

Behavioral trade-offs and habitat associations of coral-dwelling damselfishes (family Pomacentridae)

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ABSTRACT: Many coral reef fishes are intimately associated with branching corals. While these fishes rely on their host corals for shelter, fishes may exhibit behavioral trade-offs linked to spatial and temporal variations in their association with corals. This study quantified variation in coral use by 5 species of damselfishes, assessing key behavioral traits that determine the extent to which damselfishes interact with their host colonies. *In situ* behavioral observations revealed marked interspecific differences in diurnal and nocturnal behavior among 5 damselfish species. *Dascyllus aruanus* and *D. reticulatus* consistently displayed frequent and sustained interactions with and around corals (i.e. frequent colony visits and high aggressiveness towards other fishes) compared to *Chromis viridis*, *Pomacentrus moluccensis*, and *P. amboinensis* that exhibited weaker associations (i.e. few colony visits and low aggression) with host colonies. Coral bleaching impacted modal diurnal swimming positions, thereby altering damselfish–coral interactions under thermal stress. This research demonstrates that coral-associated damselfishes utilize host colonies in very different ways, with complex variations in behavior that extend beyond simple proximity to host coral. Such among-species variation is likely the result of behavioral trade-offs related to coral association. Understanding species-specific foraging and colony-use behavior is important because habitat degradation may undermine habitat associations of coral–damselfish and associated mutualistic services.

KEY WORDS: Coral–fish associations · Fish behavior · Behavioral trade-offs · Species coexistence · Colony usage · Interspecific variation

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1. INTRODUCTION

Scleractinian (hard) corals, and primarily branching corals, are critically important habitat-forming organisms on coral reefs. For example, >320 species (8%) of reef fishes world-wide associate with live scleractinian corals (Coker 2012, Coker et al. 2014), though many more species (60–65%) are reliant on coral-rich habitats and are adversely affected by coral loss (Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008, 2018). Reef fishes, along with many reef-associated motile invertebrates, rely on

corals for food and/or shelter (Holbrook & Schmitt 2002, Cole et al. 2008, Stella et al. 2011, Coker et al. 2014), as an egg-laying substrate (Munday & Jones 1998, Coker 2012), and as temporary refuge from water currents or predation (Johansen et al. 2008). Moreover, corals modulate fish competition, predation, and other biological interactions, contributing to the high number of species that co-exist within coral reef environments (Almany 2004, Messmer et al. 2011). The fundamental reliance of reef fishes on coral habitats is most evident during major environmental disturbances and episodes of coral loss, whereby

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severe (>60%) coral loss is linked to declines in abundance, biomass, and diversity of reef fishes (Wilson et al. 2006, Pratchett et al. 2016). Severe episodes of mass-coral bleaching, which almost invariably lead to elevated levels of coral mortality (e.g. Hughes et al. 2018), have been linked to extensive declines in abundance of fishes, with concomitant effects on the structure, function, and productivity of reef-fish assemblages (Pratchett et al. 2011, 2018).

The nature and variation within fish–coral associations depends upon (1) densities of fishes within individual coral hosts (Chase et al. 2014, Shantz et al. 2015); (2) levels of site fidelity and use (Jones et al. 2004, Munday 2004, Coker et al. 2014); (3) the position and persistence of fishes relative to coral colonies (Garcia-Herrera et al. 2017); (4) body size or overall biomass of resident fishes (Holbrook et al. 2008, Chase et al. 2014); and (5) behavioral trade-offs. These facets are dictated by species prioritizing essential fitness-enhancing processes of growth, reproduction, and survival. The ecological consequences of these behavioral trade-offs (Caley & Munday 2003, Sih et al. 2012) are linked to the nature of fish–coral interactions with a regard to a fishes' specialization to different environmental conditions, social structure, and positive growth/size feedbacks. For example, small-bodied coral-dwelling damselfishes can enhance the growth of their host coral, which in turn promotes fidelity by those fishes to the same coral, thus promoting residency of more fishes to larger, healthy shelters compared to overcrowded, unhealthy corals (see Holbrook et al. 2011). Furthermore, fish–habitat associations are provisional on environmental conditions. Abiotic factors such as increased sea surface temperatures, water flow conditions (Johansen et al. 2008), and sediments (Wenger & McCormick 2013) can reduce fishes' foraging distance and movement, and lead to confusion over preferred coral habitats. Alteration of fishes' behaviors, physiology, and survival due to reduced visibility, altered olfactory cues, and increased temperature could alter the selection and location of preferred colonies by fishes (Munday et al. 2008, Nagelkerken & Munday 2016, Boström-Einarsson et al. 2018). The health status of coral hosts, which can be impacted by coral bleaching (Bonin et al. 2009, Coker et al. 2014), disease (Casey et al. 2014), or degradation (algae overgrowth, loss of complexity due to breakage or death) can also lead to dramatic changes in fishes' behaviors, potentially undermining the positive effects that fishes can have for host corals, such as enhanced growth and survival (Meyer & Schultz 1985b, Holbrook et al. 2008, Shantz et al. 2015).

Aside from differences in coral reliance and habitat preferences (Wilson et al. 2006, 2008), reef fishes vary in their diurnal patterns of movement, foraging, and habitat associations. For example, coral-dwelling damselfishes forage actively during the day, and often shelter among the branches of specific host corals throughout the night (Holbrook & Schmitt 2002). Conversely, juvenile haemulids forage mainly at night, and exhibit strong site fidelity, generally resting on the periphery of specific branching coral colonies during the day (Meyer et al. 1983). Therefore, the extent to which fishes interact with, and influence conditions for, host corals varies taxonomically, spatially, and temporally (Lieberman et al. 1995, Garcia-Herrera et al. 2017). For instance, fish-derived services, like coral tissue aeration by damselfishes, are particularly important at night when coral photosynthesis is absent and hypoxic conditions can develop among the coral branches (Shashar et al. 1993, Kühl et al. 1995, Goldshmid et al. 2004, Garcia-Herrera et al. 2017). Fishes also vary in their associations with different coral species, largely based on different colony morphologies which afford different levels of shelter, shade, and protection from predation (Kerry & Bellwood 2012). As a result, taxonomic differences in coral use will influence the overall fish–coral feedback.

Obligate coral-associated fishes, such as coral-dwelling damselfishes, not only have direct interactions with host corals, but may also moderate the interactions and effects of other, more transient fishes, based on their level of aggression (McCormick & Meekan 2007). Aggressive interactions associated with territory or social dynamics, especially those that involve chases, could lead to enhanced water flow and mixing within the colony (Goldshmid et al. 2004), deter corallivores (Cole et al. 2011), as well as potentially cause abrasion damage to coral tissues. Again, aggression may be influenced by coral bleaching or thermal stress (Coker et al. 2012) and can differ between climate-sensitive and climate-robust coral assemblages (Kok et al. 2016). During crepuscular and nocturnal hours, aggressive individuals can relegate subordinate individuals towards the branch ends or outside the colony (Holbrook & Schmitt 2002, Coker et al. 2012), likely reducing the input of fish-derived nutrients to the coral colony. Colony usage traits (e.g. nocturnal position, conspecific and heterospecific aggressive interactions, and frequency of colony visits) represent tangible metrics for determining the nature of fish–coral interactions.

This study quantified spatial and temporal variations in associations between coral-dwelling damsel-

fishes and their host corals, by examining colony-associated behaviors (i.e. territoriality and foraging) and usage traits (i.e. roosting grounds or shelter). While previous studies have demonstrated the importance of corals for resident damselfishes (Pratchett et al. 2012, Coker et al. 2014) and the benefits that these fishes may confer to corals (Holbrook et al. 2008, Chase et al. 2014), interspecific variations in damselfishes' movements and behavioral strategies have not been fully considered. Importantly, species-specific differences in the nature of fishes' associations with their host corals (e.g. frequency and extent of colony visits) is directly linked with their survival strategies and potential benefits provided to host colonies. In this study, key diurnal and nocturnal behavioral traits were quantified *in situ* for 5 pomacentrid species to assess their usage and interaction with host colonies. A bleaching event occurred during sampling, so the impact of colony bleaching/thermal stress on variation in fishes' behavior was also examined. As subtle variations in behaviors can impact the outcome of interactions between fish species and association with their coral hosts, this research provides new insight into the importance of fish–coral interactions for coral reef fish populations and communities (e.g. Pruitt & Ferrari 2011, Chamberlain et al. 2014).

2. MATERIALS AND METHODS

2.1. Study system

This study considered 5 species of damselfishes (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) that associate with corals, but vary in their habitat preferences and reliance on live corals (Wilson et al. 2008, Pratchett et al. 2012). These species settle preferentially in reef habitats and in coral hosts containing conspecifics, and exhibit high levels of site fidelity (Booth et al. 2000, Booth 2002, Holbrook & Schmitt 2002), often associating with the same coral colony throughout their lives (Sale 1971, Sweatman 1983). These fishes mostly occur in groups, with the number of conspecifics cohabitating a coral colony being dependent on the size and complexity of the coral hosts (Holbrook et al. 2000, Chase et al. 2014). Average body size and biomass varied slightly among species, but all species were naturally size-matched to fit within the branches of the sampled coral colonies (Allen et al. 2003, Chase et al. 2014, Coker et al. 2014), due to their selection of their host coral over

another for residency. Additionally, these species do co-occur on the same coral hosts (Nadler et al. 2014).

Rather than considering the full suite of potential host corals, this study focused on 5 coral species: *Acropora intermedia*, *A. spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*. These corals are widely distributed on the Great Barrier Reef (GBR), are locally abundant, and are often occupied by coral-dwelling damselfishes (Holbrook et al. 2000, Pratchett et al. 2012, Coker et al. 2014). Relatively small (~20–80 cm diameter) coral colonies were selected to standardize for colony size. *In situ* coral surveys and behavioral observations took place between February and April 2016, which coincided with mass-bleaching in the northern GBR (Hughes et al. 2017, 2018). Behavioral observations were conducted at the following locations (Fig. 1a): northern sites around Ferguson reef (12° 33' S, 143° 49' E; Fig. 1b) and the Lizard Island region (14° 41' S, 145° 27' E; Fig. 1c, and see Table S1 in the Supplement at www.int-res.com/articles/suppl/m633p141_supp.pdf), where bleaching among these coral species was relatively similar (Hoogenboom et al. 2017, Hughes et al. 2017) at shallow depths. All colonies were located on sandy patch and slope/base habitat zones at a depth of 0–12 m (further details regarding locations, coral colony details, and damselfish group sizes in Table S1). Coral colonies were considered to be bleached wherever there was anomalous coloration on >50 % of the colony (following Hoegh-Guldberg 1999, Baird et al. 2009, Hughes et al. 2017), whereas colonies with normal pigmentation were considered to be healthy (or at least not bleached).

2.2. Behavioral observations

A series of behavioral traits relating to movement, diurnal and nocturnal position, and aggression were recorded for individual fishes (non-juvenile, minimum 2 cm length, group size ranged from 3–105) of each species during *in situ* observations (SCUBA diver observations and underwater video camera recordings; see Longo & Floeter 2012, Branconi et al. 2019). The focal fish behavioral traits were (1) average distance from host colony; (2) maximum distance from host colony; (3) colony visits; (4) conspecific aggression; (5) heterospecific aggression; (6) modal diurnal orientation; (7) algae-eating behavior; (8) refuge position; and (9) modal sleeping position (see Table S1). This study focused on behaviors that are linked with important foraging versus survival trade-offs as well as key benefits that fishes provide to coral colonies.

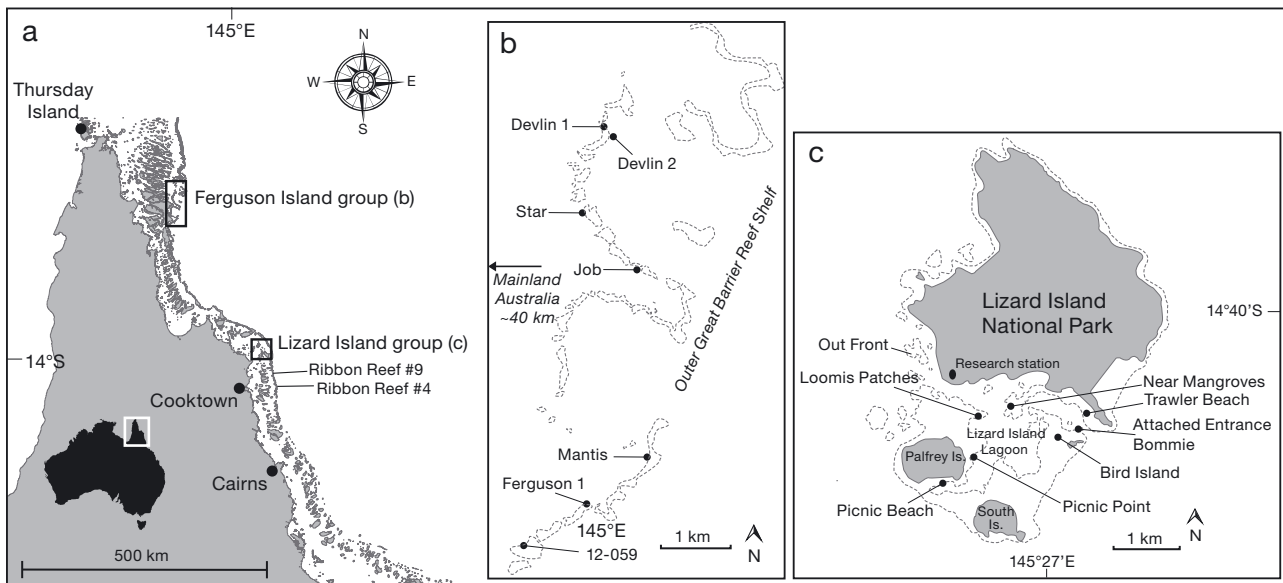


Fig. 1. Study sites along the (a) northern Great Barrier Reef for the 2 study regions: (b) the northern Ferguson Reef region and (c) Lizard Island region. Dashed lines: reefs; solid grey areas: land. Diurnal and nocturnal behavioral observations were conducted on 5 species of damselfish (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) on 5 species of coral (*Acropora spathulata*, *A. intermedia*, *Pocillopora damicornis*, *Stylophora pistillata*, and *Seriatopora hystrix*) in sand patch and slope/base habitats ranging from 0–12 m below lowest astronomical tide. Map template provided by Geoscience Australia under Creative Commons Attribution 4.0 International License

2.2.1. Diurnal variation in colony use

Behavioral observations were conducted on mid-shelf and outer-shelf reefs (Fig. 1, Table S1) on the GBR, from February–April 2016. *In situ* video recordings were used to quantify the behavioral differences between the 5 species of aggregating fishes. Semi-isolated colonies (~20–80 cm diameter) of *A. intermedia* (n = 12), *A. spathulata* (n = 17), *P. damicornis* (n = 27), *S. hystrix* (n = 10), and *S. pistillata* (n = 9) were filmed for approximately 20–40 min each between 08:00 and 17:00 h, using high-definition digital video cameras in underwater housings (Hero4 1080p; GoPro). These coral-dwelling species exhibited home ranges that encompassed a single branching coral or small reef structure; nearby suitable branching coral colonies (>1 m) were beyond average swimming distances. Two GoPro cameras on tripods were situated around the coral colony; one 1 m to the side of the colony and the other 1 m above the colony, to allow for a 360° view of fishes' movements around the coral colony. Two 1 m tape measures were affixed to aluminum poles and positioned adjacent to the focal coral colony for the duration of the observations, serving as scale bars to estimate coral size, fishes' movements, and fishes' size. For each video, a random 10 min section was selected, excluding the

first and last 5 min of the video recording in order to exclude any potential disturbances to the fishes due to diver presence during camera deployment and retrieval. This buffer time allowed fishes to acclimate to the presence of the cameras and scale bars, and was deemed appropriate due to fishes resuming natural foraging distances as observed in undisturbed colonies and from previous literature (Chase et al. 2014, Eurich et al. 2018).

Average distance was calculated as the average of the 10 observations for 1 individual damselfish per species present at a colony throughout a 10 min observation period (colony level as the replication unit); maximum distances were measured by a single observation of the maximum distance of 1 haphazardly selected damselfish per species within the 10 min observations. This method, of taking either the average or maximum from 10 observations per fish, was needed to obtain a reliable indication of a fish's average distance, due to their ever-changing movements. To avoid pseudoreplication, the multiple observations were collapsed into a single data point (averaged) prior to statistical analysis. Maximum distances on top of and to the side of the coral were connected with fishes' home range (side position = patrolling their areas and exploring new habitat; see Kent et al. 2016, Branconi et al. 2019) and foraging

behaviors (top position = accessing plankton above the colony, or access to more/better resources; see Noda et al. 1992, Mann & Sancho 2007). These maximum distances were measured by a single observation of the maximum distance of any one damselfish per species within the 10 min observations.

Diurnal swimming position categories included ‘in colony branches’ (within branching structure), ‘above colony’ (vertically on top of colony), ‘under’ (under colony structure), and ‘side’ (to the side of the colony). These categories are directly related to foraging for plankton in surrounding water currents (Liberman et al. 1995) and predator avoidance (Boström-Einarsson 2018, Boström-Einarsson et al. 2018, Gauff et al. 2018), along with the nature of certain fish-derived benefits to coral colonies (Goldshmid et al. 2004, Layman et al. 2013). Modal diurnal position was determined by recording the most commonly occupied position relative to the host coral of 1 fish per species, per individual coral colony (a ‘representative individual’) over 10 observations during the 10 min video periods for each coral colony (see Table S1). Coral species were pooled to increase sample sizes for each damselfish species. These methods were determined appropriate due to the fluctuating movement by fishes (10 observation points as replicate counts rather than repeated time points) and the directional orientation and grouping of many of the damselfishes.

Aggressive interactions were characterized by a rapid movement in the direction of another fish, often leading to fin flaring, nips, defensive darting towards unwanted visitors (Sale 1970, Parmentier et al. 2009), and/or chases around the colony (see Kok et al. 2016). Counts of aggressive interactions and colony visits were standardized per fish per 10 min. Number of colony visits was used as a proxy for diurnal colony use, and is defined as when a fish completely entered the colony. These visits were typically short in duration (all fishes exited the colony within 10 s of entering), but constitute episodes of close interaction between fish and colony. Due to the natural variation in abundance of heterospecific damselfishes in the colony and local predators, heterospecific aggressiveness was also standardized by numbers of heterospecifics present in each colony, as well as any outside fishes that interacted with the colony during the observation period (5 outsider fishes interacted with the 72 focal colonies in this experiment).

In addition, fishes’ behavior was quantified to determine whether it differed between bleached and unbleached colonies, to assess if colony bleaching/thermal stress was a factor in driving variations in fish behavior and colony usage. Very low levels of

partial colony mortality (<5%) were observed on 12 bleached colonies, and for these colonies, algal eating (biting) by damselfishes was recorded per damselfish species and are presented as averages in Section 3.1. Average colony diameter was measured for each colony using ImageJ software (Schneider et al. 2012), which was then used to calculate colony volume, assuming each colony was hemispherical in shape; colony diameter was also included in the measure of fish density and included in statistical models for each of the behavioral trait analyses.

2.2.2. Nocturnal colony use

In situ behavioral observations were used to compare modal diurnal and modal nocturnal colony occupancy by the same 5 species of fishes. Within the Lizard Island lagoon, a separate set of *P. damicornis* colonies ($n = 25$) with aggregating fishes were tagged and monitored. These corals were tagged during the day using cattle tags, and the positions of aggregating fishes present on coral colonies were observed and recorded by SCUBA divers, both during the day (08:00–17:00 h) and night (20:00–23:00 h), to ensure accurate fish numbers on each colony at night. During nocturnal observations, each tagged coral colony was inspected by SCUBA divers utilizing an underwater torch (using white and UV light) for illumination. The colony was illuminated for less than 20 s and this did not induce movement by any of the resident fishes. Due to the sedentary nature of the damselfishes at night, the position of each individual fish was recorded. Nocturnal positions of all individuals of each damselfish species were measured once for each colony of *P. damicornis*. The position of each fish relative to the coral colony was categorized as ‘in colony branches’, ‘under colony’, or ‘reef’ (not visible around colony or located in rubble beneath/near colony) to differentiate fishes’ positions.

2.2.3. Short-term reaction to startle stimulus response

To further quantify the association between aggregating fishes and their host colonies, reaction to startle stimulus trials were performed *in situ*, on natural, non-manipulated coral colonies ($n = 43$), hosting 1023 damselfishes in the field. A SCUBA diver rapidly approached a coral colony with aggregating fishes present until the diver was within 25 cm of the colony, at which point the fishes moved to their selected point

of refuge. A point of refuge was categorized as 'in colony branches' (retreat within physical colony structure or branches), 'under colony' (retreat to under the colony or into substrate structure), or 'outside colony' (swimming away into the water column). Startle stimulus trials were performed in replicates of 4 (see Table S1), to fully capture the refuge position of these continually moving damselfishes, with 90 s between replicates to allow focal fishes to return to normal behavior. Fishes resumed normal foraging behaviors within 30 s of startle stimulus. No equipment was placed near the colony, the startle stimulus was similar to a diver swimming over the colony (minimal colony interference), and the interval of 90 s between replicates was included as an extra precaution.

2.3. Data analysis

Behavioral observations were analyzed using R statistical software (R Development Core Team 2019). Behavioral traits of fishes (average distance, maximum above and maximum side distance from colony) were analyzed using Gaussian generalized linear models (GLM) with each behavioral trait as the dependent variable (log + 1 transformed); fish species, colony health, and fish density as independent variables; and colony number as a random factor (to account for any repeated measures of multiple fish within individual coral colonies). Bleaching category was included as a co-factor in select analyses based on evidence of behavioral changes due to bleaching/thermal stress and associated changes in colony health (Coker et al. 2009, Pratchett et al. 2018). Fish density (total number of resident fishes per unit colony volume) was included in these analyses, as swimming distances of damselfish can be influenced by both colony size and total number of fish per colony (Forrester 1991). Model selection was based on Akaike's information criterion (AIC) values after Burnham & Anderson (2002), Zuur & Ieno (2016), and Zuur et al. (2009, 2010). Assumptions for model validity were checked through residual plots (QQ-normal plot for normality and scatter plots of residuals vs. fitted for linearity), as well as calculations of dispersion (comparing model mean with variance). Statistical results were interpreted using the numerical output of the statistical model, after model validation. Following formal model selection, inclusion of colony health and fish density did not significantly improve the fit of the model to the data. As a result, for average distance, maximum distance above and maximum side distance, the best model only included fish

species as an independent variable (see model comparison in Tables S1–S3). Based on GLMs, differences among the 5 fish species were assessed using estimated marginal means (R package 'emmeans') multiple comparison post hoc (with a Tukey's HSD correction).

Colony visits were analyzed using a Poisson distribution GLM, with colony visits as a dependent variable, colony health as an independent variable, colony number as a random factor, and fish number per species as an offset. The Poisson distribution was selected following AIC model comparison and because the data were counts of events (visits). Fish number per species and fish density per colony were included as offsets in the model to standardize these counts (Yan et al. 2009).

Aggression data were analyzed using GLMs, to determine if conspecific and heterospecific aggressions were different among species and influenced by colony health. In conspecific aggression models, fish species, colony volume, and colony health were included as covariables, and the number of fishes per species as an offset to standardize conspecific aggressions per individual fish, per the number of conspecifics to whom they could display aggression. For heterospecific aggression, fish species, colony health, and colony volume were covariables and the number of fish per species and the number of other fish on the colony (number of heterospecific fish available to be aggressed towards) as an offset. Accordingly, values for conspecific aggression data are displayed as standardized per number of conspecifics, and heterospecific aggression figure data are displayed as standardized per number of fishes per colony and number of heterospecifics. Model selection was again performed by comparing AIC values (Zuur et al. 2009, 2010, Zuur & Ieno 2016); including colony health and fish species did not significantly improve either model for conspecific or heterospecific aggression. Assumptions for model validity were again checked through residual plots, as well as calculations of dispersion.

Diurnal behavioral observational data were converted into modal position categories to represent the area around host colonies in which the fish were most often located. Modal positions were analyzed using chi-squared (χ^2) tests comparing the number of observations of occupancy in each position within healthy and bleached colonies to expectations based on random chance (null hypothesis: fish spent equal time in each of the position categories; see Pearson 1990). Again, the multiple initial observations of diurnal position (10 observation points during observation period per fish species) were converted to a

single value (mode) to avoid pseudoreplication of the data whilst accounting for variability in colony occupancy over time due to normal swimming and foraging activities. Values for modal diurnal position are displayed as proportions of all colonies per fish species with 2 different health categories: healthy and bleached. Modal nocturnal positions (observed on 25 colonies, separate from the diurnal colonies), with coral colonies pooled were analyzed with separate χ^2 tests by damselfish species. Colony bleaching was not included in the tests, as all colonies selected for nocturnal behaviors were healthy (non-bleached) during the observation period. Data for nocturnal positions are presented as average proportion of time in each position category.

Startle refuge responses were analyzed using a zero-inflated generalized linear mixed model (GLMM) with a negative binomial distribution to account for the over-dispersed (zero-inflated) count data; this combines the negative binomial distribution and a logit distribution. In the GLMM, the number of fish per shelter position was the dependent variable, with fish species and shelter position as fixed factors (additive model), colony number as a random factor, and startle number nested within colony, with total fish per species per colony as an offset. This model included all observations of all of the fish present in each colony whilst accounting for the repeated measures of individual fish within colonies. Colony bleaching was not included in the tests, as all selected colonies were healthy (non-bleached) during the observation period. Again, Tukey's HSD tests were used to compare the startle refuge positions of the 5 fish species around host colonies.

All modelling was performed in the statistical software R (R Development Core Team 2019) using the packages 'MASS' (Venables & Ripley 2002), 'nnet' (Venables & Ripley 2002), 'lme4' (Bates et al. 2015), 'lmerTest' (Kuznetsova et al. 2017), 'glmmTMB' (Brooks et al. 2017), 'nlme' (Pinheiro et al. 2014), and 'emmeans' (Searle et al. 1980).

3. RESULTS

3.1. Diurnal and nocturnal positions

All damselfish species considered in this study (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) spent the majority of daylight hours (>80% of time) swimming within 30 cm of their host corals, presumably

feeding in the adjacent water column (Fig. 2a), while sheltering on or within coral hosts during the night (Fig. 2b). The different species of fishes occupied different regions of the space above and around coral colonies, and there was strong evidence that the modal spatial position of fish relative to colonies was non-random (Fig. 2a). Three of the species (*C. viridis*, *D. aruanus*, and *D. reticulatus*) spent >50% of their time positioned directly above the colony (pooled over colony health status). In contrast, *P. amboinensis*

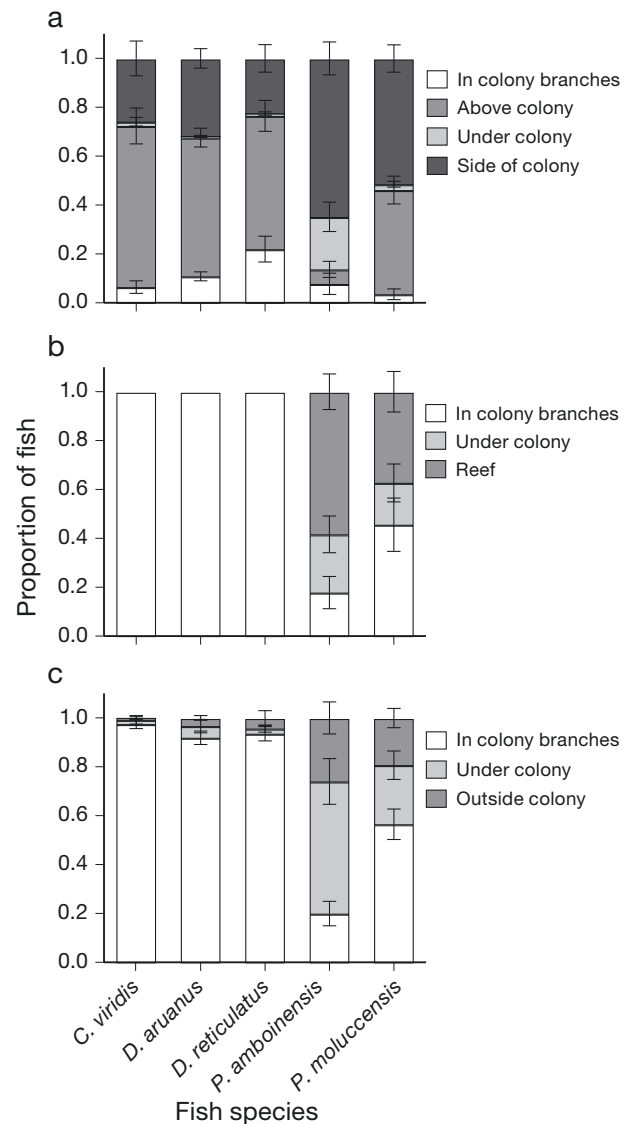


Fig. 2. Average position (proportion \pm SE) of 5 damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) in relation to natural host colonies of small branching coral colonies (*Acropora intermedia*, *A. spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, *Stylophora pistillata*): (a) modal diurnal (~08:00–17:00 h) swimming positions, (b) modal nocturnal (20:00–23:00 h) roosting positions, and (c) startle refuge positions

spent most of its time to the side or under the colony. Coral bleaching/thermal stress had an impact on the position of all damselfish species (Fig. 3, Table S2), with use of the side spatial position becoming more

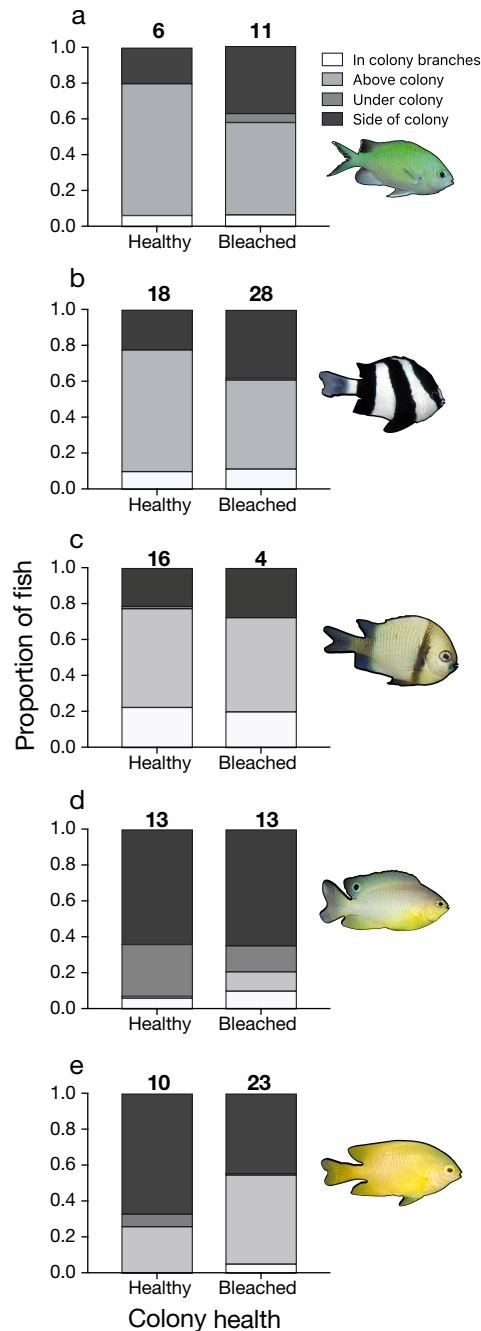


Fig. 3. Average diurnal (~08:00–17:00 h) modal position of (a) *Chromis viridis*, (b) *Dascyllus aruanus*, (c) *D. reticulatus*, (d) *Pomacentrus amboinensis*, and (e) *P. moluccensis* in relation to host colonies (*Acropora intermedia*, *A. spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*) of 2 different health categories: healthy and bleached. Coral sample size per health category are displayed above bars

prevalent. Specifically, *C. viridis*, *D. aruanus*, and *D. reticulatus* mostly swam above healthy colonies, but when on bleached colonies displayed weaker preference for the above position and increased swimming to the side and under the colony (*C. viridis*, $n = 17$ colonies, chi-square [bleaching status]: $\chi^2 = 29.33$, $df = 3$, $p < 0.001$; *D. aruanus*, $n = 46$ colonies, $\chi^2 = 41.06$, $df = 3$, $p < 0.001$; *D. reticulatus*, $n = 20$ colonies, $\chi^2 = 16.50$, $df = 3$, $p < 0.001$). *P. amboinensis* spent most of its time to the side and under healthy colonies and switched to having a stronger preference for swimming above bleached colonies ($n = 26$ colonies, chi-square [bleaching status]: $\chi^2 = 25.05$, $df = 3$, $p < 0.001$). *P. moluccensis* preferred swimming to the side and under healthy colonies, but demonstrated a stronger preference for swimming above and within the branches of bleached colonies, and a weaker preference for swimming under bleached colonies ($n = 33$ colonies, $\chi^2 = 23.98$, $df = 3$, $p < 0.001$).

Targeted algae-eating behavior was observed on 66% of the bleached colonies with partial filamentous algal growth (8 of 12 colonies). Algae eaten varied by damselfish species, with *Dascyllus* spp. engaged in algae eating on 83% (bites on 6 of 9 and 1 of 1 colonies for *D. aruanus* and *D. reticulatus*, respectively) of affected colonies and *Pomacentrus* spp. only on 58% (2 of 3 and 3 of 6 colonies for *P. amboinensis* and *P. moluccensis*, respectively) of filamentous algae colonies; sample sizes were too low (0 bites on 1 algae-covered colony) to report accurate *C. viridis* algae-eating behavior.

Nocturnal modal position (all damselfishes measured once on 25 colonies) around the colony was species-specific (Fig. 2b). *C. viridis*, *D. aruanus*, and *D. reticulatus* slept exclusively within the colony branches (*C. viridis*, $n = 103$ fish on 5 colonies, $\chi^2 = 8.50$, $df = 2$, $p = 0.014$; *D. aruanus*, $n = 120$ fish on 24 colonies, $\chi^2 = 48.00$, $df = 2$, $p < 0.001$; and *D. reticulatus*, $n = 28$ fish on 6 colonies, $\chi^2 = 12$, $df = 2$, $p = 0.0025$). *P. amboinensis* ($n = 31$ fish on 10 colonies, $\chi^2 = 1.50$, $df = 2$, $p < 0.027$) and *P. moluccensis* ($n = 39$ fish on 9 colonies, $\chi^2 = 2.67$, $df = 2$, $p = 0.264$) did not display strong preferences in modal position of the 3 roosting positions. *P. amboinensis* and *P. moluccensis* were both found more commonly outside the colony branches at night, often sleeping semi-motionless within the surrounding reef structure or under the coral colony.

Modal diurnal and modal nocturnal positions were congruent with startle refuge, with fish species exhibiting preference for refuge location (GLMM: $p < 0.001$; Tables 1, S3 & S4, Fig. 2c). When startled, *C. viridis* ($n = 544$ fish on 15 colonies), *D. aruanus* ($n =$

Table 1. Post hoc test (R package 'emmeans') for multiple comparisons of colony visits ($\log + 1$ fish⁻¹ per 10 min, for each damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) from host branching coral colonies, with p-values. Values are based off model selection practice using df and Akaike's information criterion scores; the best model included colony visits (dependent variable), fish species (independent variable), coral colony (random factor), and fish number per species as an offset. Significant p-values are in **bold**

Comparison	p-value (adjusted)
<i>C. viridis</i> – <i>D. aruanus</i>	<0.0001
<i>C. viridis</i> – <i>D. reticulatus</i>	<0.0001
<i>C. viridis</i> – <i>P. amboinensis</i>	<0.0001
<i>C. viridis</i> – <i>P. moluccensis</i>	<0.0001
<i>D. aruanus</i> – <i>D. reticulatus</i>	0.9999
<i>D. aruanus</i> – <i>P. amboinensis</i>	<0.0001
<i>D. aruanus</i> – <i>P. moluccensis</i>	<0.0001
<i>D. reticulatus</i> – <i>P. amboinensis</i>	<0.0001
<i>D. reticulatus</i> – <i>P. moluccensis</i>	<0.0001
<i>P. amboinensis</i> – <i>P. moluccensis</i>	0.9990

190 fish on 28 colonies), and *D. reticulatus* (n = 67 fish on 10 colonies) all retreated into the colony branches >91 % of the time. *P. moluccensis* (n = 148 fish on 31 colonies) and *P. amboinensis* (n = 74 fish on 17 colonies) showed more variance in their refuge positions, with *P. amboinensis* preferring to hide under the colony and *P. moluccensis* only retreating into the colony branches ~50 % of the time, but still favoring retreating into the colony 57 % of the time, and displaying equal preference between under or outside the colony as secondary refuge positions (Fig. 2c, Tables S3 & S4).

The number of colony visits (within the branches of the host colony) were significantly different between damselfish species (GLM: $p < 0.001$; Table S5). Neither colony bleaching nor fish density affected colony visits for any damselfish species (GLM: bleaching status, $p > 0.05$, fish density, $p > 0.05$). *D. aruanus* and *D. reticulatus* displayed the highest mean (\pm SE) number of colony visits, with 14.5 ± 1.8 and 15.3 ± 2.9 visits per 10 min, respectively (Fig. 4). *C. viridis* (4.6 ± 1.3 visits per 10 min), *P. amboinensis* (1.3 ± 0.3 visits per 10 min), and *P. moluccensis* (1.7 ± 0.4 visits per 10 min) exhibited fewer than 5 colony visits fish⁻¹ per 10 min block, indicating that these species spend less overall time within the colony branches during daylight hours. Overall, *C. viridis*, *D. aruanus*, and *D. reticulatus* exhibited significantly higher visits than *P. amboinensis* or *P. moluccensis* (post hoc comparisons are presented in Table 1).

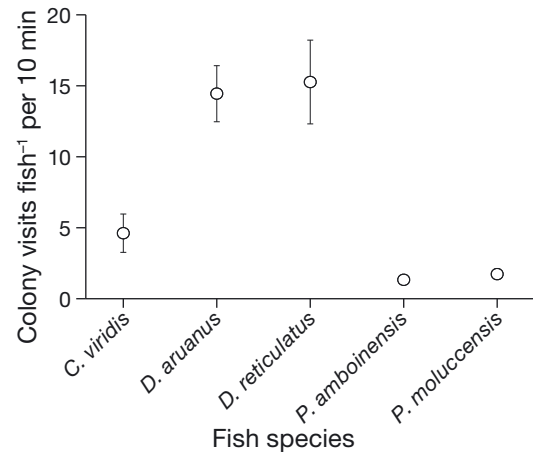


Fig. 4. Mean (\pm SE) number of visits of fish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) to coral colonies. Data are standardized per fish, per coral colony, and per 10 min observation period

3.2. Proximity of fish to coral colonies

During the day, fishes were observed continually swimming, eating plankton in the water column, and darting into the colonies to avoid nearby predators. Activity levels ranged from continual swimming due to foraging behavior, to resting and stationary behavior, where fishes would remain nearly motionless within 10 cm of their host coral (Fig. 5). Average distance from host colony significantly differed between damselfish species (GLM: $p < 0.05$; Tables 2 & S6, Fig. 5a), and neither colony bleaching status ($p > 0.05$) nor fish density ($p < 0.05$) influenced this aspect of fish behavior for any of the 5 damselfish species (Table S6). *C. viridis* and *D. aruanus* generally had significantly larger average distances from their host colony compared with the 2 *Pomacentrus* species (see Table 2 for post hoc comparisons). The maximum distance that fishes moved above the colony (Fig. 5b) and the maximum distance moved from the side of the colony (Fig. 5c, Tables S7 & S8) displayed similar differences among species to the average distance each species maintained away from the colony (GLM: above, $p < 0.001$; side, $p < 0.05$). *C. viridis* (21 ± 4.6 cm), *D. aruanus* (23 ± 3.6 cm), and *D. reticulatus* (19 ± 4.2 cm) all displayed considerably further average (Table 1, Fig. 4a) and maximum positions away from their host colony compared to *P. amboinensis* (8.9 ± 1.6 cm) and *P. moluccensis* (8.3 ± 1.4 cm, see Table 2 for post hoc comparisons among species). Diver observations also recorded some *D. aruanus* temporarily moving >3 m to neighboring colonies. Again, colony

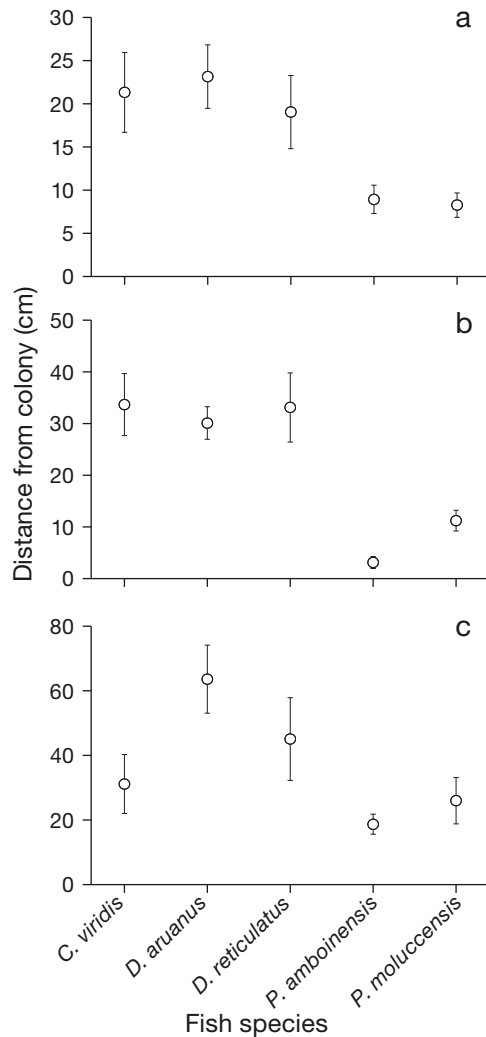


Fig. 5. Mean (\pm SE) species-specific damselfish (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) distances from host coral colony: (a) average distance, (b) maximum distance above, and (c) maximum side distance from colony. Note different y-axes to allow for visualization of variance between fish species

bleaching and fish density did not impact maximum distance to the above (GLM: $p > 0.05$) or side (GLM: $p > 0.05$) positions for any damselfish species.

3.3. Aggressiveness and territoriality

The frequency of aggression towards conspecifics was highest for *D. aruanus* (1.1 ± 0.13 interactions fish⁻¹ per 10 min, standardized to the number of conspecifics; Fig. 6a) and *D. reticulatus* (0.67 ± 0.13 interactions fish⁻¹ per 10 min), which were significantly higher than for the other damselfishes (GLM:

Table 2. Post hoc test (R package 'emmean') for multiple comparisons with adjusted p-values for each damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) distance from its resident colony: average distance, maximum distance above the colony, and maximum distance from the side of the colony; based on a lognormal generalized linear model of average distance, maximum distance above, maximum distance to the side (dependent), and fish species (in dependent variable). Significant p-values are in **bold**

Comparison	Average distance	Max. distance above	side
<i>C. viridis</i> – <i>D. aruanus</i>	1.0000	1.0000	0.2019
<i>C. viridis</i> – <i>D. reticulatus</i>	0.8401	0.9954	0.6999
<i>C. viridis</i> – <i>P. amboinensis</i>	0.0193	<0.0001	0.9950
<i>C. viridis</i> – <i>P. moluccensis</i>	0.0063	0.0001	0.9978
<i>D. aruanus</i> – <i>D. reticulatus</i>	0.7679	0.9996	0.9556
<i>D. aruanus</i> – <i>P. amboinensis</i>	0.0015	<0.0001	0.0267
<i>D. aruanus</i> – <i>P. moluccensis</i>	0.0002	<0.0001	0.0197
<i>D. reticulatus</i> – <i>P. amboinensis</i>	0.2095	<0.0001	0.3568
<i>D. reticulatus</i> – <i>P. moluccensis</i>	0.1248	0.0002	0.3604
<i>P. amboinensis</i> – <i>P. moluccensis</i>	0.9995	<0.0001	0.9999

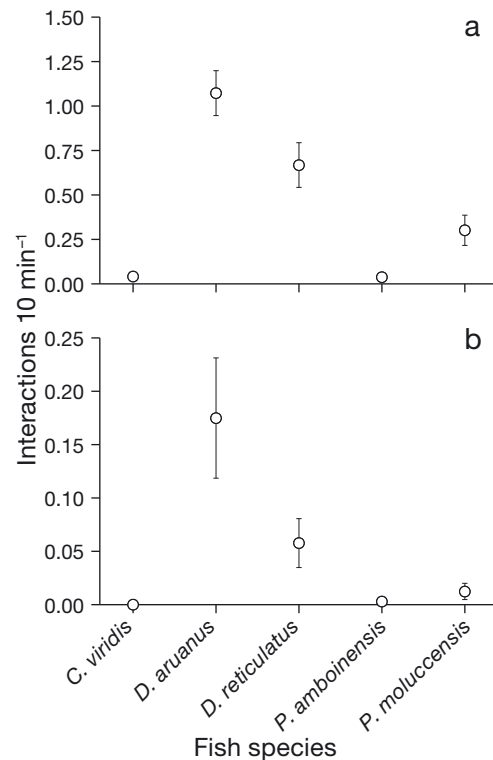


Fig. 6. Mean (\pm SE) aggressive interactions of damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) per 10 min period: (a) with conspecifics, standardized to number of conspecifics present, and (b) with heterospecifics, standardized to number of conspecifics and number of heterospecifics

Table 3. Post hoc test (R package ‘emmean’) for multiple comparisons of conspecific and heterospecific aggressions, fish⁻¹ per 10 min for each damselfish species (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) from host branching coral colonies, with p-values. Values are based off model selection practice using df and Akaike’s information criterion scores. The most parsimonious model was based on a log-normal generalized linear model that included aggressions (dependent variable), fish species (independent variable), and coral colony (random factor). Both conspecific and heterospecific aggression were standardized to number of each fish species; heterospecific aggressions also included the offset term ‘other fish on the colony’ as offsets. Significant p-values are in **bold**

Comparison	Conspecific aggression	Heterospecific aggression
<i>C. viridis</i> – <i>D. aruanus</i>	<0.0001	<0.0001
<i>C. viridis</i> – <i>D. reticulatus</i>	0.0499	<0.0015
<i>C. viridis</i> – <i>P. amboinensis</i>	0.9996	0.7543
<i>C. viridis</i> – <i>P. moluccensis</i>	0.6798	0.5527
<i>D. aruanus</i> – <i>D. reticulatus</i>	0.0231	0.6141
<i>D. aruanus</i> – <i>P. amboinensis</i>	<0.001	<0.0001
<i>D. aruanus</i> – <i>P. moluccensis</i>	<0.001	<0.0001
<i>D. reticulatus</i> – <i>P. amboinensis</i>	0.0120	0.0497
<i>D. reticulatus</i> – <i>P. moluccensis</i>	0.3818	0.2081
<i>P. amboinensis</i> – <i>P. moluccensis</i>	0.4343	0.9961

$p > 0.05$; Tables 3 & S9), and were indicative of territorial damselfishes. *C. viridis* and *P. amboinensis* displayed particularly low aggression towards conspecifics, both with <0.1 interactions fish⁻¹ per 10 min. *P. moluccensis* displayed medium levels of aggression (0.29 ± 0.08 interactions fish⁻¹ per 10 min). Colony bleaching ($p > 0.992$) and colony volume ($p > 0.962$) had no effect on total aggressive interactions.

Aggressiveness with heterospecifics was also significantly different among species (GLM: $p < 0.05$; Table S10), with *D. aruanus* again displaying 2- to 10-fold more aggressive interactions than other damselfish species (0.17 ± 0.06 interactions fish⁻¹ per 10 min). All other damselfish species displayed low heterospecific aggressive interactions, with *C. viridis* displaying zero interactions (Fig. 6b). Post hoc analysis revealed significant differences for both *D. aruanus* and *D. reticulatus* and all other damselfish species (Table 3). *D. reticulatus* (0.057 ± 0.02 interactions fish⁻¹ per 10 min) and *P. moluccensis* (0.12 ± 0.01 interactions fish⁻¹ per 10 min) had medium scores for aggression, while *C. viridis* and *P. amboinensis* had nearly zero heterospecific interactions (0.00 ± 0.00 and 0.003 ± 0.002 interactions fish⁻¹ per 10 min, respectively). Neither colony bleaching nor colony volume had any effect on heterospecific aggressive interactions ($p > 0.05$).

4. DISCUSSION

While coral-dwelling damselfishes have known affinities for specific species of branching corals (e.g. Wilson et al. 2008, Pratchett et al. 2012), this study demonstrates that there are important interspecific differences in the nature of these habitat associations. Importantly, the 5 species of damselfishes considered in this study (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis*, and *P. moluccensis*) exhibited marked differences in the proportion of time spent inside host colonies, the frequency with which they returned to host colonies, and the distance they ventured away from host colonies. These different behavioral strategies are likely linked to trade-offs (e.g. choosing between feeding versus sheltering) and their functional reliance on corals (discussed below). *D. aruanus* and *D. reticulatus* exhibited high usage and interactions with their coral hosts; their tight social network is likely derived from the physical structure of their host coral and their swimming positions and usage (Forrester 1991, Booth 1995), with priorities of foraging. *Pomacentrus* spp. showed less colony usage (i.e. maintenance or submissive behaviors involving the coral) and may have prioritized other fitness-enhancing behaviors such as survival or feeding, with less dependency on coral hosts (Fricke 1980, Fishelson 1998, Branconi et al. 2019). Differences in direct (distance from colony or colony visits) and indirect (aggressive) behavioral strategies with respect to fishes interacting with their shelter resource may also be linked to fishes’ habitat specialization (Eurich et al. 2018), dependency upon the coral used for the habitat structure (Bay et al. 2001), shelter, swimming ability (Johansen et al. 2008), and foraging (Liberman et al. 1995). *P. amboinensis* are observed to use a small subset of live coral taxa, yet used individual colonies much less compared to the other 4 *Pomacentrus* species (Pratchett et al. 2012, this study). Conversely, *D. reticulatus* was the most specialized of the focal species and exhibited very high usage and dependency (Wilson et al. 2008, Pratchett et al. 2012). By measuring the nature of the damselfish–coral interaction, this research highlights the potential functional importance of particular species of damselfishes, their strategies of habitat use, and the prevalence of the interaction on coral reefs at the colony and seascape levels.

Apparent differences in behavioral modes and habitat associations among coral-dwelling damselfishes most likely relate to fundamental cost–benefit trade-offs among foraging (i.e. position and access to prey; see Coates 1980, Foster 1985, Biro et al. 2010,

Wen et al. 2013, White et al. 2013), proximity to shelter and vulnerability to predation (Coker et al. 2009), mating/reproduction (i.e. increased breeding partners and egg-laying substrate, but high aggression/competition; see Forrester 1991, Coker 2012, Coker et al. 2012), and social requirements (Fricke 1977, Forrester 1991). While close association with host colonies may reduce vulnerability to predation (Coker et al. 2009), constrained movement reduces prey access for plankton feeders and increases vulnerability to habitat loss (Pratchett et al. 2012, 2016), while also increasing competition for resources and aggression (Sale 1972, Jones 1987, Coker 2012). Variations in the average and maximum distance that fishes venture from host colonies are also linked to processes of group living, zooplankton foraging, and territories (Fricke 1977, Shpigel & Fishelson 1986, Fishelson 1998, Meekan et al. 2010). As such, additional traits measured in this study (e.g. frequency of colony visits, nocturnal roosting position, and territoriality) may be better functional indicators of colony use. Although *D. aruanus* and *D. reticulatus* often ventured furthest from their host corals, they exhibited high colony usage behaviors (e.g. high colony visits, preferentially roosted within the colony branches, and actively defended the colony). Furthermore, of the fish species in this study that showed the lowest usage behaviors with their host corals, *P. amboinensis* stayed closest to the coral, yet barely interacted with the colony for shelter or sleeping and did not defend coral colonies within its home range. When associated with colonies, *Dascyllus* spp. trade-off increased foraging distances for predator protection, while *Pomacentrus* spp. may trade-off optimal plankton feeding locations (top of colony) for alternative foraging areas around the base of the colony that are more protected (Wen et al. 2013) with lower flow, thereby conserving energy (Johansen et al. 2008, 2015). Additionally, the average size or boldness of these 2 species may be less compared to the *Dascyllus* spp., reducing their average distance from shelter (Biro et al. 2010).

Aggression of these damselfish species links to the strength of the dominance hierarchies, and how persistent they are in maintaining their colony (i.e. territoriality; see Harrington 1993, Leal et al. 2015). With high conspecific and heterospecific aggression, it is evident that a host colony is entrenched in the social networks of these 2 *Dascyllus* spp. For instance, alpha male territory is demarcated by the optimal foraging location with respect to the host colony and surrounding currents (Fricke 1977, Shpigel & Fishelson 1986, Fishelson 1998, Meekan et al. 2010); which in turn explains the average and maximum distances ventured

by these damselfishes. Furthermore, this strong usage and interactions by *Dascyllus* spp. is displayed by their high heterospecific aggression; these damselfishes challenge outsiders or large corallivorous predators that pose a threat to their coral interaction (Gochfeld 2010, Cole et al. 2011) and foraging/mating territory. The other 3 damselfish species examined in this study stayed much closer to their host corals (consistent with low boldness levels), relied less on the physical coral colony for mediating social hierarchies and shelter, and were more flexible to temporarily exploit or re-colonize nearby colonies if other damselfishes or predators excluded them from particular colonies. Although bleaching/thermal stress did not impact any aspect of the measured aggression of the damselfishes, it is likely that aggressive behavior would considerably change with coral mortality or coral re-organization, due to increased competition for habitat and altered territory boundaries (Coker et al. 2009, 2012, Kok et al. 2016, Boström-Einarsson 2018).

While many reef fishes are fundamentally reliant on coral habitats, there is also evidence that fishes confer important benefits on host corals, such as nutrient subsidies (Meyer et al. 1983, Meyer & Schultz 1985a, Holbrook et al. 2008), hydrodynamic modulation/ventilation (Goldshmid et al. 2004, Garcia-Herrera et al. 2017), and colony defense (Gochfeld 2010, Chase et al. 2014), resulting in enhanced coral health and growth (Meyer & Schultz 1985b, Holbrook et al. 2011, Shantz et al. 2015). Services are likely species-specific; although not explicitly quantified, among the fishes considered in this study, *C. viridis*, *D. aruanus*, and *D. reticulatus* are likely to contribute the most to nutrient provision, enhancing water flow and aeration of colony tissues due to their species-specific nocturnal roosting (where aeration is the most effective; Goldshmid et al. 2004, Berenshtein et al. 2015) within colony branches and frequent diurnal colony visits (or diurnal chases around the colony; see Kok et al. 2016). Coral-associated fishes are increasingly vulnerable to ongoing coral loss, mainly caused by climate-induced coral bleaching (Jones et al. 2004, Pratchett et al. 2012); however, these fishes may be important in providing resilience to coral bleaching (Suefuji & van Woesik 2001, Chase et al. 2018). Several fishes were observed on bleached colonies that had filamentous algae growing on them, which is consistent with other studies showing fishes remaining with their hosts during partial degradation (observed by Feary et al. 2007, Bonin et al. 2009, Coker et al. 2009). In this study, targeted biting of algae by *D. aruanus*, *D. reticulatus*, *P. amboinensis*, and *P. moluccensis* on bleached corals was recorded, a behavior which has previously been

documented only in coral-dwelling gobies (Dixon & Hay 2012). Although probably not sufficient to prevent algae growing on the coral colony, target algae biting could help slow rates of algal overgrowth and limit partial mortality of coral tissues after bleaching. Furthermore, subtle differences in swimming position due to colony bleaching may lead to different association strengths. An interaction breakdown due to colony death and subsequent structural degradation would result in reduced swimming time spent by fishes within colony branches (Coker et al. 2009) as well as reductions in colony refuge from predators by fishes (i.e. especially on dead and algae-covered colonies, Boström-Einarsson et al. 2018).

A previous study of a Red Sea damselfish species found that *D. marginatus* spent 18–34 % of its time between coral branches during the day and 100 % at night, for a total of 68–84 % of its time within the colony (Garcia-Herrera et al. 2017). These values are estimated to be similar to *C. viridis*, *D. aruanus*, and *D. reticulatus* (this study estimated 60–80 % within-colony time due to 50 % of time within branches at night and frequent colony visits, corresponding to high sheltering time). *P. amboinensis* and *P. moluccensis* would likely spend less time within colony branches (30–50 % within-colony time, due to lower roosting within colonies and fewer colony visits, corresponding to less sheltering time; see Garcia-Herrera et al. 2017). This higher residency time is likely to be a major factor in determining the extent to which fishes are dependent upon corals and possible fish-derived services. For example, large schools of generalist fishes (e.g. Haemulidae or Lutjanidae spp.), while representing significant biomass, are likely to have little impact on the health of numerous corals contained within their large foraging areas. By comparison, the persistence of a few small-bodied coral-dwelling damselfishes, on and with specific host corals, can have significant effects on nutrient provisioning and growth of host colonies (Holbrook et al. 2008, Chase et al. 2014). Finally, it is possible that fishes' behavioral strategies, trade-offs, and potential benefits differ around colonies of various coral species and in different water flow environments (Holbrook et al. 2008). For instance, distance of fish from substrate would likely vary between larger branched *Acropora intermedia* colonies, compared with more compact *Seriatopora hystrix*. However, distance from colony branches and colony visits remain unchanged, likely due to abundance of food and startle refuge distance (Tables S7 & S8). Distinguishing the foraging distance of fishes around different sizes (Pereira et al. 2015, Pereira & Munday 2016) and species of corals

may elucidate fine-scale patterns of occupancy and usage, as well as survival of these interactions after habitat loss (Pratchett et al. 2012).

This study illustrated that coral-dwelling fishes vary in their associations with host corals, which is likely to influence their cost–benefit ratios associated with colony usage (i.e. roosting location, foraging ground, social group network). These behavioral variations are exemplified by contrasting the association of *D. aruanus*, which shelters within the coral throughout the night and regularly returns to the coral even during feeding, compared to *P. amboinensis*, which infrequently visits the colony and exhibits less fidelity for roosting within the colony. This interspecific trait variation (as well as intraspecific variations) between aggregating damselfish species at the colony level could alter community dynamics through reduced fish–coral interaction abundances and interaction strengths (Bolnick et al. 2011, Pruitt & Ferrari 2011). Nevertheless, changes in coral colony health (i.e. bleaching), can alter key behaviors, such as swimming position around coral colonies, fish interaction strengths, and fish survival during and after bleaching events. The present study highlights the fact that fishes utilize colonies in different ways and for different purposes and that there is a need to consider not only which fish species are present, but also a range of diurnal and nocturnal movements, and social fish behavioral traits dictating the mechanisms impacting their coral use. Scientific literature currently focuses on how changes in coral complexity influence fish communities, but limited information exists on the reverse feedback of how fish-derived behaviors translate into beneficial services for coral colonies and populations. The results of this study emphasize the complexity of quantifying the nature of fish–coral interactions (how fishes utilize colonies), particularly in terms of the species-specific variations, and the context-dependency of these interactions across temporal scales and their response to global environmental change. Abiotic stressors will disrupt these habitat associations (Wong & Candolin 2015, Pratchett et al. 2019) and eventually erode the function of fishes within reef habitats (Graham et al. 2006, Kiers et al. 2010).

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