cleaner behaviour is towards species across years

Family	Species	Years observed cleaned	Years observed on reef	Total clean frequency	Total clean duration (s)	Time per clean (s)	Rank range: clean frequency	Rank range: time per clean
Acanthuridae	*Acanthurus bahianus*	8	8	**187**	3041	16.3	2–14	4–13
	Acanthurus chirurgus	5	8	11	125	11.4	17–22	6–25
	Acanthurus coeruleus	7	8	**98**	2183	22.3	1–13	2–11
Aulostomidae	*Aulostomus maculatus*	5	8	17	163	9.6	15–19	5–21
Balistidae	*Melichthys niger*	1	8	*1*	24	**24.0**	23	4
Blenniidae	*Ophioblennius atlanticus*	1	5	6	55	9.2	16	18
Chaetodontidae	*Chaetodon capistratus*	8	8	29	163	5.6	9–22	9–22
	Chaetodon striatus	7	8	56	699	12.5	1–16	1–26
Haemulidae	*Haemulon carbonarium*	5	8	9	191	21.2	11–24	1–27
	Haemulon flavolineatum	8	8	96	2222	**23.1**	3–19	4–20
	Haemulon sciurus	2	7	2	25	12.5	21–24	2–18
	Haemulon chrysargyreum	3	8	23	233	10.1	9–19	6–16
Holocentridae	*Holocentrus adscensionis*	2	8	*1*	13	13.0	15–21	3–16
	Myripristis jacobus	1	7	*1*	5	5.0	21	18
Labridae	*Bodianus rufus*	2	8	2	40	20.0	21–23	7–10
	Halichoeres bivittatus	5	8	8	13	*1.6*	18–24	25–31
	Halichoeres maculipinna	7	8	26	228	8.8	9–19	5–25
	Halichoeres radiatus	6	8	18	251	13.9	7–24	1–25
	Thalassoma bifasciatum	3	8	4	15	3.8	22–24	25–25
Lutjanidae	*Lutjanus analis*	4	4	9	257	**28.6**	15–24	1–21
	Lutjanus synagris	1	2	3	70	**23.3**	15	7
	Ocyurus chrysurus	1	6	2	52	**26.0**	19	3
Monacanthidae	*Aluterus scriptus*	4	7	16	488	**30.5**	12–23	2–15
	Cantherhines macrocerus	7	8	69	1433	20.8	3–15	1–14
	Cantherhines pullus	3	8	6	144	**24.0**	17–19	1–24
Mullidae	*Mulloidichthys martinicus*	5	8	**100**	1222	12.2	4–11	2–21
	Pseudupeneus maculatus	2	6	2	10	5.0	21–23	21–24
Muraenidae	*Echidna catenata*	1	3	*1*	2	2.0	22	25
	Gymnothorax moringa	1	1	*1*	2	2.0	23	30
Pempheridae	*Pempheris schomburgkii*	1	6	2	24	12.0	17	11
Pomacentriade	*Abudefduf saxatilis*	4	8	19	256	13.5	10–24	9–28
	Abudefduf taurus	2	8	2	62	**31.0**	19–24	5–19
	Microspathodon chrysurus	8	8	**113**	1205	10.7	1–18	8–24
	Stegastes partitus	6	8	70	394	5.6	4–15	5–27
	Stegastes spp.[a]	8	8	**1176(235.2)**	5903(1180.6)	5.0	2–11	14–26
Scaridae	*Scarus guacamaia*	2	6	3	11	3.7	17–23	21–29
	Scarus iseri	8	8	**166**	1246	7.5	1–13	11–23
	Scarus taeniopterus	8	8	**144**	1766	12.3	3–12	8–17
	Scarus vetula	8	8	**240**	2405	10.0	1–10	6–16
	Sparisoma aurofrenatum	8	8	**238**	2892	12.2	1–15	5–17
	Sparisoma chrysopterum	2	5	2	19	9.5	22–23	9–21
	Sparisoma rubripinne	7	8	26	399	15.3	8–21	1–28
	Sparisoma viride	8	8	**122**	2274	18.6	1–15	4–16

Table 1 continued

Family	Species	Years observed cleaned	Years observed on reef	Total clean frequency	Total clean duration (s)	Time per clean (s)	Rank range: clean frequency	Rank range: time per clean
Serranidae	*Cephalopholis cruentata*	3	3	7	250	**35.7**	15–18	2–12
	Cephalopholis fulva	1	2	4	28	7.0	18	19
	Epinephelus adscensionis	2	2	9	283	**31.4**	15–15	1–8
Tetradontidae	*Canthigaster valentini*	4	7	5	53	10.6	9–24	2–26

[a]*Stegastes* spp. represents five different damselfish species: *Stegastes adustus*, *S. diencaeus*, *S. leucostictus*, *S. planifrons* and *S. variabilis*. Total counts are provided for this group, whilst bracket values indicate these totals divided by five to act as a conservative comparable measure

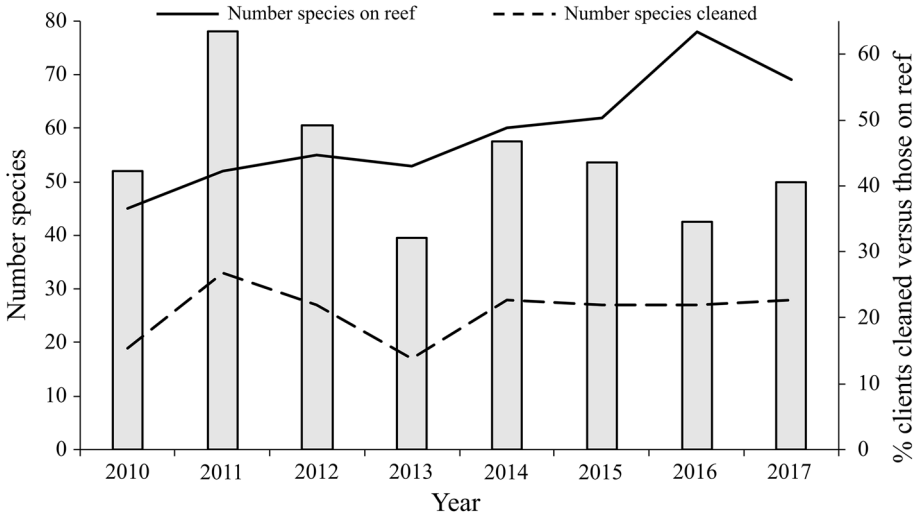

Fig. 1 Relationship between the number of fish species on Booby Reef, Man O' War Bay Tobago and those cleaned by sharknose gobies (*E. evelynae*) over 8 yr. Bars represent proportion of clients cleaned versus those available on the reef

($z = 1.81$, $p = 0.033$) and the Serranidae ($z = 4.92$, $p < 0.001$) were cleaned for significantly longer than the other eight families (Fig. 3). Three families (Acanthuridae $z = 4.84$, $p < 0.001$, Lutjanidae $z = 1.97$, $p = 0.024$ and Serranidae $z = 8.64$, $p < 0.001$) did not receive the same cleaning durations across years (Fig. 3), and those families which were cleaned for longer were not cleaned for the same duration each year (rho = 0.66, $p = 0.022$). The cleaning frequency of a given family was unrelated to its cleaning duration (rho = 0.03). Patterns in cleaning frequencies and cleaning durations were not more consistent for clients grouped at a family versus species level (cleaning frequency: difference between means = − 2.75, 95% CI_b [− 4.06, − 1.46]).

Discussion

From our unique 8-yr long-term study of cleaning on a Caribbean reef, we show that there are no clear patterns in cleaning frequencies and durations of particular clients across years, i.e. no reef fish species is consistently the most important client of sharknose gobies (*E. evelynae*). Only around 40% of cleaned species were consistently cleaned relative to others across each year and ca. one-third of species were cleaned for consistently the same duration or at the same frequency across years. Given that no client species alone appears to play a consistently key role in maintaining cleaner–client interactions, we thus propose that the key players in cleaner–client relationships are likely to be context dependent, and so patterns are a function of the dynamic nature of coral reef fish communities.

Cleaners are hypothesised to be supergeneralists; interacting with, and relying on a highly diverse number of species (Sazima et al. 2010). Here we provide evidence for

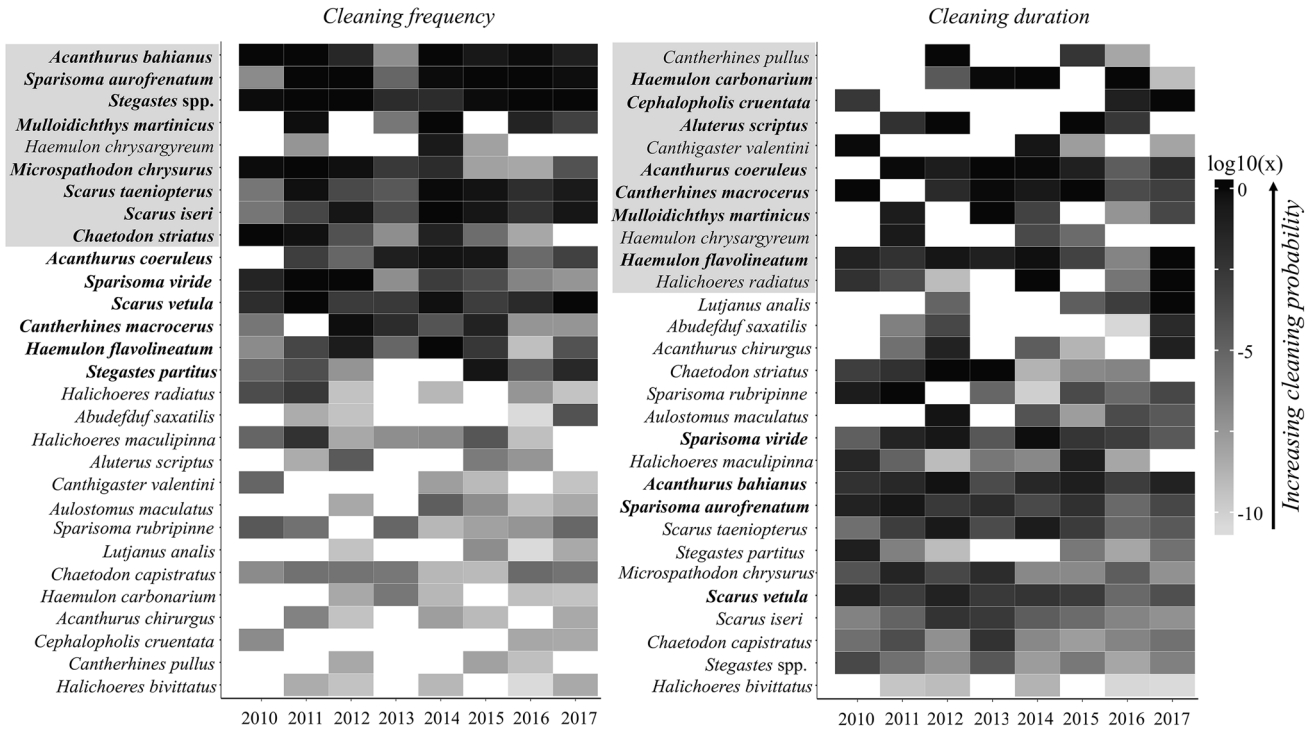

Fig. 2 Sharknose goby (*E. evelynae*) probabilities of cleaning (log10 transformed) for different client species over 8 yr based on observed cleaning frequencies and the mean time per clean (cleaning duration). Darker colours represent higher probabilities of cleaning. Species are ordered based on their relative standard error (RSE) of cleaning frequency or duration calculated across years, with top species showing more variation in their received cleaning behaviour across years. The names of the species that show significant ($p < 0.05$) variations in cleaning probabilities across years are shown in the grey boxes. Species that were cleaned significantly more frequently/for longer than the others are highlighted in bold

this notion showing that sharknose gobies do not consistently interact more with a single client species. Instead a number of species from different families were key clients for these cleaners, suggesting that a number of different client species play an important role in maintaining these cleaning interactions. Within families, species exhibit similar traits as a result of relatedness, and some previously described cleaning patterns have been confounded by phylogenetic artefacts (e.g. Grutter and Poulin 1998; Barbu et al. 2011), although this has not always been the case (e.g. Soares et al. 2008a). Here we found no difference in cleaning variations towards species versus their family groupings, likely as a result of the diversity and number of client species and families interacting with the cleaners (Guimarães et al. 2007). Dedicated cleaners, like the sharknose goby, are thought to rely solely on client-gleaned material for nutrition (Vaughan et al. 2017), and clients are asymmetric in the nutritional content they host (Eckes et al. 2015): different client species differ in the abundance and diversity of ectoparasite species on their bodies (Grutter 1994). Thus, the presence of different species will represent different food rewards and hence nutritional gains to the cleaner. For example, larger (Poulin and Rohde 1997), group living and/or sedentary (Patterson and Ruckstuhl 2013) species, including those from the Acanthuridae, Haemulidae and Scaridae families, are likely to host greater numbers of ectoparasites/higher quality food resources relative to other clients. This may explain why they were regularly cleaned for longer than others. Ascertaining which client traits are important for cleaning has been a focus of previous literature, but again results have been inconsistent. For example, client body size has been shown to influence cleaner behaviour in some studies (e.g. Whiteman and Côté 2002a; Grutter et al. 2005; Silvano et al. 2012), but not in others (e.g. Grutter and Poulin 1998; Arnal et al. 2000). The payoffs of certain traits will ultimately depend upon the presence, and relative abundance of both clients and their ectoparasites within the environment (Cheney and Côté 2005), which will, however, vary temporally. Thus, when investigating which client traits are more important to a cleaner, the client and parasite relative abundances within an area should also be considered (Floeter et al. 2007). If we can determine which, if any, client traits are consistently important to a cleaner and always influence the interaction dynamics, we can gain a greater understanding of how cleaning mutualisms are maintained and function.

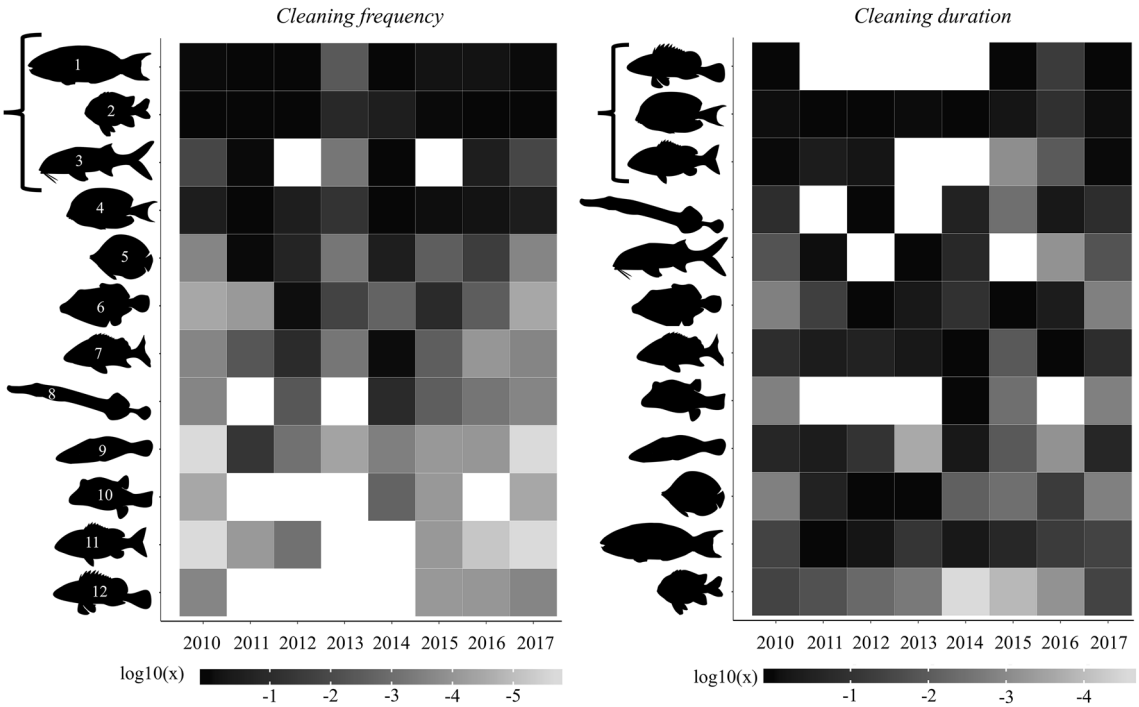

Fig. 3 Sharknose goby (*E. evelynae*) probabilities of cleaning (log10 transformed) for different client families over 8 yr based on observed cleaning frequencies and the mean time per clean (cleaning duration). Darker colours represent higher probabilities of cleaning. Families are ordered based on their relative standard error (RSE) of cleaning frequency or duration calculated across years, with top species showing more variation in their received cleaning behaviour across years. Those families showing significant ($p < 0.05$) variations in cleaning probabilities across years are shown using brackets. Only those families which were cleaned across 3 or more years are shown. 1 = Scaridae, 2 = Pomacentridae, 3 = Mullidae, 4 = Acanthuridae, 5 = Chaetodontidae, 6 = Monacanthidae, 7 = Haemulidae, 8 = Aulostomidae, 9 = Labridae, 10 = Tetraodontidae, 11 = Lutjanidae, 12 = Serranidae

Previous studies have demonstrated the positive role of client abundance on the reef on cleaning frequencies (e.g. Floeter et al. 2007) but only few consider the local abundance (Côté and Molloy 2003; Dunkley et al. 2018). Clients visit cleaners at their stations, and thus their local abundance is perhaps expected to be a larger contextual driver of cleaning patterns than the reef abundance. The local abundance of a client may also explain preference switching between years. Frequently cleaned sedentary clients from the families Pomacentridae (e.g. *Stegastes* spp. and *Microspathodon chrysurus*) and Haemulidae (e.g. *Haemulon flavolineatum*), for example, are often cleaned simply as a result of their proximity to cleaning stations. This has been shown for the longfin damselfish (*S. diencaeus*), which visits cleaning gobies less frequently the further away they are from a cleaning station (Cheney and Côté 2001). The presence of these sedentary species in close proximity to a cleaner ensures a frequent supply of food, but cleaning of these species likely represents repeated visits of the same few individuals. Indeed, often the same damselfish repeatedly visits the same cleaner (Côté et al. 1998) and individual damselfish with cleaning stations in their territories have been shown to host fewer ectoparasites (Cheney and Côté 2003). These repeated visits from the same individual client may explain why we found that those species/families that were cleaned more frequently or for longer were also the most variable in their cleaning patterns: food availability on the host may be limited.

Some species were on the reef every year but were not always observed as clients (e.g. *Abudefduf saxatilis*, Pomacentridae, and *Acanthurus chirurgus*, Acanthuridae). Again, these differences could reflect species-specific differences in ectoparasite abundance and diversity across years, influencing their need to seek out cleaning stations (Grutter 2001). However, only a maximum of two-thirds of fish species were cleaned by sharknose gobies in a given year. Cleaning by sharknose gobies is not the only method of parasite control observed on coral reefs (e.g. flashing, Wyman and Walters-Wyman 1985; Sikkel et al. 2000, and mucus production, Grutter et al. 2011) and on our reef we consistently observed the presence of three other cleaner species across study years: juvenile blueheaded wrasse (all years), juvenile Spanish hogfish (*Bodianus rufus*; all years) and juvenile French angelfish (*Pomacanthus paru*; 2010, 2015, 2016 and 2017). These cleaner species are facultative cleaners (Vaughan et al. 2017), and their client base can overlap with the dedicated cleaner species on the reef

(Johnson and Ruben 1988; Sazima et al. 1999; Dunkley et al. 2018; Quimbayo et al. 2018). The effect of co-occurring cleaner species may have large implications on species interactions patterns and also influences the dynamics of other mutualistic interactions (Palmer et al. 2015).

Overall, we show that no client species was consistently the most important species for sharknose goby cleaners, showing that their cleaning behaviour is highly plastic across 8 yr of study on the same reef, and is vulnerable to context-dependent changes. Despite sharknose goby cleaners representing one of the simplest cleaner–client interactions (in contrast to the bluestreak wrasse, *L. dimidiatus*), our understanding of cleaning is still largely limited in what maintains and drives patterns of cleaning. Our results suggest that cleaner preference is not driven by fish species identities, and instead we should now consider combinations of other biotic context-dependent factors when investigating cleaning dynamics (as suggested by Palmer et al. 2015): partner identity (functional identity of both the cleaner and client, which will link to their ectoparasite assemblages and cleaner visitation patterns), partner abundance (both at the cleaning station and on the reef) and the presence of co-occurring third party species (both clients and cleaners). All these factors, among others, together likely influence which client species is important to a cleaner at any one time point, and our long-term data set provides a unique opportunity to determine how stable cleaning patterns are over time. By determining which factors are consistently important in governing cleaner–client interactions, in terms of who interacts with whom and how, we will gain a better understanding of how resilient these interactions will be in response to the impending monumental shifts in reef and marine ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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