

The selective cleaning behaviour of juvenile blue-headed wrasse (*Thalassoma bifasciatum*) in the Caribbean

Katie Dunkley*, Jo Cable¹, Sarah E. Perkins¹

School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff, CF10 3AX, UK



ARTICLE INFO

Keywords:

Caribbean
Cleaner wrasse
Coral reef
Elacatinus evelynae
Facultative
Thalassoma bifasciatum

ABSTRACT

Through the removal of parasites, dead skin and mucus from the bodies of visiting reef fish (clients), cleaner fish have a significant ecosystem function in the ecology of coral reefs. Cleaners gain nutrition from these interactions and through offering a 'service' are afforded protection from predators. Given these benefits, it is unclear why more fish do not engage in cleaning, and why part-time cleaning strategies exist. On coral reefs, dedicated species clean throughout their life, whereas some species are facultative, employing opportunistic and/or temporary cleaning strategies. Here, we investigate the cleaning behaviour of a facultative species to assess the relative importance of this interaction to the cleaner. Using a combination of focal and event sampling from a coral reef in Tobago, we show that cleaning is not an essential food source for facultative juvenile blue-headed wrasse (*Thalassoma bifasciatum*), as cleaning rate was unrelated to their foraging rate on the substrate. These wrasse displayed two cleaning strategies: stationary versus wandering cleaning, with cleaning frequency being highest for stationary cleaners. A specific cleaning location facilitated increased cleaning frequency, and wrasse cleaning rate decreased as cleaner or client abundance increased. We also compared juvenile blue-headed wrasse cleaning behaviour to a resident dedicated cleaner, the sharknose goby (*Elacatinus evelynae*), and showed that, in comparison, juvenile wrasse clean a narrower client range, predominately cleaning three species of gregarious free-ranging surgeonfish (*Acanthurus* spp.). The wrasse, however, frequently approached these clients without cleaning, which suggests that their selective cleaning strategy may be driven by the acquisition of a particular parasitic food source. Juvenile blue-headed wrasse are generalist foragers, and may thus be limited in their cleaning behaviour by their nutritional requirements, the availability of a suitable cleaning site, and fish density, which ultimately means that they do not adopt more dedicated cleaning roles within the reef community.

1. Introduction

In abundant and species rich environments where competition for food is high, different feeding strategies have developed to spatiotemporally partition the available resources between species (Sale, 1977). Generalist feeders are characterised by a diverse diet or consume a broad dietary niche whilst specialists show a preference for specific food types or have a narrower dietary range (Bridcut and Giller, 1995; Amundsen et al., 1996). As predicted by foraging theory, specialist feeding strategies develop when there are benefits derived from feeding on specific food types (Stephens and Krebs, 1986). However, given the tangible benefits, other species must be limited in their feeding strategies or else they too would be expected to adopt these beneficial specialist strategies.

The abundance and diversity of species supported within coral reef environments makes them one of the most complex habitats in the

world (Reaka-Kudla, 1997) and multiple feeding strategies have developed to partition food resources. Most coral reef species are generalist feeders (Sale, 1977; Froese and Pauly, 2017) but cleaning, a symbiotic interaction ubiquitously observed in coral reef communities (White et al., 2007), represents a specialist feeding strategy where a cleaner removes ectoparasites and other material from the body of a heterospecific, a client (Feder, 1966). Dedicated cleaner species (formerly known as obligate cleaners; Vaughan et al., 2016) specialise in cleaning behaviour gaining all their nutrition from client derived material (Poulin and Grutter 1996), and since these cleaners interact with a large diversity of clients on a daily basis, including potential predators, dedicated cleaners are also afforded protection from predators (Potts, 1973a; Darcy et al., 1974; Losey, 1979; Côté, 2000). Within a reef environment, several fish species may act as cleaners (Côté, 2000), adopting differing cleaning strategies. Facultative cleaners are not solely dependent on cleaning for nutrition (Itzkowitz, 1979; Vaughan

* Corresponding author.

E-mail address: DunkleyK@cardiff.ac.uk (K. Dunkley).

¹ Joint senior authors.

et al., 2016), and many such species only clean when juvenile. Although a greater diversity of facultative as opposed to dedicated cleaners is known (Côté, 2000), research predominantly focuses on the latter (Côté and Soares, 2011): namely the Caribbean cleaning gobies, *Elacatinus* spp. (e.g. Whiteman and Côté, 2002; Côté and Molloy, 2003; Soares et al., 2008a,b) and the bluestreak cleaner wrasse, *Labroides dimidiatus* (e.g. Grutter, 1995a, 1999; Gingins and Bshary, 2014; Wilson et al., 2014). The extent to which a facultative cleaner gleans food from clients and the wider environment, varies spatio-temporally and between species (Vaughan et al., 2016). Some more specialised facultative species (e.g. *Pomacanthus paru* and *Thalassoma noronhanum*) are considered just as central within the reef community as their dedicated counterparts (Francini-Filho and Sazima, 2008; Sazima et al., 2010; Quimbayo et al., 2017) as they clean just as often, interacting with as many client species. Other facultative species exhibit more opportunistic and/or temporary cleaning behaviours, and are considered less specialised in cleaning (Vaughan et al., 2016). Investigating why these facultative cleaners do not adopt more dedicated cleaning strategies, given the benefits of cleaning (nutritional, Poulin and Grutter, 1996; and predator protection, Potts, 1973a; Darcy et al., 1974; Losey, 1979; Côté, 2000), will further our knowledge of why part-time cleaning strategies exist.

Blue-headed wrasse (*Thalassoma bifasciatum*) are a prominent member of the Caribbean reef fauna (Feddern, 1965) and only clean when juvenile (Feddern, 1965; Cheney and Côté, 2003). These facultative cleaners occupy the same reefs as the dedicated sharknose goby cleaners (*Elacatinus evelynae*). Both species are considered principle cleaners in the Caribbean (Michael, 2002; Cheney and Côté, 2003) but the frequency of observed juvenile blue-headed wrasse cleaning is variable across reefs (Feddern, 1965; Darcy et al., 1974; Itzkowitz, 1979; Johnson and Ruben, 1988; Walsh et al., 2017) and it has been suggested that these cleaners play a minor role on the reef despite being highly abundant (Johnson and Ruben, 1988). Although ectoparasites have been recovered from the stomachs of these wrasse cleaners (Randall, 1967), their reliance on cleaning as a food source has not been quantified. Itzkowitz (1979) described different cleaning strategies exhibited by juvenile blue-headed wrasse on the same reef in Jamaica; stationary versus wandering cleaners, but the prevalence of these strategies is also unknown. In comparison to other facultative cleaners (e.g. *Thalassoma noronhanum*; see Francini-Filho et al., 2000; Quimbayo et al., 2017), these wrasse are considered less specialised in their cleaning, adopting a more opportunistic approach (Itzkowitz, 1979; Johnson and Ruben, 1988).

Here, we investigated the relative importance of cleaning to juvenile blue-headed wrasse to further knowledge on why part-time cleaning strategies exist. Using the behaviour of the resident dedicated cleaner species (sharknose goby) occupying the same reef in Tobago as a comparison, we investigated the cleaning strategies of the facultative wrasse through behavioural observations. To investigate why these wrasse cleaners do not adopt more specialised cleaning roles within the community, we must assess what limits their cleaning. Space is the most competitive resource on coral reefs (Sale, 1977) and although cleaning represents an opportunistic foraging strategy for juvenile blue-headed wrasse, the prevalence of cleaning strategies of a species can vary spatially (Vaughan et al., 2016), with cleaning stations being an important requisite for other cleaner species (Whiteman and Côté, 2002; Huebner and Chadwick, 2012). Thus, we hypothesised that cleaning by these wrasse will also vary spatially with the frequency of cleaning differing between wandering versus stationary cleaners. The prevalence of feeding strategies within a population and between species is also regulated by density dependent competition, as more individuals adopting a strategy, and competing for resources, will reduce the benefits gained by each individual (Krebs, 1979; Krebs et al., 1993). Thus it was hypothesised that the prevalence of juvenile blue-headed wrasse cleaning would also be limited by the number of wrasse cleaners (increased competition) but would be positively influenced by an

increase in the number of clients, reducing competition. The importance of cleaning to a species can be assessed by investigating the cleaners wider diet (Whiteman and Côté, 2002). Juvenile blue-headed wrasse predominantly feed on benthic organisms (Feddern, 1965) and so it is hypothesised that if cleaning does provide a compulsory component of their diet, the foraging rate of individual wrasse on the substrate would be negatively influenced by their respective cleaning rates. The material gleaned from different clients during cleaning interactions, also provides differing nutritional content (Eckes et al., 2015) and thus like other cleaners (*Elacatinus* spp. see Soares et al., 2007; Francini-Filho and Sazima, 2008) it is hypothesised that juvenile blue-headed wrasse will clean certain client species more frequently than others to meet their nutritional requirements.

2. Methods

2.1. Study site and species

Observations on juvenile blue-headed wrasse (*Thalassoma bifasciatum*) and sharknose goby (*Elacatinus evelynae*) cleaning behaviour were collected from Pirates Bay Reef in Charlotteville, Man-O-War Bay, Tobago (11° 19' 00" N, 60° 33' 00" W) in January to February 2017 by daily snorkelling between the hours of 08:00 and 17:30. The shallow reef area sampled (30 m × 50 m, reef top depth 0.5–2 m) is on the east side of the bay about 100 m offshore. The fringing reef is mainly composed of rocky sandy substrate, the encrusting zooxanthid (*Palythoa caribaeorum*) and living hard coral (*Siderastrea* spp. and *Montastraea* spp.; Mallela et al., 2010), providing suitable habitats for sharknose goby cleaning stations (Soares et al., 2008a). These small dedicated cleaning gobies (max 4.5 cm fork length), the predominant Caribbean cleaner fish, are characterised by conspicuous black and blue lateral stripes on the body (Cheney and Côté, 2003). They occupy the same reefs as the more facultative juvenile blue-headed wrasse cleaners (max 15 cm fork length). These cleaners are characterised by their yellow body colouration and black spot on the dorsal fin (Feddern, 1965). All work was approved by Cardiff University's animal ethics committee linked to Home Office licence PPL 302876, and supported by the Tobago Ministry of Food Production Fisheries Division.

2.2. Cleaner-client interactions

To compare the abundance of juvenile blue-headed wrasse and sharknose gobies on the reef, 30 m × 2 m belt transects (n = 12) were laid along the reef, and the number of each cleaner species were counted along each transect. To quantify wrasse cleaning behaviour, focal individuals (n = 94) were observed for up to 10 min or until focal fish were lost. Individual wrasse could not be identified due to their uniform body patterning and free swimming behaviour across the reef, but it is unlikely that the same individual was observed multiple times due to their high abundance on the reef; our unpublished fish abundance surveys conducted over the last four years at Pirates Bay Reef have consistently recorded over 150 individuals of free-ranging juvenile blue-headed wrasse per 50 min survey. To compare cleaning behaviours, we observed at least ten individual sharknose gobies occupying ten marked cleaning stations (n = 10.7 × 10 min observations per station ± 2.04; mean ± S.E.). The number of gobies occupying these stations ranged from one to seven but only one focal fish was observed at a time, and it is unknown whether the same individual goby was observed multiple times. For both cleaner species, the frequency of cleaning events per unit time was recorded. A cleaning event began when a cleaner and single client physically interacted, ending when either the cleaner or client terminated the interaction (Floeter et al., 2007). In contrast to the sharknose goby cleaners (Côté, 2000), juvenile blue-headed wrasse reportedly do not rely solely on gleaned material as a food source (Feddern, 1965) and therefore the non-cleaning substrate foraging rate of juvenile wrasse was also recorded during these 10 min

focal observations.

As cleaning was rarely observed during juvenile blue-headed wrasse focal observations, an event sampling method, which is more likely to capture rarer behaviours (Altmann, 1974), was also used to quantify the frequency of wrasse cleaning behaviour across the reef. The occurrence of cleaning events by juvenile wrasse was recorded during 10 min random swims over the reef study area ($n = 49$). When a cleaning event was observed we recorded the species of the client. At one site on the reef, which was characterised by large flat boulders covered with the encrusting *Palythoa caribaeorum* zooxanthid, we consistently and frequently observed juvenile blue-headed wrasse cleaning interactions. To supplement snorkelling observations, two underwater video cameras (QUMOX SJ4000 Action Cams) were used to document wrasse cleaning behaviour at this station over 10 days. Event and focal surveys did not include this cleaning station so that a comparison could be made between juvenile blue-headed wrasse wandering and stationary cleaners (Itzkowitz, 1979).

2.3. Cleaner-client interactions: video analysis

Following a 30 s period after the observer had placed a camera at the cleaning station, videos ($n = 10$, ≈ 39 min per video) were analysed at 1 min intervals for 10 s ($n = 359$ observations). We recorded the number and species of clients posing (stationary postures where an individual presents their body to cleaners; Feder, 1966; Losey, 1971) and the number of cleaning events (visible peck on the client's body) by each juvenile blue-headed wrasse observed in the video. Due to the static nature of the camera, not all cleaning events could be observed, so we recorded when a cleaner associated with a client but subsequently went out of view. The percentage of view blocked by the reef substrate was recorded to account for differences in video position as a result of rugose habitat. Cleaners were also recorded associating with and inspecting clients without cleaning.

2.4. Data analysis

Data analysis was conducted using the statistical software R, version 3.2.2 (R Core Team, 2015). All Generalised Linear Mixed Model (GLMMs) were run using the `glmer` call in the `lme4` package (Bates et al., 2015). All models were refined by stepwise deletion with the removal of non-significant terms (Crawley, 2007). Fit was assessed using residual plots as recommended by Pinheiro and Bates (2000) with all continuous variables standardised to facilitate model convergence.

The total time for each focal observation accounted for the amount of time a cleaner was out of view, and thus varied across observations. A binomial GLMM with a probit link function compared the difference in cleaning frequency, whilst accounting for observation time, between juvenile blue-headed wrasse and sharknose goby cleaners. Due to differences in data collection method for the video observations, this model only considered cleaning frequency across the reef. This data was collected using two methods; focal observations quantified sharknose goby and free swimming juvenile blue-headed wrasse cleaning frequency, whilst event sampling further quantified blue-headed wrasse cleaning. Thus observation method (focal and event) was included as a random factor to control for these differences in data collection method. This model accounted for repeated observations at the same sharknose goby cleaning station by including station number as a random factor. Cleaner species, time into study period and minutes into day were included in the model, with relevant two-way interactions, as fixed effects. To compare the diversity and evenness of clients, Shannon's diversity indices were calculated based on average cleaning rates across sharknose goby and juvenile blue-headed wrasse event and focal observations using the 'vegan' package (Oksanen et al., 2013). A Wilcoxon matched pairs test compared cleaner species abundance along each transect.

Client species cleaned were assigned maximum fork lengths using

Humann and DeLoach (2014) and recorded as either solitary or gregarious (associate with > 3 individuals) and sedentary or free ranging, using FishBase (Froese and Pauly, 2017). To account for overdispersion, a quasibinomial Generalised Linear Model (GLM) with a logit link function determined whether the proportion of cleaning events, observed within each cleaner species, differed towards assigned functional traits of their clients. The two different data collection methods (focal and event) were combined, and the model included the fixed effects: cleaner species and the interactions with client: social behaviour, range and maximum size. Correcting for overdispersion, another quasibinomial GLM with a logit link function determined whether the cleaning rate (accounting for observation length), day into study and minutes into day influenced individual wrasse substrate foraging counts.

For video observations, a Poisson GLMM with a log link function determined whether the number of clients and wrasse cleaners influenced the frequency of observed cleaning interactions. Time into the day (in minutes), time into study and amount of view blocked by substrate were also included in the model as fixed factors. As repeat observations were made within the same video, video number was included as a random effect. A similar model with the same fixed and random terms determined whether juvenile cleaner wrasse and client abundance influenced the number of cleans per client per cleaner. A Gaussian family was specified with an identity link function. Preliminary analyses found the amount of observation view blocked by substrate did not influence observed results and so is not further included here.

3. Results

3.1. Cleaning frequency

Despite being more abundant on the reef than sharknose goby cleaners (median: 6.5 juvenile blue-headed wrasse; 3 sharknose gobies/30 m, $Z = 60$, $N = 12$, $p = 0.018$), significantly more cleaning events were observed by sharknose gobies (0.11 ± 0.01 cleans per minute; mean \pm S.E.), compared to juvenile wrasse observed across the reef (0.02 ± 0.004 cleans per minute; $\beta = 0.60$, $\chi^2_1 = 20.06$, $p < 0.001$). For both cleaner species, this effect was consistent across the day ($\chi^2_1 = 0.377$, $p = 0.539$) and study period ($\chi^2_1 = 0.12$, $p = 0.729$). At one location on the reef, however, juvenile blue-headed wrasse cleaning rate (1.57 ± 0.37 cleaning events per minute) was over 14x greater than all other rates observed for both cleaners across the reef (sharknose goby: 0.11 ± 0.01 cleaning events per minute, juvenile blue-headed wrasse: 0.02 ± 0.004 cleaning events per minute). At this station, wrasse cleaners also inspected clients but did not clean them within the observation period (1.42 ± 0.30 inspections per minute).

3.2. Cleaning station

In each 10 s period of video analysed, 4.18 ± 0.18 clients (mean \pm S.E., maximum observed = 19 individuals) posed for 1.90 ± 0.06 juvenile blue-headed wrasse cleaners (maximum observed = 5 individuals). Juvenile wrasse only cleaned three species from the same family (*Acanthurus* spp.; Fig. 1) even though 11 client species from seven families posed for the cleaners at this location. When juvenile wrasse cleaners were absent from their cleaning station, posing behaviour ($n = 87$) was still observed by six species (predominantly *Acanthurus* spp.) across all video observations.

Cleaning frequency significantly increased with the number of juvenile blue-headed wrasse cleaners ($\beta = 0.49$, $\chi^2_1 = 19.35$, $p < 0.001$) and clients ($\beta = 0.29$, $\chi^2_1 = 7.14$, $p = 0.008$) present at the juvenile blue-headed wrasse cleaning station. This effect was not influenced by time of day ($\chi^2_1 = 0.81$, $p = 0.369$) or time into the study ($\chi^2_1 = 3.22$, $p = 0.727$). However, an increased number of clients ($\chi^2_1 = 12.57$, $p < 0.001$) or cleaners ($\chi^2_1 = 5.73$, $p = 0.017$) at the wrasse cleaning location (Fig. 2) resulted in a significant decrease (albeit low R^2 values;

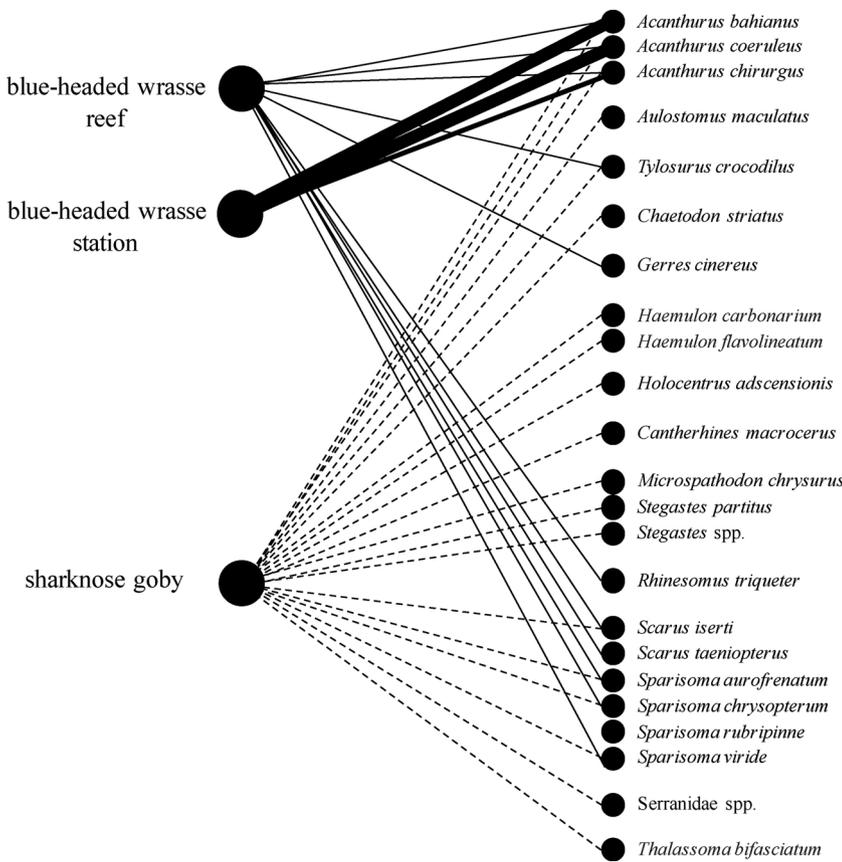


Fig. 1. Network showing clients cleaned by sharknose goby and juvenile blue-headed wrasse cleaners (either swimming free on the reef or at a specific locality). Sharknose gobies were never observed cleaning in open water. Edge thickness represents the cleaning rate per minute for each cleaner and client species. Clients are grouped based on family.

Fig. 2) in cleans per client for each juvenile cleaner present, with the decline more marked when the number of clients increased ($\beta = -0.03$) compared to the number of cleaners ($\beta = -0.02$). There was no interaction effect between the number of juvenile wrasse cleaners and clients at the station ($\chi^2_1 = 1.07$, $p = 0.302$). The cleaning rate of each juvenile blue-headed wrasse was not influenced by time of day ($\chi^2_1 = 0.11$, $p = 0.746$) but did decrease across the study period ($\beta = -0.03$, $\chi^2_1 = 5.31$, $p = 0.021$).

3.3. Substrate foraging

Those juvenile blue-headed wrasse observed cleaning, also foraged on the substrate within the same focal observation period. Cleaning rate was not significantly correlated with the substrate foraging rate of these focal individuals ($\chi^2_1 = 0.004$, $p = 0.95$). Juvenile wrasse foraged on the substrate at the same rate across the day ($\chi^2_1 = 1.36$, $p = 0.244$) and

study period ($\chi^2_1 = 3.27$, $p = 0.071$).

3.4. Clients

Across the reef, sharknose gobies cleaned a greater diversity of clients at a higher evenness than juvenile blue-headed wrasse (Shannon’s diversity = 2.40 cf. 2.03, evenness = 0.69 cf. 0.58, respectively). Sharknose gobies cleaned 19 species from 11 families whilst juvenile wrasse cleaned 11 species from five families, both cleaner species overlapped in the species that they cleaned (**Fig. 1**). From snorkelling observations across the reef, juvenile blue-headed wrasse and sharknose gobies cleaned both gregarious and solitary clients (**Fig. 3a**) in similar proportions ($\chi^2_1 = 0.61$, $p = 0.44$). The clients’ swimming range, however, did influence the proportion of cleaning events between cleaner species ($\chi^2_1 = 7.48$, $p = 0.006$), with wrasse only cleaning free-ranging clients, whilst sharknose gobies cleaned both

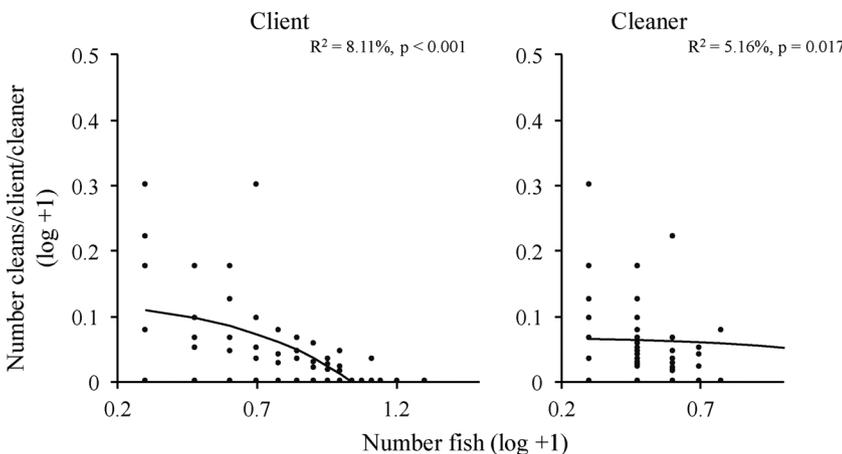


Fig. 2. Number of cleaning events ($n = 74$) per client per juvenile blue-headed wrasse, showing a negative relationship with the number of clients and cleaners present.

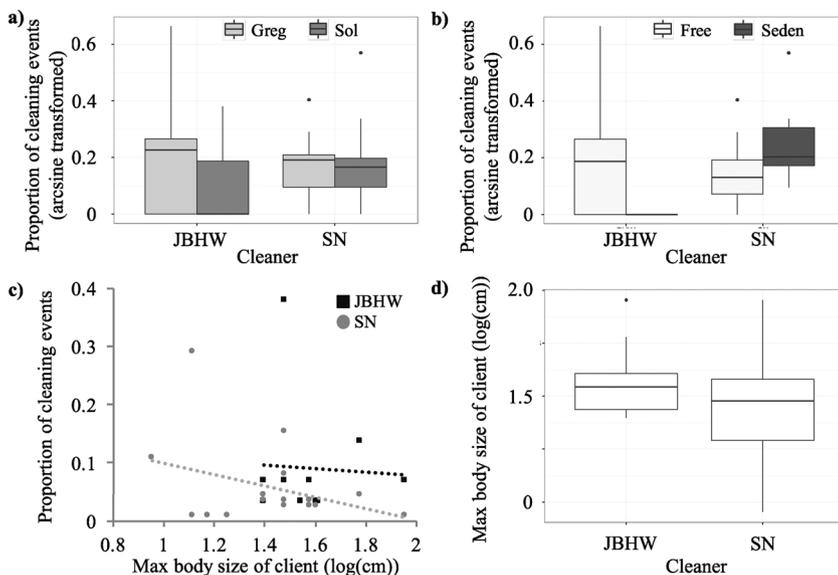


Fig. 3. Proportion of juvenile blue-headed wrasse (JBHW) and sharknose goby (SN) total cleaning events elicited by a) gregarious vs solitary clients with median and inter-quartile ranges (proportion values are arcsine square root transformed) b) free ranging vs sedentary clients with median and inter-quartile ranges (proportion values are arcsine square root transformed) and c) clients of differing max body size on Pirates Bay Reef, Tobago. D) Size range of clients cleaned by both cleaner species, with median and inter-quartile ranges.

free ranging and sedentary clients, but a higher proportion of sedentary clients (Fig. 3b). For both cleaner species, the maximum body size of the client did not influence the proportion of cleaning events received ($\chi^2_1 = 0.73$, $p = 0.393$; Fig. 3c). However, juvenile wrasse cleaned clients at the upper end of the sharknose goby client's body size range (Fig. 3d). From video observations of the cleaning station, juvenile blue-headed wrasse only cleaned three gregarious free-ranging herbivorous species (Fig. 1) at the lower end of their client size range (30–38 cm; Fig. 3c), despite 11 species posing.

4. Discussion

Overall, juvenile blue-headed wrasse cleaned less frequently than sharknose goby cleaners and foraged predominantly on the substrate across the reef. A specific cleaning station facilitated an increased cleaning frequency by these wrasse, where just three larger bodied free ranging client species were cleaned despite posing by a total of 11 species. At this juvenile wrasse station, total cleaning frequency increased with the number of cleaners or clients present, but individual cleaning rate decreased as the number of other fish increased.

We recorded a dual cleaning strategy for juvenile blue-headed wrasse (confirming Itzkowitz, 1979); cleaning by wandering individuals across the reef and cleaning by individuals or groups at a specific location. We quantified, for the first time, the frequency of these two different cleaning strategies. Wrasse cleaning behaviour varied spatially, with a high frequency of cleaning observed at the single cleaning station, whilst cleaning was rarely observed by wandering individuals. In contrast to the numerous sharknose goby cleaning stations on our study reef, the presence of only one juvenile wrasse cleaning station limits our knowledge on how widespread the different wrasse cleaning strategies are. However, on a similar sized reef (50 m × 50 m, Booby Reef), again within the Man O'War Bay, we also observed one juvenile blue-headed wrasse cleaning station. Anecdotal observations at this second cleaning station also showed an increased cleaning frequency by wrasse in comparison to resident sharknose gobies, which in combination with observations by Itzkowitz (1979), suggests that this cleaning strategy adopted by juvenile blue-headed wrasse is more widespread. It is not clear why cleaning was so frequent at the two locations on our study reefs; cleaning stations are usually associated with topological features of the reef (e.g. Potts, 1973a), but there was no obvious unique characteristics of our observed juvenile blue-headed wrasse stations. Itzkowitz (1979) suggested that juvenile blue-headed wrasse clients do not learn specific locations for

cleaning and act opportunistically, but we observed clients posing at the wrasse stations consistently across years in the absence of cleaners, suggesting that the presence of a cleaning station facilitates more frequent access for these cleaners to their clients. Further observations of juvenile blue-headed wrasse cleaning behaviour across multiple reefs would quantify the prevalence of these cleaning stations and help assess their functions. The number of juvenile cleaners at the cleaning station varied (as also shown by Itzkowitz, 1979), but given that these cleaners cannot be individually identified, it is unclear whether these were the same or different individuals (Deady et al., 1995), representing individual plasticity or inter-individual differences in cleaning strategies. Thus, a further study where marked individuals are observed, will help to elucidate why and how these part-time cleaning strategies exist.

Previously, it has been suggested that facultative cleaners only use cleaning stations already occupied by dedicated cleaners (Johnson and Ruben, 1988; Whiteman and Côté, 2002). In the absence of dedicated cleaners however, facultative cleaners occupy their own stations or share stations with other facultative species (Quimbayo et al., 2012; Walsh et al., 2017). In contrast to Johnson and Ruben (1988) and Walsh et al. (2017), we only observed blue-headed wrasse simultaneously associating with sharknose gobies and clients in 3% of observed cleaning interactions at our juvenile blue-headed wrasse cleaning station, and no such association was observed elsewhere on the reef. Further, no other facultative cleaner species (e.g. *Pomacanthus paru* or *Bodianus rufus*) were observed on the study reef. In aquaculture, where facultative cleaners (e.g. ballan wrasse, *Labrus bergylta*; goldsinny, *Ctenolabrus rupestris* and lumpfish, *Cyclopterus lumpus*) are deployed to biologically control ectoparasites of farmed fish (e.g. sea lice, *Lepeophtheirus salmonis* and *Caligus* spp. infecting farmed Atlantic salmon, *Salmo salar*, see Rae, 2002), the simultaneous use of two cleaner species is thought to enhance their cleaning efficiency (Powell et al., 2017). However, from the current study it appears that other cleaner species are not required to facilitate facultative cleaning.

To our knowledge, we provide the first *in situ* evidence that the local abundance of fish on the reef influences the observed patterns of facultative cleaning for juvenile blue-headed wrasse. At the wrasse cleaning station, the overall cleaning frequency increased with the number of cleaners or clients, whilst the cleaning efficiency of juvenile blue-headed wrasse (cleaning rate per fish) decreased when more fish (both cleaners and clients) were present. Previous *ex situ* studies also show a decreased cleaning efficiency when the number of facultative cleaners increases (Groner et al., 2013; Skiftesvik et al., 2013; Imsland et al., 2014a). A high density of fish may increase the chance of a

predatory attack (Wittenberger and Hunt, 1985), or, these facultative cleaners may experience a ‘confusion effect’, whereby the presence of a large number of individuals may make it difficult for the cleaner to assess the client availability (Krakauer, 1995; Ward et al., 2004). In contrast, dedicated cleaners are afforded protection from predators throughout their lifespan (Potts, 1973a; Darcy et al., 1974; Losey, 1979; Côté, 2000) and interact with a large number of clients daily (e.g. *Elacatinus figaro* engage in 110 cleaning interactions per day; Sazima et al., 2000); the cleaning efficiency of dedicated captive barber gobies (*Elacatinus figaro*) increased when the number of clients increased (de Souza et al., 2014). For cleaners deployed in aquaculture, finding optimal cleaner client ratios (e.g. 1 cleaner: 20 farmed fish; Skiftesvik et al., 2013) is key to increasing deployed cleaners ectoparasite removal efficiency (Deady et al., 1995; Imsland et al., 2014a; Leclercq et al., 2014; Imsland et al., 2015). However, consideration of the overall numbers of both cleaners and clients in fish farm pens may enhance the efficiency of cleaning rates.

Unlike other facultative wrasse cleaners (e.g. *Thalassoma noronhanum* see Francini-Filho and Sazima, 2008; Quimbayo et al., 2017, and *Bodianus rufus* see Johnson and Ruben, 1988), juvenile blue-headed wrasse clean less frequently than resident dedicated goby cleaners (Johnson and Ruben, 1988; current study). When not cleaning, juvenile *Thalassoma* wrasse feed on benthic reef organisms (Feddern, 1965; Narvaez et al., 2015) and in this study wrasse predominantly fed on the benthos, and did not alter their substrate foraging rates when also cleaning, suggesting that they are generalist foragers with cleaning only supplementing their diet. For other facultative cleaners (e.g. juvenile *Pomacanthus paru*; Sazima et al., 1999), gleaned material forms a predominant dietary source. Morphologically, juvenile wrasse may not be as efficient at removing parasites compared to more frequent cleaners: *Elacatinus genie* gobies are better at removing monogenean ectoparasites (*Neobenedenia melleni*) from clients than juvenile blue-headed wrasse (Cowell et al., 1993). Additionally, for larger facultative cleaner species, ectoparasite consumption alone does not lead to satiation (Leclercq et al., 2014), and although similar sized dedicated cleaner wrasse (e.g. *Labroides dimidiatus*) do rely on gleaned material (Côté, 2000), they can consume up to 1200 gnathiids daily (Grutter, 1996). Thus, nutrition gained from gleaned material is unlikely to replace that gained from substrate foraging for juvenile blue-headed wrasse; hence their minor role as reef cleaners (Johnson and Ruben, 1988) and generalist feeding strategy. The lack of relationship between cleaning and substrate foraging rate found in this study, provides further evidence that these juvenile wrasse clean opportunistically (Itzkowitz, 1979; Johnson and Ruben, 1988) as an extension of their existing benthic foraging behaviour (Poulin and Grutter, 1996). Such opportunistic behaviour is commonly observed by deployed commercial facultative cleaners which “ignore” clients to forage on detritus or commercial feed (Deady et al., 1995; Imsland et al., 2014b; Leclercq et al., 2014).

Rather than relying on cleaning for nutrition, juvenile blue-headed wrasse may instead use cleaning to gain a particular food type. Unlike other more specialised facultative cleaners (e.g. *Pomacanthus paru*; Sazima et al., 1999), and despite being more generalist foragers, these wrasse cleaners were more selective in their cleaning than the resident specialist sharknose gobies, which cleaned a larger client range and all client types and body sizes (as in Darcy et al., 1974; Johnson and Ruben, 1988; Francini-Filho and Sazima, 2008). Facultative cleaners tend to clean non-threatening, herbivorous and detritivorous clients (e.g. Francini-Filho & Sazima 2008; Quimbayo et al., 2012) and despite 11 species posing for juvenile wrasse, they predominantly cleaned three focal herbivorous species within the surgeonfish family. The predominant cleaning of surgeonfish species; blue tang (*Acanthurus coeruleus*) and ocean surgeonfish (*Acanthurus bahianus*), was also anecdotally observed at another juvenile blue-headed wrasse cleaning station on a different reef in Man-O-War Bay. These free-ranging, gregarious clients may host a high prevalence of parasites (Patterson and Ruckstuhl, 2013) and/or high quality mucus; surgeonfish mucus has

high caloric content (Arnal et al., 2001). Juvenile wrasse were also observed approaching and inspecting these client species but not cleaning (also noted by Feddern, 1965; Johnson and Ruben, 1988), suggesting that these cleaners search for a particular food source on their preferred client species. Different types of gleaned material differ in their nutritional content, and client species vary in the quantities of these materials (Eckes et al., 2015). Unlike the facultative cleaner *Thalassoma lunare*, and more similarly to *Thalassoma klunzingeri* (Barbu et al., 2011), juvenile blue-headed wrasse were unlikely preferentially feeding on client mucus during their cleaning interactions, as clients were rarely observed jolting (client jolts are indicative of cleaners removing scales or mucus e.g. Barbu et al., 2011). Instead, different client species are infected with specific parasite assemblages (Grutter, 1994), which may explain why, body length did not influence juvenile blue-headed wrasse and sharknose goby cleaning rates (confirming Grutter and Poulin, 1998; Arnal et al., 2000). The conspicuous gnathiid and copepod crustaceans are the most cited ectoparasites in cleaning interactions (Cheney and Côté, 2003; Grutter, 2010; Côté and Soares, 2011), and the role of other ectoparasites, such as monogeneans (Grutter, 1994, 1995b), remains relatively unexplored. Parasite diversity and abundance varies spatially amongst reefs (Cheney and Côté, 2003; Sellers et al., 2015), and if the food source rather than the host species influences the selective cleaning behaviour of this facultative cleaner, this may explain why different studies have recorded variable frequencies of their cleaning (Feddern, 1965; Darcy et al., 1974; Walsh et al., 2017). Molecular analysis of stomach content would provide useful nutritional information on juvenile blue-headed wrasse diet to further quantify the importance of cleaning to this facultative species.

This current study suggests that cleaning is not key for juvenile blue-headed wrasse nutrition, which explains why they only adopt a minor cleaning role on the reef. Although these cleaners are opportunistic adopting a more generalist foraging strategy, they are also selective in their client choice, suggesting that the availability of certain supplementary food types, may be driving the frequency of their cleaning behaviour. A specific cleaning station facilitated juvenile blue-headed wrasse cleaning frequency, providing a stable location for visiting clients. However, the presence of more clients or cleaners inhibited wrasse cleaning rates restricting the facultative nature of their cleaning behaviour. Cleaning behaviour observed for this wrasse species, appears to parallel cleaning observed in aquaculture where maintaining and enhancing the feeding efficiency of deployed cleaner fish is a major challenge (Imsland et al., 2016). Like the wandering juvenile blue-headed wrasse, deployed cleaners are facultative, rarely adopting cleaning behaviours in their natural environments (Potts, 1973b), suggesting that perhaps the cleaning efficiency of existing deployed cleaner species cannot be substantially increased, and alternative species should be sought. Future work should determine the food types (e.g. parasites) driving the selective nature of juvenile wrasse cleaning behaviour and identify whether certain habitat features of cleaning stations determine spatial variation in cleaning.

Acknowledgements

This project was funded by a Natural Environment Research Council GW4+ studentship to KD (NE/L002434/1). We thank Patricia Turpin (President of Environment Tobago) for field facilities, and Kathryn Whittey and Environment Research Charlotteville (ERIC) for field support. We thank the anonymous reviewers for their comments on the draft of this manuscript.

References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–266. <http://dx.doi.org/10.1163/156853974X00534>.
- Amundsen, P.A., Gabler, H.M., Staldvik, F.J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990)

- method. *J. Fish Biol.* 48, 607–614. <http://dx.doi.org/10.1111/j.1095-8649.1996.tb01455.x>.
- Arnal, C., Côté, I.M., Sasal, P., Morand, S., 2000. Cleaner-client interactions on a Caribbean reef: influence of correlates of parasitism. *Behav. Ecol. Sociobiol.* 47, 353–358. <http://dx.doi.org/10.1007/s002650050676>.
- Arnal, C., Côté, I., Morand, S., 2001. Why clean and be cleaned? The importance of client ectoparasites and mucus in a marine cleaning symbiosis. *Behav. Ecol. Sociobiol.* 51, 1–7. <http://dx.doi.org/10.1007/s002650100473>.
- Barbu, L., Guinand, C., Alvarez, N., Bergmüller, R., Bshary, R., 2011. Cleaning wrasse species vary with respect to dependency on the mutualism and behavioural adaptations in interactions. *Anim. Behav.* 82, 1067–1074. <http://dx.doi.org/10.1016/j.anbehav.2011.07.043>.
- Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. *lme4: Linear Mixed-effects Models Using Eigen and S4*. R Package Version 1.1-9. <https://CRAN.R-project.org/package=lme4>.
- Bridcut, E.E., Giller, P.S., 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. *Can. J. Fish. Aquat. Sci.* 52, 2543–2552. <http://dx.doi.org/10.1139/f95-845>.
- Cheney, K.L., Côté, I.M., 2003. Do ectoparasites determine cleaner fish abundance? Evidence on two spatial scales. *Mar. Ecol. Prog. Ser.* 263, 189–196. <http://dx.doi.org/10.3354/meps263189>.
- Côté, I.M., Molloy, P.P., 2003. Temporal variation in cleanerfish and client behaviour: does it reflect ectoparasite availability? *Ethology* 109, 487–499. <http://dx.doi.org/10.1046/j.1439-0310.2003.00883.x>.
- Côté, I.M., Soares, M.C., 2011. *Gobies as cleaners. The Biology of Gobies*. Science Publishers, St. Helier, pp. 525–551.
- Côté, I.M., 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanogr. Mar. Biol.* 38, 311–355.
- Cowell, L.E., Watanabe, W.O., Head, W.D., Grover, J.J., Shenker, J.M., 1993. Use of tropical cleaner fish to control the ectoparasite *Neobenedenia melleni* (Monogenea: Capsalidae) on seawater-cultured Florida red tilapia. *Aquaculture* 113, 189–200. [http://dx.doi.org/10.1016/0044-8486\(93\)90473-C](http://dx.doi.org/10.1016/0044-8486(93)90473-C).
- Crawley, M.J., 2007. Statistical modelling. In: *Crawley, M.J. (Ed.), The R Book*. Wiley, England UK, pp. 323–386.
- Darcy, G.H., Maisel, E., Ogden, J.C., 1974. Cleaning preferences of the gobies *Gobiosoma evelynae* and *G. prochilos* and the juvenile wrasse *Thalassoma bifasciatum*. *Copeia* 375–379. <http://dx.doi.org/10.2307/1442531>.
- Deady, S., Varian, S.J., Fives, J.M., 1995. The use of cleaner-fish to control sea lice on two Irish salmon (*Salmo salar*) farms with particular reference to wrasse behaviour in salmon cages. *Aquaculture* 131, 73–90. [http://dx.doi.org/10.1016/0044-8486\(94\)00331-H](http://dx.doi.org/10.1016/0044-8486(94)00331-H).
- de Souza, R.A., da Anunciacao, W.F., Lins, S.M., Sanches, E.G., Martins, M.L., Tsuzuki, M.Y., 2014. Can barber goby *Elacatinus figaro* control *Neobenedenia melleni* infections on dusky grouper *Epinephelus marginatus*? *Aquacult. Res.* 45, 619–628. <http://dx.doi.org/10.1111/are.12002>.
- Eckes, M., Dove, S., Siebeck, U.E., Grutter, A.S., 2015. Fish mucus versus parasitic gnaithiid isopods as sources of energy and sunscreens for a cleaner fish. *Coral Reefs* 34, 823–833. <http://dx.doi.org/10.1007/s00338-015-1313-z>.
- Fedderm, H.A., 1965. The spawning, growth, and general behavior of the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Bulletin of Marine Science. Bull. Mar. Sci.* 15, 896–941.
- Feder, H.M., 1966. Cleaning symbiosis in the marine environment. In: *Henry, S.M. (Ed.), Symbiosis*. Academic Press, New York, pp. 327–380.
- Floeter, S.R., Vázquez, D.P., Grutter, A.S., 2007. The macroecology of marine cleaning mutualisms. *J. Anim. Ecol.* 76, 105–111. <http://dx.doi.org/10.1111/j.1365-2656.2006.01178.x>.
- Francini-Filho, R.B., Sazima, I., 2008. A comparative study of cleaning activity of two reef fishes at Fernando de Noronha Archipelago, tropical West Atlantic. *Environ. Biol. Fishes* 83, 213–220. <http://dx.doi.org/10.1007/s10641-007-9322-6>.
- Francini-Filho, R.B., Moura, R.L., Sazima, I., 2000. Cleaning by the wrasse *Thalassoma noronhanum*, with two records of predation by its grouper client *Cephalopholis fulva*. *J. Fish Biol.* 56, 802–809. <http://dx.doi.org/10.1006/jfbi.1999.1197>.
- Froese, R., Pauly, D., 2017. *FishBase*. World Wide Web Electronic Publication. www.fishbase.org.
- Gingins, S., Bshary, R., 2014. Pairs of cleaner fish prolong interaction duration with client reef fish by increasing service quality. *Behav. Ecol.* 26, 350–358. <http://dx.doi.org/10.1093/beheco/aru194>.
- Groner, M.L., Cox, R., Gettinby, G., Revie, C.W., 2013. Use of agent-based modelling to predict benefits of cleaner fish in controlling sea lice, *Lepeophtheirus salmonis*, infestations on farmed Atlantic salmon, *Salmo salar* L. *J. Fish Dis.* 36, 195–208. <http://dx.doi.org/10.1111/jfd.12017>.
- Grutter, A.S., Poulin, R., 1998. Cleaning of coral reef fishes by the wrasse *Labroides dimidiatus*: influence of client body size and phylogeny. *Copeia* 120–127. <http://dx.doi.org/10.2307/1447707>.
- Grutter, A.S., 1994. Spatial and temporal variations of the ectoparasites of seven reef fish species from Lizard Island and Heron Island, Australia. *Mar. Ecol. Prog. Ser.* 115, 21–30. <http://dx.doi.org/10.3354/meps115021>.
- Grutter, A.S., 1995a. Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Mar. Ecol. Prog. Ser.* 118, 51–58. <http://dx.doi.org/10.3354/meps118051>.
- Grutter, A.S., 1995b. Comparison of methods for sampling ectoparasites from coral reef fishes. *Mar. Freshwater Res.* 46, 897–903. <http://dx.doi.org/10.1071/MF950897>.
- Grutter, A.S., 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Mar. Ecol. Prog. Ser.* 130, 61–70. <http://dx.doi.org/10.3354/meps130061>.
- Grutter, A.S., 1999. Cleaner fish really do clean. *Nature* 398, 672–673. <http://dx.doi.org/10.1038/19443>.
- Grutter, A.S., 2010. Cleaner fish. *Curr. Biol.* 20, 547–549. <http://dx.doi.org/10.1016/j.cub.2010.04.013>.
- Huebner, L.K., Chadwick, N.E., 2012. Reef fishes use sea anemones as visual cues for cleaning interactions with shrimp. *J. Exp. Mar. Biol. Ecol.* 416, 237–242. <http://dx.doi.org/10.1016/j.jembe.2012.01.004>.
- Humann, P., DeLoach, N., 2014. *Reef Fish Identification*. New World Publications.
- Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Foss, A., Vikingstad, E., Elvegård, T.A., 2014a. The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar* L.). *Aquaculture* 424, 18–23. <http://dx.doi.org/10.1016/j.aquaculture.2013.12.033>.
- Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2014b. Notes on the behaviour of lumpfish in sea pens with and without Atlantic salmon present. *Journal of Ethology* 32, 117–122. <http://dx.doi.org/10.1007/s10164-014-0397-1>.
- Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2015. Feeding preferences of lumpfish (*Cyclopterus lumpus* L.) maintained in open net-pens with Atlantic salmon (*Salmo salar* L.). *Aquaculture* 436, 47–51. <http://dx.doi.org/10.1016/j.aquaculture.2014.10.048>.
- Imsland, A.K., Reynolds, P., Eliassen, G., Mortensen, A., Hansen, Ø.J., Puvanendran, V., Hangstad, T.A., Jónsdóttir, Ó.D., Emaus, P.A., Elvegård, T.A., Lemmens, S.C., 2016. Is cleaning behaviour in lumpfish (*Cyclopterus lumpus*) parentally controlled? *Aquaculture* 459, 156–165. <http://dx.doi.org/10.1016/j.aquaculture.2016.03.047>.
- Itzkowitz, M., 1979. The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum* (Pisces: Labridae). *J. Zool.* 187, 403–413. <http://dx.doi.org/10.1111/j.1469-7998.1979.tb03377.x>.
- Johnson, W.S., Ruben, P., 1988. Cleaning behavior of *Bodianus rufus*, *Thalassoma bifasciatum*, *Gobiosoma evelynae*, and *Periclimenes pedersoni* along a depth gradient at Salt River Submarine Canyon, St. Croix. *Environ. Biol. Fishes* 23, 225–232. <http://dx.doi.org/10.1007/BF00004913>.
- Krakauer, D.C., 1995. Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behav. Ecol. Sociobiol.* 36, 421–429. <http://dx.doi.org/10.1007/s002650050165>.
- Krebs, J.R., 1979. Foraging strategies and their social significance. *Social Behavior and Communication*. Springer US, pp. 225–270.
- Krebs, J.R., Davies, N.B., Parr, J., 1993. *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications.
- Leclercq, E., Davie, A., Migaud, H., 2014. Delousing efficiency of farmed ballan wrasse (*Labrus bergylta*) against *Lepeophtheirus salmonis* infecting Atlantic salmon (*Salmo salar*) post-smolts. *Pest Manag. Sci.* 70, 1274–1282. <http://dx.doi.org/10.1002/ps.3692>.
- Losey, G.S., 1971. Communication between fishes in cleaning symbiosis. In: *Cheng, T.C. (Ed.), Aspects of the Biology of Symbiosis*. University Park Press, Baltimore, pp. 45–76.
- Losey, G.S., 1979. Fish cleaning symbiosis: proximate causes of host behaviour. *Anim. Behav.* 27, 669–685. [http://dx.doi.org/10.1016/0003-3472\(79\)90004-6](http://dx.doi.org/10.1016/0003-3472(79)90004-6).
- Mallela, J., Parkinson, R., Day, O., 2010. An assessment of coral reefs in Tobago. *Caribbean J. Sci.* 46, 83–87. <http://dx.doi.org/10.18475/cjos.v46i1.a10>.
- Michael, S.W., 2002. *Reef Fishes: A Guide to Their Identification, Behavior, and Captive Care*. N.J.T. F. H. Publications, Neptune City, NJ pp. 624.
- Narvaez, P., Furtado, M., Neto, A.I., Moniz, I., Azevedo, J.M.N., Soares, M.C., 2015. Temperate facultative cleaner wrasses selectively remove ectoparasites from their client-fish in the Azores. *Mar. Ecol. Prog. Ser.* 540, 217–226. <http://dx.doi.org/10.3354/meps11522>.
- Oksanen, J.F.G., Blanchet, R., Kindt, P., Legendre, P.R., Minchin, R.B., O'Hara, G.L., Simpson, P., Solymos, M., Henry, H., Stevens, H.W., 2013. *Vegan: Community Ecology Package*. R package version 2.0-8.
- Patterson, J.E., Ruckstuhl, K.E., 2013. Parasite infection and host group size: a meta-analytical review. *Parasitology* 140, 803–813. <http://dx.doi.org/10.1017/S0031182012002259>.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York, NY.
- Potts, G.W., 1973a. The ethology of *Labroides dimidiatus* (cuv. & val.) (Labridae, Pisces) on Aldabra. *Anim. Behav.* 21, 250–291. [http://dx.doi.org/10.1016/S0003-3472\(73\)80068-5](http://dx.doi.org/10.1016/S0003-3472(73)80068-5).
- Potts, G.W., 1973b. Cleaning symbiosis among British fish with special reference to *Crenilabrus melops* (Labridae). *J. Mar. Biol. Assoc. U.K.* 53, 1–10. <http://dx.doi.org/10.1017/S0025315400056587>.
- Poulin, R., Grutter, A.S., 1996. Cleaning symbioses: proximate and adaptive explanations. *Bioscience* 46, 512–517. <http://dx.doi.org/10.2307/1312929>.
- Powell, A., Treasurer, J.W., Pooley, C.L., Keay, A.J., Lloyd, R., Imsland, A.K., Garcia de Leaniz, C., 2017. Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities. *Rev. Aquacult.* 0, 1–20. <http://dx.doi.org/10.1111/raq.12194>.
- Quimbayo, J.P., Floeter, S.R., Noguchi, R., Rangel, C.A., Gasparini, J.L., Sampaio, C.L., Ferreira, C.E., Rocha, L.A., 2012. Cleaning mutualism in Santa Luzia (Cape Verde archipelago) and São Tomé Islands, tropical eastern Atlantic. *Mar. Biodivers. Rec.* 5, e118. <http://dx.doi.org/10.1017/S175526721200108X>.
- Quimbayo, J.P., Nunes, L.T., Ozekoski, R., Floeter, S.R., Moraes, R.A., Fontoura, L., Bonaldo, R.M., Ferreira, C.E.L., Sazima, I., 2017. Cleaning interactions at the only atoll in the South Atlantic. *Environ. Biol. Fishes* 100, 865–875. <http://dx.doi.org/10.1007/s10641-017-0612-3>.
- R Core Team, 2015. *R: A Language and Environment for Statistical Computing*. <http://www.R-project.org>.
- Rae, G.H., 2002. Sea louse control in Scotland, past and present. *Pest Manag. Sci.* 58, 515–520. <http://dx.doi.org/10.1002/ps.491>.
- Randall, J.E., 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5,

- 665–847.
- Reaka-Kudla, M.L., 1997. The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla, M.L., Wilson, D.E., Wilson, E.O. (Eds.), *Biodiversity II: Understanding and Protecting Our Biological Resources*. Joseph Henry Press, Washington, DC, pp. 83–108.
- Sale, P.F., 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111, 337–359. <http://dx.doi.org/10.1086/283164>.
- Sazima, I., Moura, R.L., Sazima, C., 1999. Cleaning activity of juvenile angelfish, *Pomacanthus paru*, on the reefs of the Abrolhos Archipelago, western South Atlantic. *Environ. Biol. Fishes* 56, 399–407. <http://dx.doi.org/10.1023/A:1007531925845>.
- Sazima, I., Sazima, C., Francini-Filho, R.B., Moura, R.L., 2000. Daily cleaning activity and diversity of clients of the barber goby, *Elacatinus figaro*, on rocky reefs in southeastern Brazil. *Environ. Biol. Fishes* 59, 69–77. <http://dx.doi.org/10.1023/A:1007655819374>.
- Sazima, C., Guimarães, P.R., Dos Reis, S.F., Sazima, I., 2010. What makes a species central in a cleaning mutualism network? *Oikos* 119, 1319–1325. <http://dx.doi.org/10.1111/j.1600-0706.2009.18222.x>.
- Sellers, A.J., Ruiz, G.M., Leung, B., Torchin, M.E., 2015. Regional variation in parasite species richness and abundance in the introduced range of the invasive lionfish, *Pterois volitans*. *PLoS One* 10, e0131075. <http://dx.doi.org/10.1371/journal.pone.0131075>.
- Skiftesvik, A.B., Bjelland, R.M., Durif, C.M., Johansen, I.S., Browman, H.I., 2013. Delousing of Atlantic salmon (*Salmo salar*) by cultured vs. wild ballan wrasse (*Labrus bergylta*). *Aquaculture* 402–403, 113–118. <http://dx.doi.org/10.1016/j.aquaculture.2013.03.032>.
- Soares, M.C., Cardoso, S.C., Côté, I.M., 2007. Client preferences by Caribbean cleaning gobies: food, safety or something else? *Behav. Ecol. Sociobiol.* 61, 1015. <http://dx.doi.org/10.1007/s00265-006-0334-6>.
- Soares, M.C., Bshary, R., Cardoso, S.C., Côté, I.M., 2008a. Does competition for clients increase service quality in cleaning gobies? *Ethology* 114, 625–632. <http://dx.doi.org/10.1111/j.1439-0310.2008.01510.x>.
- Soares, M.C., Bshary, R., Cardoso, S.C., Côté, I.M., 2008b. The meaning of jolts by fish clients of cleaning gobies. *Ethology* 114, 209–214. <http://dx.doi.org/10.1111/j.1439-0310.2007.01471.x>.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press.
- Vaughan, D.B., Grutter, A.S., Costello, M.J., Hutson, K.S., 2016. Cleaner fishes and shrimp diversity and a re-evaluation of cleaning symbioses. *Fish Fish.* 1–19. <http://dx.doi.org/10.1111/faf.12198>.
- Walsh, C.A., Pinheiro, H.T., Rocha, L.A., Goodbody-Gringley, G., 2017. Cleaning service gaps in Bermuda, North Atlantic. *Ecology* 98, 1973–1974. <http://dx.doi.org/10.1002/ecy.1841>.
- Ward, A.J., Hart, P.J., Krause, J., 2004. Assessment and assortment: how fishes use local and global cues to choose which school to go to. *Proc. R. Soc. Lond. B: Biol. Sci.* 271, S328–S330. <http://dx.doi.org/10.1098/rsbl.2004.0178>.
- White, J.W., Grigsby, C.J., Warner, R.R., 2007. Cleaning behavior is riskier and less profitable than an alternative strategy for a facultative cleaner fish. *Coral Reefs* 26, 87–94. <http://dx.doi.org/10.1007/s00338-006-0161-2>.
- Whiteman, E.A., Côté, I.M., 2002. Cleaning activity of two Caribbean cleaning gobies: intra- and interspecific comparisons. *J. Fish Biol.* 60, 1443–1458. <http://dx.doi.org/10.1006/jfbi.2002.1947>.
- Wilson, A.D., Krause, J., Herbert-Read, J.E., Ward, A.J., 2014. The personality behind cheating: behavioural types and the feeding ecology of cleaner fish. *Ethology* 120, 904–912. <http://dx.doi.org/10.1111/eth.12262>.
- Wittenberger, J.F., Hunt, G.L., 1985. The adaptive significance of coloniality in birds. *Avian Biol.* 8, 1–78.