

Variation in the parasite communities of three co-occurring herbivorous coral reef fishes

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Abstract

Parasites are important, diverse, and abundant components of natural ecosystems and can influence the behaviour and health of their hosts, inter- and intraspecific interactions, and ultimately community structure. Coral reefs are one of the world's most biodiverse ecosystems, yet our understanding of the abundance, diversity, and composition of parasite communities of coral reef fishes is limited. Here, the authors aimed to compare the abundance, richness and composition of parasite communities among three co-occurring herbivorous coral reef fishes (the barred rabbitfish *Siganus doliatus*, Ward's damsel *Pomacentrus wardi* and the obscure damsel *Pomacentrus adelus*) from an inshore reef of the Great Barrier Reef (GBR). In total, 3978 parasites (3869 endoparasites and 109 ectoparasites) from 17 families were recovered from 30 individuals of each of the three fish species (mean = 44 ± 22 s.e. parasites per fish; range = 0–1947 parasites per fish). The parasite communities of *P. wardi* and *P. adelus* were characterised by pennellid copepods, derogenid and lecithasterid digeneans and were distinct from those of *S. doliatus* that were characterised by a higher abundance of attractotrematid and gyliuchenid digeneans. The abundance and family richness of all parasites were greatest in *S. doliatus* (abundance: 22.1 ± 5.0 parasites per fish; richness: 3.2 ± 0.3 families per fish), intermediate in *P. wardi* (abundance: 4.8 ± 1.1 parasites per fish; richness: 2.3 ± 0.3 families per fish) and lowest in *P. adelus* (abundance: 1.4 ± 0.4 parasites per fish; richness: 0.9 ± 0.2 families per fish). Similarly, the abundance of endoparasites was greatest in *S. doliatus* (19.7 ± 5.1 endoparasites per fish), intermediate in *P. wardi* (2.6 ± 0.7 endoparasites per fish) and lowest in *P. adelus* (1.2 ± 0.4 endoparasites per fish). Ectoparasite abundances were also lowest for *P. adelus* (0.2 ± 0.1 ectoparasites per fish), and *S. doliatus* and *P. wardi* had comparable abundances of ectoparasites (1.3 ± 0.3 and 2.1 ± 0.5 parasites per fish, respectively). Similarities between the parasite assemblages of the two pomacentrids may be related to their similar behaviours and/or diets vs. those of the larger-bodied and more mobile rabbitfish. Investigating the causes and consequences of variation in parasite communities across a broader range of fish species will be critical to understand the potential role of parasites in coral reef ecosystems.

KEYWORDS

abundance, diet, ectoparasite, endoparasite, host fish size, richness

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1 | INTRODUCTION

Parasites are ubiquitous, abundant, and diverse components of natural ecosystems and are increasingly recognised for their roles in ecosystem functioning (Marcogliese, 2004; Mouritsen & Poulin, 2005; Preston *et al.*, 2016). Within an ecosystem, parasites play important roles in trophic interactions and energy transfer, with parasitism, in its broadest sense, suggested to be the most common means of food acquisition among organisms (Dunne *et al.*, 2013; Lafferty, Allesina *et al.*, 2008; Lafferty *et al.*, 2006; Price, 1977). In estuarine ecosystems, for example, parasites have been found to contribute more to overall ecosystem biomass than predatory birds and fishes, due to their high productivity and food conversion ratios (Kuris *et al.*, 2008). Parasites are also highly diverse, with approximately 40% of all known species estimated to be parasitic at some stage within their life cycle (Dobson *et al.*, 2008; Rohde, 1984). Moreover, the host specificity of most parasites means that the diversity of the parasite community often reflects the biodiversity of the ecosystem itself (Cribb *et al.*, 1994b; Hudson *et al.*, 2006; Marcogliese, 2004). Despite the diversity, ubiquity, and potential importance of parasites in ecosystem function, they are often overlooked within ecological studies. Including parasites and host–parasite interactions within ecological research will improve our understanding of the function, health and resilience of these ecosystems. This is particularly important for those ecosystems vulnerable to growing anthropogenic and climatic stressors, such as coral reefs.

Coral reefs are one of the world's most biodiverse ecosystems and are estimated to support a diverse community of parasites, up to 10-fold greater than the number of coral reef fish species (Cribb *et al.*, 1994a; Rohde, 1976). Despite considerable research focus on the taxonomy of some families of marine parasites (Bray & Cribb, 1998; Kritsky *et al.*, 2007), and on the interactions between cleaner organisms (*i.e.*, cleaner wrasse and shrimps) and parasitic gnathiid isopods (Grutter *et al.*, 2019; Sikkil *et al.*, 2006), relatively few studies have described the parasite communities of coral reef fishes in their entirety or how these communities vary among fish species (Duong *et al.*, 2019; Muñoz *et al.*, 2007; Vignon & Sasal, 2010). Quantifying the parasite communities of coral reef fishes and establishing their “baseline” composition will not only increase our understanding of coral reef biodiversity but also provide insights into the mechanisms structuring their parasite communities. Moreover, establishing community baselines will allow us to identify how changes in reef condition and disturbances such as coral bleaching, cyclones and terrestrial runoff can influence parasite communities and, for those parasites that utilise multiple host species, be used as a means of monitoring system recovery (Overstreet, 2007).

Of the few studies that have quantified the parasite communities of adult coral reef fishes, most have focused on piscivorous (Vignon & Sasal, 2010: Lutjanidae 3 spp., Serranidae 5 spp.), invertivorous (Muñoz *et al.*, 2007: Labridae 14 spp.) and omnivorous species (Lo *et al.*, 1998: Pomacentridae 4 spp.; Sun *et al.*, 2012: ambon damsel *Pomacentrus amboinensis* Bleeker 1868). Few studies have quantified the parasite communities of herbivorous reef fish, with exceptions

being the marbled spinefoot *Siganus rivulatus* Forskål & Neibuhr 1775 (Red Sea; Dzikowski *et al.*, 2003), the whitecheek surgeonfish *Acanthurus nigricans* (L. 1758) and the detritivorous striped-fin surgeonfish *Ctenochaetus marginatus* (Valenciennes, 1835) (Line Islands Archipelago; Wood *et al.*, 2015). Herbivorous coral reef fishes, through their feeding actions, help maintain a healthy balance between coral and algal assemblages on coral reefs and facilitate the recruitment of corals and other benthic organisms (Burkepile & Hay, 2008; Hughes *et al.*, 2007). There is, however, considerable variation in diet and feeding ecology among herbivorous fishes (*e.g.*, Hoey *et al.*, 2013; Rasher *et al.*, 2013). Given ingested material is a major source of infection by internal (or endo-) parasites (Aponte *et al.*, 2014; King *et al.*, 2008; Vitone *et al.*, 2004), differences in diet and feeding ecology are likely to influence their parasite communities.

The aim of this study was to quantify and compare the parasite communities of three common and co-occurring herbivorous coral reef fishes from inshore reefs of the Great Barrier Reef (GBR): the barred spinefoot *Siganus doliatus* Guérin-Méneville 1829–38, a gregarious and mobile algal cropping species; and two territorial, algal farming damselfish: Ward's damsel *Pomacentrus wardi* Whitley 1927 and the obscure damsel *Pomacentrus adelus* Allen 1991.

2 | METHODS

2.1 | Ethical statement

The care and use of experimental animals complied with the Queensland government's animal welfare laws, guidelines and policies as approved by James Cook University's Animal Ethics Committee, A2449. Fish were killed using an anaesthetic overdose so that their endoparasite communities could be determined. Euthanasia and organ inspection is currently the only means to identify the entire fish parasite community.

2.2 | Fish collection

Three common, co-occurring herbivorous coral reef fishes, namely *S. doliatus*, *P. adelus* and *P. wardi*, were selected for this study, as they are abundant on inshore reefs of the GBR (Emslie *et al.*, 2012; Hoey *et al.*, 2013). *S. doliatus* is a relatively large [up to 25 cm total length (TL); Kuitert & Tonozuka, 2001] species that typically forms conspecific pairs or, less commonly, larger conspecific or mixed species schools (Woodland, 1990). *S. doliatus* has a relatively large home range (1.53 ± 0.13 s.e. ha; Brandl & Bellwood, 2013) that likely encompasses a range of habitat types (*e.g.*, coral, macroalgae, rubble, sand). *P. adelus* and *P. wardi* are two common species of herbivorous, farming (or “territorial”) damselfishes on the GBR (maximum TL: *P. adelus*: 8 cm; *P. wardi*: 10 cm; Allen *et al.*, 2015). Both species are solitary and highly site-attached with small territory sizes (*c.* 0.6–2.0 m²; Ceccarelli *et al.*, 2005, 2006) and typically form pairs only to breed (Breder & Rosen, 1966). Although previous studies have investigated the

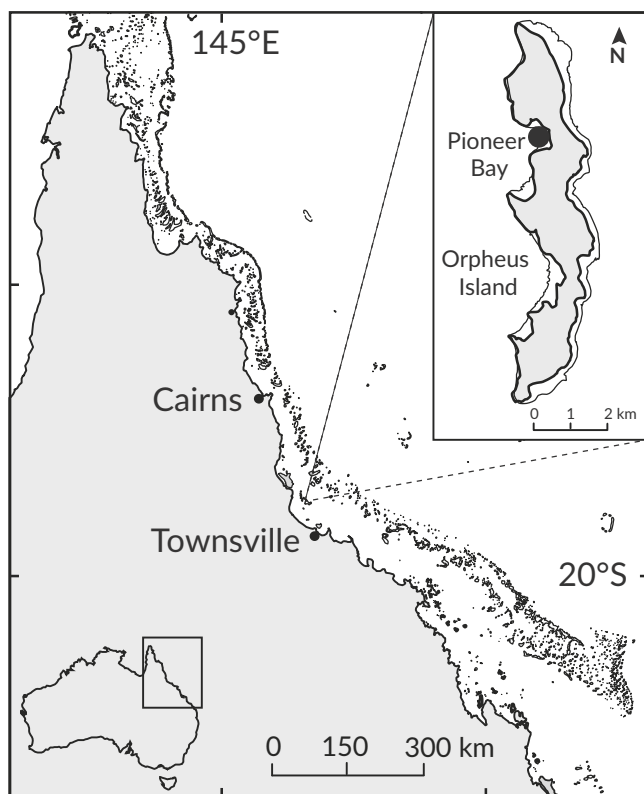


FIGURE 1 Map of the Great Barrier Reef. Inset: Orpheus Island within the central Great Barrier Reef; black circle indicates the fish collection location at Pioneer Bay

prevalence and composition of specific parasite taxa for *S. doliius* (Kritsky *et al.*, 2007; Nolan & Cribb, 2006) and *P. wardi* (Bray *et al.*, 1993; Gunter & Adlard, 2008), no studies have documented the entire ecto- and endoparasite communities of *S. doliius* or *P. wardi*, and no parasite species are recorded for *P. adelus*.

Thirty individuals of each species were collected from the reef crest and outer reef flat (1–3 m depth) of Pioneer Bay, Orpheus Island, within the central GBR in July and August 2017. Orpheus Island is a high continental island c. 16 km from the Queensland coast that has extensive fringing reef development on the western (leeward) margin (Figure 1). A sample size of 30 individuals has been shown to achieve approximately 95% confidence of recovering parasite taxa with a prevalence of greater than 10% (Post & Millest, 1991). Individuals were collected using a weak clove oil solution, barrier nets and hand-nets, and immediately placed individually in sealed aquarium-grade bags, provided with supplemental oxygen and transported to Orpheus Island Research Station (OIRS). At OIRS each fish was transferred into an aquarium filled with filtered, UV-sterilised sea water and supplemental aeration. Given differences in body size (*S. doliius*: mean TL = 22.3 ± 2.8 cm s.e.; *P. wardi*: mean TL = 7.3 ± 1.7 cm s.e.; *P. adelus*: mean TL = 6.9 ± 1.5 cm s.e.), the pomacentrids were placed in individual 10 l aquaria, and *S. doliius* were placed in individual 15 l aquaria. Static, as opposed to flow-through, systems were used to ensure that any dislodged parasites were retained within each aquarium. Water exchanges were conducted every 24 h whereby

approximately 80% of the water from each aquarium was siphoned; filtered through a 63 µm sieve to capture dislodged parasites; and replaced with fresh, filtered UV-sterilised sea water. Any parasites captured on the sieve were preserved in a 70% ethanol solution for subsequent identification. Fish were fed twice daily *ad libitum*; the two pomacentrid species were fed commercial pellets (NRD 5/8 pellets, INVE Aquaculture Nutrition, Nonthaburi, Thailand), and *S. doliius* were fed commercially supplied, dried *Pyropia* sp. (*i.e.*, nori). Fish were held in aquaria for a maximum of 6 days before being transported to James Cook University for necropsy. Before transport, fish were not fed for 24 h to minimise nitrogenous waste during transport; they were placed in separate, sealed aquarium-grade bags filled with fresh, filtered UV-sterilised sea water and supplemental oxygen. Aquarium water was filtered, and any captured parasites were preserved as described earlier.

2.3 | Fish dissection

Fish were killed in a 0.15% solution of 2-phenoxyethanol, subsequently measured (TL and wet mass) and photographed, and the entire body surface, including inside the oral cavity and buccal folds, was inspected for ectoparasites under a dissection microscope (range: 6.7–45× magnification as required). Gills were then removed and placed in filtered sea water for inspection under the dissecting microscope at 6.7–45× magnification. After gill removal, each fish was placed in individual freshwater baths for 5 min. The contents of each bath were then filtered through a 63 µm sieve to collect any dislodged ectoparasites. Parasitological analyses of visceral organs (*i.e.*, heart, liver, spleen, gall bladder, white muscle, brain, stomach and intestines) were conducted following Hutson *et al.* (2007) and Cribb and Bray (2010). For both pomacentrid species, a sample of white muscle tissue (surrounding the visceral cavity) and the entire heart, liver, gall, spleen and brain were squashed onto slides, forming a tissue layer approximately one cell thick. Slides were examined for parasites under a compound microscope at 200× magnification (400× magnification for the gall bladder). Due to the larger organs of *S. doliius*, a sample of the white muscle tissue (surrounding the visceral cavity), heart, liver and spleen was removed consistently from the same area, squashed onto a slide and examined as described earlier. The brain and gall bladder of *S. doliius* were squashed as whole organs. Due to the size of the digestive tract of *S. doliius*, the stomach and intestines were each cut open, sectioned and shaken vigorously in physiological saline, and the settled contents and tissues were examined under a dissection microscope (Cribb & Bray, 2010). For the two pomacentrid species, the stomach and intestines were dissected and inspected under a dissecting microscope at 6.7–45× magnification.

The abundance of all parasites was quantified, the exceptions being ceratomyxid myxozoans (f. Ceratomyxidae) and ancyrocephalid monogeneans (f. Ancyrocephalidae). The extremely high abundances of these taxa in the gall bladder and on the gills, respectively, made accurate estimates of abundance unfeasible, and therefore only presence/absence data were recorded. All parasites found during

dissections were preserved in 70% ethanol. Due to logistical considerations, 13 *S. doliatius* were killed in a 0.15% solution of 2-phenoxyethanol and immediately frozen for dissection later. During dissection, the frozen *S. doliatius* were defrosted overnight in a refrigerator and dissected the following morning following the protocol described earlier.

Parasites were identified to the lowest taxonomic ranking using morphological characters with the assistance of taxonomic keys and/or soliciting taxonomic expertise on parasite groups (see Supporting Information).

2.4 | Statistical analysis

Statistical analyses were conducted using family-level assignments of the parasite taxa to provide objective comparisons among the three fish species, unless otherwise indicated (Locke *et al.*, 2011; Poulin & Leung, 2010).

Due to non-normality of parasite abundance data, PERMANOVA (permutational multivariate analysis of variance) was used to test for differences in parasite community composition (infection intensity of each parasite family) among the three fish species (fixed categorical variable with three levels). PERMANOVA was conducted using the vegan package in R (Oksanen *et al.*, 2020), and *post hoc* comparisons among species were conducted using the RVAideMemoire package (Hervé, 2020). Model validation was confirmed using stress values and stress plots. Differences in the composition of the parasite communities among fish species were visualised using non-metric multidimensional scaling (nMDS). This technique produces an ordination of community composition data for each fish, based on the Bray–Curtis dissimilarity matrix of parasite infection intensity data (*i.e.*, excluding uninfected fish; see A. O. Bush *et al.*, 1997) using the vegan package in R (Oksanen *et al.*, 2020). Infection intensity data were square root transformed and Wisconsin double standardised to reduce the influence of extreme values. As individual fish without parasitic infection, infected only by nematodes or infected by encysted and excysted parasitic worms (see later) were removed from the analysis, nMDS was used to compare the communities of 27 × *S. doliatius*, 24 × *P. wardi* and 13 × *P. adelus*.

Parasite abundance and richness were compared among the three species using a series of generalised linear mixed models (GLMM) or generalised linear models (GLM). To compare the abundance of total parasites and endoparasites among the three fish species (*S. doliatius*, *P. wardi* and *P. adelus*), separate GLMMs were used, with fish species as a fixed factor. An observation-level random effect was included to model extra variation present in the data. The abundance of ectoparasites, the two most common parasite taxa independently (graffillid turbellarians and pennellid copepods), and encysted and excysted parasitic worms was compared among the three fish species using GLMs, with fish species included as a fixed factor. The natural log of TL was included as an offset in the model comparing pennellid abundance between the two damselfish species (pennellids did not infect *S. doliatius*); nonetheless, it was not included in models comparing all three fish species due to collinearity of fish species and TL. Total

parasite and endoparasite abundance were modelled against a Poisson distribution, and the abundance of ectoparasites, pennellid copepods and graffillid turbellarians, and encysted and excysted worms was modelled against a negative binomial distribution. A single *S. doliatius* was removed from the total and endoparasite abundance analysis, as the abundance of gyliauchenid digeneans in its gastrointestinal tract ($n = 1916$ gyliauchenids) was an order of magnitude greater than the average abundance of all 30 *S. doliatius* investigated (mean = 110.8 gyliauchenids per fish ± 64 s.e. – including heavily infected individual). A single, anomalous *S. doliatius* was also removed from the encysted and excysted abundance analysis, as the abundance of encysted and excysted worms was *c.* 3.5 times greater (94 individuals) than the next highest abundance (27 individuals).

The number of parasite families found to infect the three fish species (*i.e.*, parasite richness) was modelled using a GLM against a Poisson distribution, with fish species included as a fixed factor. Parasite richness data were significantly under-dispersed (DHARMA non-parametric dispersion test; $P < 0.05$; Hartig, 2021), and as such the standard errors for the Poisson distribution are overestimated (Harris *et al.*, 2012). The overall prevalence of parasitic infection (*i.e.*, proportion of hosts infected), as well as the prevalence of ecto- and endoparasitic infection, was compared among species ($n = 30$ individuals per species) using a GLM of presence/absence data against a binomial distribution.

Assumptions of the error distributions for candidate models were examined using residual plots, χ^2 goodness-of-fit tests and dispersion (the ratio of the variance to the mean). Residual diagnostics, zero inflation and overdispersion were also tested for each model using the DHARMA package (Hartig, 2021). AICc was used for model selection with the model with the fewest parameters, and AICc value within 2 units of the lowest was selected. Tukey's *post hoc* analyses comparing parasite abundances, family richness and prevalence among fish species were conducted using the emmeans package (Lenth, 2021). All statistical analyses were performed using R software, version 3.5.1 (R Core Team, 2018). The parasite taxa for which only presence/absence data were recorded (*i.e.*, ceratomyxid myxozoans and ancyrocephalid monogeneans) were excluded from analyses of abundance and community composition. Conversely, parasite taxa that could not be identified to family (*i.e.*, nematodes and encysted and excysted parasitic worms) were removed from species richness and community composition analyses.

3 | RESULTS

A total of 3978 metazoan parasites were recorded from 17 families (7 families of ectoparasites and 10 families of endoparasites) across the 90 fish examined (Table 1; see Supporting Information Figure S1). From these 90 fish (including a heavily infected *S. doliatius* with 1916 gyliauchenids), gyliauchenid digeneans accounted for 84% of all parasites recorded. Encysted and excysted parasitic worms were also highly abundant, accounting for 8% of all parasites recorded (total = 315 individuals, including a heavily infected *S. doliatius* with 94 encysted and excysted worms); nonetheless, these could not be identified to family with any certainty. The abundance of parasites

TABLE 1 Summary of all known host–parasite records for *Siganus doliatus*, *Pomacentrus wardi* and *Pomacentrus adelus* from the Indo-Pacific Region

Host species	Class/family	Taxon	Record	Microhabitat	Location
<i>S. doliatus</i>					
Ectoparasites					
	Malacostraca				
	Corallanidae	<i>Argathona cf. macronema</i> *	Current study	Body surface	PI
	Cymothoidae	<i>Anilocra</i> sp.	Grutter (1994)	Body surface ⁺	GBR
	Gnathiidae	<i>Gnathia</i> spp. •	Grutter (1994)	Body surface/gills ⁺	LI; HI
			Current study	Body surface	PI
		<i>Gnathia falcipines</i> •	C. M. Jones <i>et al.</i> (2007)	Body surface/gills ⁺	LI
	Hexanauplia				
	Bomolochidae	<i>Acanthocolax/Orbitacolax</i> sp. nov.	Grutter (1994)	Body surface ⁺	LI, HI
	Caligidae	<i>Lepeophtheirus</i> sp.	Grutter (1994)	Body surface/gills ⁺	LI, HI
		<i>Caligus</i> sp. •	Grutter (1994)	Body surface/gills ⁺	LI, HI
		<i>Caligus cf. uniartus</i> *•	Current study	Body surface	PI
	Trematoda				
	Transversotrematidae	<i>Transversotrema licinum</i>	Grutter (1994)	Body surface ⁺	LI
	Monogenea				
	Ancyrocephalidae	<i>Glyphidohaptor sigani</i>	Kritsky <i>et al.</i> (2007)	Gills	HI
		<i>Pseudohaliotrema sphincteroporos</i>	P. D. Olson and Littlewood (2002)	Gills	GI
		<i>Pseudohaliotrema</i> sp. 1•	Current study	Gills	PI
		<i>Pseudohaliotrema</i> sp. 2•	Current study	Gills	PI
		<i>Tetrancistrum</i> sp.*	Current study	Gills	PI
	Capsalidae	<i>Capsalidae</i> sp. nov.*•	Current study*	Body surface	PI
		“Benedeninae” •	Grutter (1994)	Body surface/gills ⁺	HI
	Neophora				
	Piscinquinilidae	<i>Ichthyophaga</i> sp.	Lockyer <i>et al.</i> (2003)	Body surface/gills ⁺	GI
	Piscinquinilidae or Graffillidae	<i>Ichthyophaga</i> sp. or <i>Paravortex</i> sp.	Grutter (1994)	Body surface/gills ⁺	LI, HI
	Graffillidae	<i>Paravortex</i> sp.	Current study	Body surface/gills	PI
Endoparasites					
	Chromadorea				
	Raphidascarididae	<i>Hysterothylacium</i> sp.*	Current study*	Heart, stomach, intestines	PI
		<i>Raphidascarididae</i> sp.*	Current study*	Intestines	PI
	Trematoda				
	Bucephalidae	<i>Bucephalidae</i> sp.	Current study*	Stomach, intestine	PI
	Gy liauchenidae	<i>Flagellotrema reburus</i>	Hall and Cribb (2008)	Intestine	HI
		<i>Gy liauchen zanchi</i>	Hughes-Stamm <i>et al.</i> (1999)	Intestine	HI
			Current study	Intestine	PI
		“ <i>Medousogy liauchen</i> ” <i>cydippe</i>	Hall (2004)	Intestine	HI
			Current study	Stomach, intestine	PI
		<i>Ptychogy liauchen thetidis</i>	Hall and Cribb (2004)	Intestine	LI, HI
			Current study	Intestine	PI
		<i>Ptychogy liauchen thistilbardi</i>	Bray and Cribb (2000)	Intestine	N, NC

(Continues)

TABLE 1 (Continued)

Host species	Class/family	Taxon	Record	Microhabitat	Location
	Lecithasteridae	<i>Hysteroleicithoides frontilatus</i> (now <i>Hysteroleicithoides epinepheli</i>)	Bray and Cribb (2000)	Stomach/intestine	LI, NC
		<i>Machidatrema leonae</i>	Bray and Cribb (2000)	Stomach	HI
		<i>Thulinia microrchis</i>	Bray et al. (1993)	Stomach	HI
	Microscaphidiidae	<i>Hexangium cf. sigani</i> *	Current study*	Intestine	PI
	Aporocotylidae	<i>Phthinomita hallae</i>	Nolan and Cribb (2006)	Heart	HI
		<i>Phthinomita jonesi</i>	Nolan and Cribb (2006)	Heart	LI
		<i>Phthinomita sasali</i>	Nolan and Cribb (2006)	Heart	P, GBR
	Atractotrematidae	<i>Atractotrematrema sigani</i> *	Current study*	Stomach, intestine	PI
	Enoplea				
	Capillariidae	<i>Capillariidae</i> sp.	Moravec (2001)	Digestive tract	NC
	Myxozoa				
	Ceratomyxidae	<i>Ceratomyxa</i> sp. 1*	Current study*	Gall	PI
		<i>Ceratomyxa</i> sp. 2*	Current study*	Gall	PI
		<i>Ceratomyxa</i> sp. 3*	Current study*	Gall	PI
<i>P. wardi</i>					
Ectoparasites					
	Malacostraca				
	Gnathiidae	<i>Gnathia</i> sp.*	Current study*	Body surface	PI
	Hexanauplia				
	Pennellidae	<i>Pennellidae</i> sp.*	Current study*	Body surface	PI
	Monogenea				
	Ancyrocephalidae	genus species	Rohde and Hobbs (1988)	Gills	CB/LI
		<i>Pseudohaliotrema</i> sp. 1*	Current study*	Gills	PI
	Neophora				
	Graffillidae	<i>Paravortex</i> sp.*	Current study	Body surface/gills	PI
Endoparasites					
	Trematoda				
	Derogenidae	<i>Derogenidae</i> sp.*	Current study*	Intestine	PI
	Lecithasteridae	<i>Hysteroleicitha nahaensis</i> •	Barker et al. (1994)	N/A	HI
		<i>Lecithaster stellatus</i> •	Bray et al. (1993)	Intestine	GBR
		<i>Lecithasteridae</i> sp. •	Current study*	Intestine	PI
	Lepocreadiidae	<i>Lepotrema monile</i>	Bray and Cribb (1998)	N/A	HI
	Bivesiculidae	<i>Bivesicula claviformis</i> *	Current study*	Intestine	PI
	Cryptogonimidae	<i>Mitotrema anthostomatum</i>	Cribb et al. (1996)	N/A	HI
	Faustulidae	<i>Faustulidae</i> sp. nov.*	Current study*	Intestine	PI
	Heterophyidae	<i>Galactosomum bearupi</i>	Beuret et al. (2000)	Brain	HI
	Chromadorea				
	Camallanidae	<i>Spirocamallanus</i> sp.	Lester and Sewell (1989)	Intestine	HI
	Myxozoa				
	Ceratomyxidae	<i>Ceratomyxa sewelli</i>	Gunter and Adlard (2008)	Gall	LI
		<i>Ceratomyxa moseri</i>	Gunter and Adlard (2008)	Gall	LI
		<i>Ceratomyxa</i> sp. 4 •	Current study	Gall	PI
		<i>Ceratomyxa</i> sp. 5 •	Current study	Gall	PI

TABLE 1 (Continued)

Host species	Class/family	Taxon	Record	Microhabitat	Location
<i>P. adelus</i>					
Ectoparasites					
	Hexanauplia				
	Pennellidae	Pennellidae sp.*	Current study	Body surface	PI
	Monogenea				
	Ancyrocephalidae	<i>Pseudohaliotrema sp. 1*</i>	Current study*	Gills	PI
	Neophora				
	Graffillidae	<i>Paravortex sp.*</i>	Current study	Body surface/gills	PI
Endoparasites					
	Trematoda				
	Derogenidae	Derogenidae sp.*	Current study	Intestine	PI
	Lecithasteridae	Lecithasteridae sp.*	Current study	Intestine	PI
		<i>Hysterolecitha sp.*</i>	Current study	Stomach	PI
	Faustulidae	Faustulidae sp. nov.*	Current study	Intestine	PI
	Chromadorea				
	Raphidascarididae	<i>Hysterothylacium sp.*</i>	Current study*	Intestine	PI
		Raphidascarididae sp.	Current study*	Stomach	PI
	Myxozoa				
	Ceratomyxidae	<i>Ceratomyxa sp. 6*</i>	Current study	Gall	PI

Note: Host records identified within the present study are highlighted in bold. Novel host records are indicated by “****”; known parasite microhabitats that were not specified in the original study are indicated by the symbol “+”; records from the present study that may be the same species as those identified in previous studies are indicated by “*.”

Abbreviation: CB, Capricorn Bunker; GBR, Great Barrier Reef; GI, Green Island; HI, Heron Island; LI, Lizard Island; N, Noumea; NC, New Caledonia; P, Palau; PI, Palm Island Group.

was highly variable among and within species, ranging from 0 to 1947 parasites per fish in *S. doliatus*, 0–22 in *P. wardi* and 0–8 parasites per fish in *P. adelus*. Ceratomyxid myxozoans and encysted and excysted parasitic worms were the most prevalent parasites recorded, with encysted and excysted worms found in 63% of all fish examined and ceratomyxid myxozoans present in 48% of all fish examined (see Supporting Information Figure S2). Overall parasite prevalence was high, with 100% of *S. doliatus* ($n = 30$), 97% of *P. wardi* ($n = 29$) and 83% of *P. adelus* ($n = 25$) examined having parasite infections.

3.1 | Parasite community composition

There was a clear separation of the parasite community of *S. doliatus* from those of the two pomacentrid species (PERMANOVA: pseudo- $F_{2,61} = 7.85$, $P < 0.01$; Figure 2), with a high degree of overlap in the parasite communities of *P. adelus* and *P. wardi* (PERMANOVA: pseudo- $F_{2,61} = 7.85$, $P > 0.05$). Relatively high abundances of caligid copepods, corallanid isopods and microscaphid, attractotrematid and gyliauchenid digeneans characterised the parasite community of *S. doliatus*, whereas those of *P. adelus* and *P. wardi* were characterised by high relative abundances of pennellid copepods and bivesiculid, derogenid, and lecithasterid digeneans (see Table 1 for a full list of host–parasite records).

3.2 | Parasite abundance and family richness

Total parasite abundance (excluding ceratomyxid myxozoans, ancyrocephalid monogeneans, and the outlier *S. doliatus* with 1947 parasites) varied significantly among the three fish species and was greatest in *S. doliatus* (adjusted mean = 22.1 ± 5.0 s.e. parasites per fish; GLMM: $z_{2,86} = 13.79$, $P < 0.01$), lowest in *P. adelus* (adjusted mean = 1.4 ± 0.4 s.e. parasites per fish; GLMM: $z_{2,86} = -7.93$, $P < 0.01$) and intermediate in *P. wardi* (adjusted mean = 4.8 ± 1.1 s.e. parasites per fish; GLMM: $z_{2,86} = -4.76$, $P < 0.01$; Figure 3a).

The family richness of parasite communities also varied among species, with *S. doliatus* and *P. wardi* infected by a significantly greater number of parasite families (*S. doliatus* adjusted mean = 3.2 ± 0.3 s.e. families per fish, GLM: $z_{2,87} = 5.68$, $P < 0.01$; *P. wardi* adjusted mean = 2.3 ± 0.3 s.e., GLM: $z_{2,87} = 3.95$, $P < 0.01$) than *P. adelus* (adjusted mean = 0.9 ± 0.2 s.e. families per fish; Figure 3b).

3.3 | Ecto- and endoparasite abundance

The abundance of both ecto- and endoparasites differed significantly among species. Ectoparasite abundance was lower on *P. adelus* (adjusted mean = 0.2 ± 0.1 s.e. ectoparasites per fish, GLM: $z_{2,86} = -3.413$, $P < 0.01$) than on the other two species, with *P. wardi*

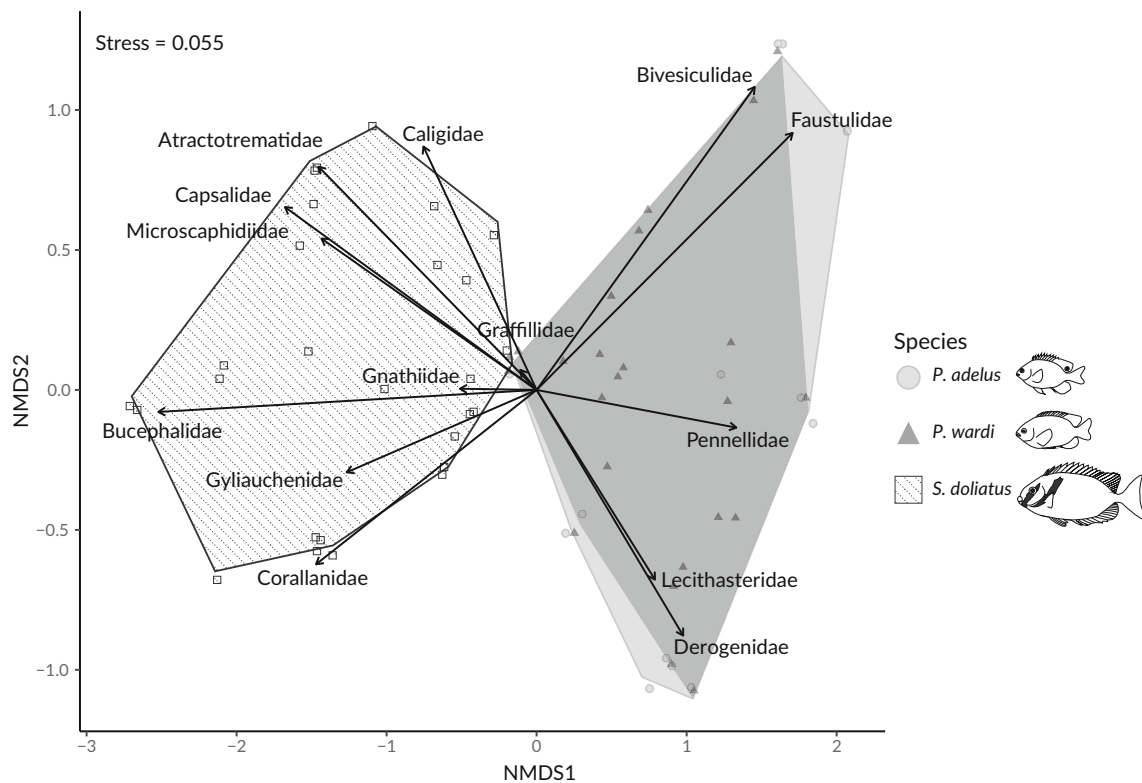


FIGURE 2 Two-dimensional solution from non-metric multidimensional scaling showing the differences in the overall parasite communities of *Siganus doliatus* ($n = 25$), *Pomacentrus wardi* ($n = 24$) and *Pomacentrus adelus* ($n = 13$) from Pioneer Bay, Orpheus Island, central Great Barrier Reef. The solution is based on Bray–Curtis dissimilarities of square root transformed infection intensity data (*i.e.*, only infected hosts). Each point represents individual fish. Polygons represent each fish species. Vectors represent the partial regression coefficients of the original variables (parasite family) with the two dimensions. Vector length is proportional to the degree of correlation between the parasite family and the ordination. See Figures S3 and S4 for additional ordinations. ● *Pomacentrus adelus*, ▲ *Pomacentrus wardi*, □ *Siganus doliatus*

(adjusted mean = 2.1 ± 0.5 s.e. ectoparasites per fish) and *S. doliatus* (adjusted mean = 1.3 ± 0.3 s.e. ectoparasites per fish) having similar abundance of ectoparasites (Tukey's *post hoc* comparison: z -ratio = 1.27, $P > 0.05$; Figure 4a). In contrast, the abundance of endoparasites was significantly greater in *S. doliatus* (adjusted mean = 19.7 ± 5.1 s.e. endoparasites per fish, GLMM: $z_{2,86} = 7.24$, $P < 0.01$) than in the two pomacentrid species, which were infected with similar abundances of endoparasites (*P. wardi*: adjusted mean = 2.6 ± 0.7 s.e. endoparasites per fish; *P. adelus*: 1.2 ± 0.4 s.e. endoparasites per fish; Tukey's *post hoc* comparison: z -ratio = -2.01 , $P > 0.05$; Figure 4b).

3.4 | Abundance of common parasite taxa and early life stages

Graffillid turbellarians and pennellid copepods were the most abundant parasite taxa, although the latter was recorded only from the two pomacentrid species. The abundance of both graffillid turbellarians and pennellid copepods varied among fish species. *P. adelus* had the lowest abundance of graffillid turbellarians (adjusted mean = 0.1 ± 0.1 s.e. graffillid turbellarians per fish) relative to *P. wardi* (adjusted mean = 0.9 ± 0.3 s.e., GLM: $z_{2,87} = 3.01$, $P < 0.01$) and *S. doliatus*

(adjusted mean = 0.7 ± 0.2 s.e., GLM: $z_{2,87} = 2.63$, $P < 0.05$; Figure 5a). Similarly, the abundance of pennellid copepods was significantly lower in *P. adelus* (adjusted mean = 0.1 ± 0.1 s.e. pennellid copepods per fish) than in *P. wardi* (adjusted mean = 1.2 ± 0.3 s.e., GLM: $z_{1,58} = 3.44$, $P < 0.01$; Figure 5b).

Encysted and excysted worms accounted for approximately 56%, 44% and 5% of the total parasite abundance of *P. adelus*, *P. wardi* and *S. doliatus*, respectively. The abundance of encysted and excysted worms (excluding the outlier *S. doliatus* with 94 encysted and excysted worms) varied significantly among fish species. *Siganus doliatus* and *P. wardi* were infected with significantly higher abundances of encysted and excysted worms relative to *P. adelus* (*P. adelus*: adjusted mean = 1.2 ± 0.4 s.e. encysted and excysted worms per fish; *P. wardi*: 2.9 ± 0.8 s.e. encysted and excysted worms per fish; *S. doliatus*: 3.3 ± 0.9 s.e. encysted and excysted worms per fish, GLM: $z_{2,86} = 2.49$, $P < 0.05$; Supporting Information Figure S2).

3.5 | Overall prevalence

No significant difference in total parasite prevalence or endoparasite prevalence was detected among species (total parasite prevalence: GLM: $z_{2,87} = 3.29$, $P > 0.05$; endoparasite prevalence: GLM:

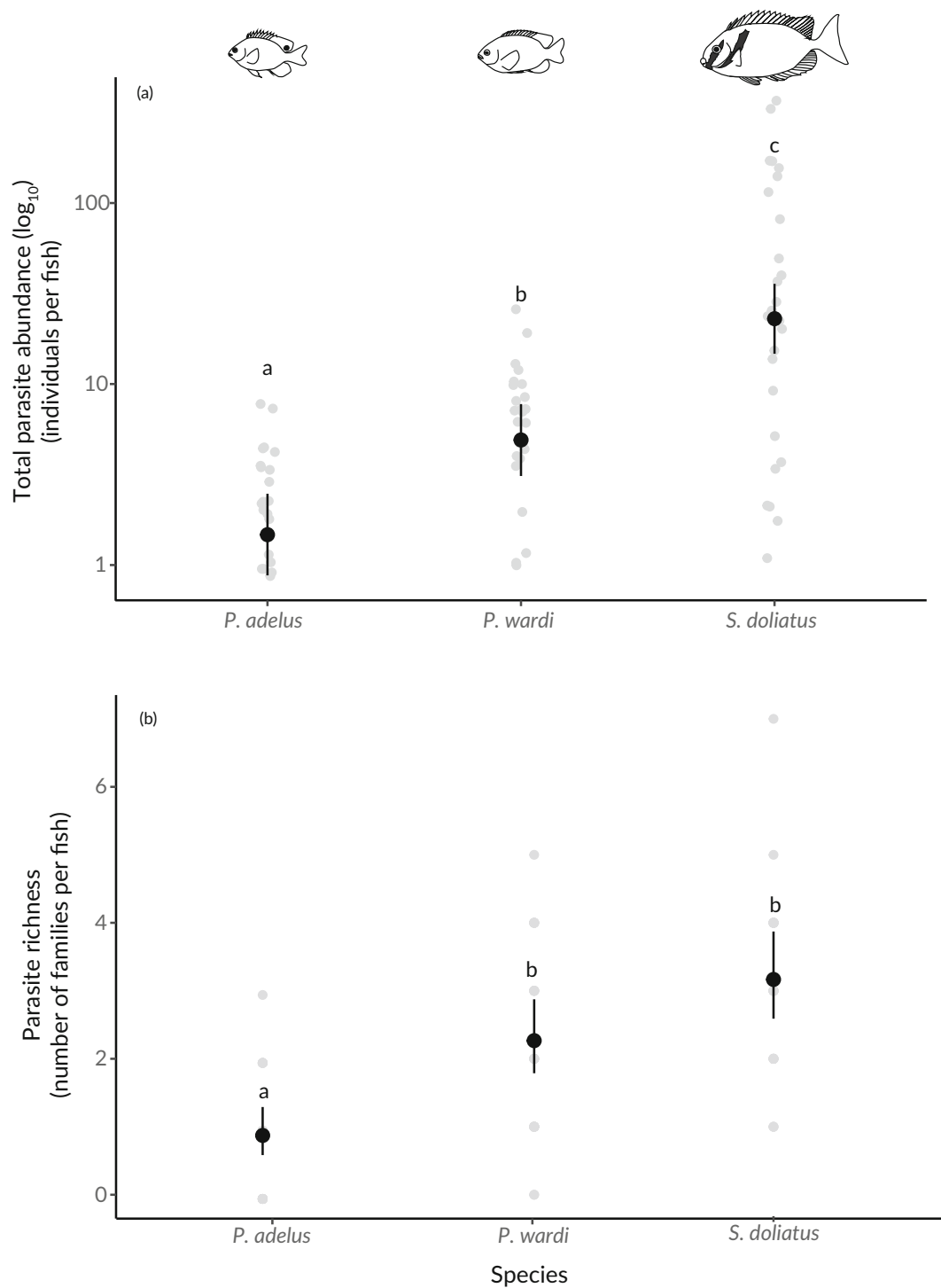


FIGURE 3 Differences in (a) total parasite abundance and (b) family richness (number of parasite families) among three co-occurring herbivorous fishes, *Pomacentrus adelus*, *Pomacentrus wardi* and *Siganus doliatus*, from Pioneer Bay, Orpheus Island, central Great Barrier Reef. Lines represent 95% C.I.; black points represent adjusted means; grey points represent raw data. Letters represent significant differences between species [Tukey's honestly significant difference (HSD), $P < 0.05$]

$z_{2,87} = 2.45$, $P > 0.05$; see Supporting Information). Nonetheless, the proportion of hosts infected with ectoparasites was significantly greater in *S. doliatus* (adjusted mean = 0.7 ± 0.1 s.e.) and *P. wardi* (adjusted mean = 0.7 ± 0.1 s.e.) relative to *P. adelus* (adjusted mean = 0.3 ± 0.1 s.e., GLM: $z_{2,87} = -2.45$, $P < 0.01$).

3.6 | Host-parasite records and novel taxa

Two probable novel species were also recorded in this study, an ectoparasitic capsalid monogenean, *Capsalidae* sp. nov., found on the skin of *S. doliatus*, and an endoparasitic digenean, *Faustulidae* sp. nov., in

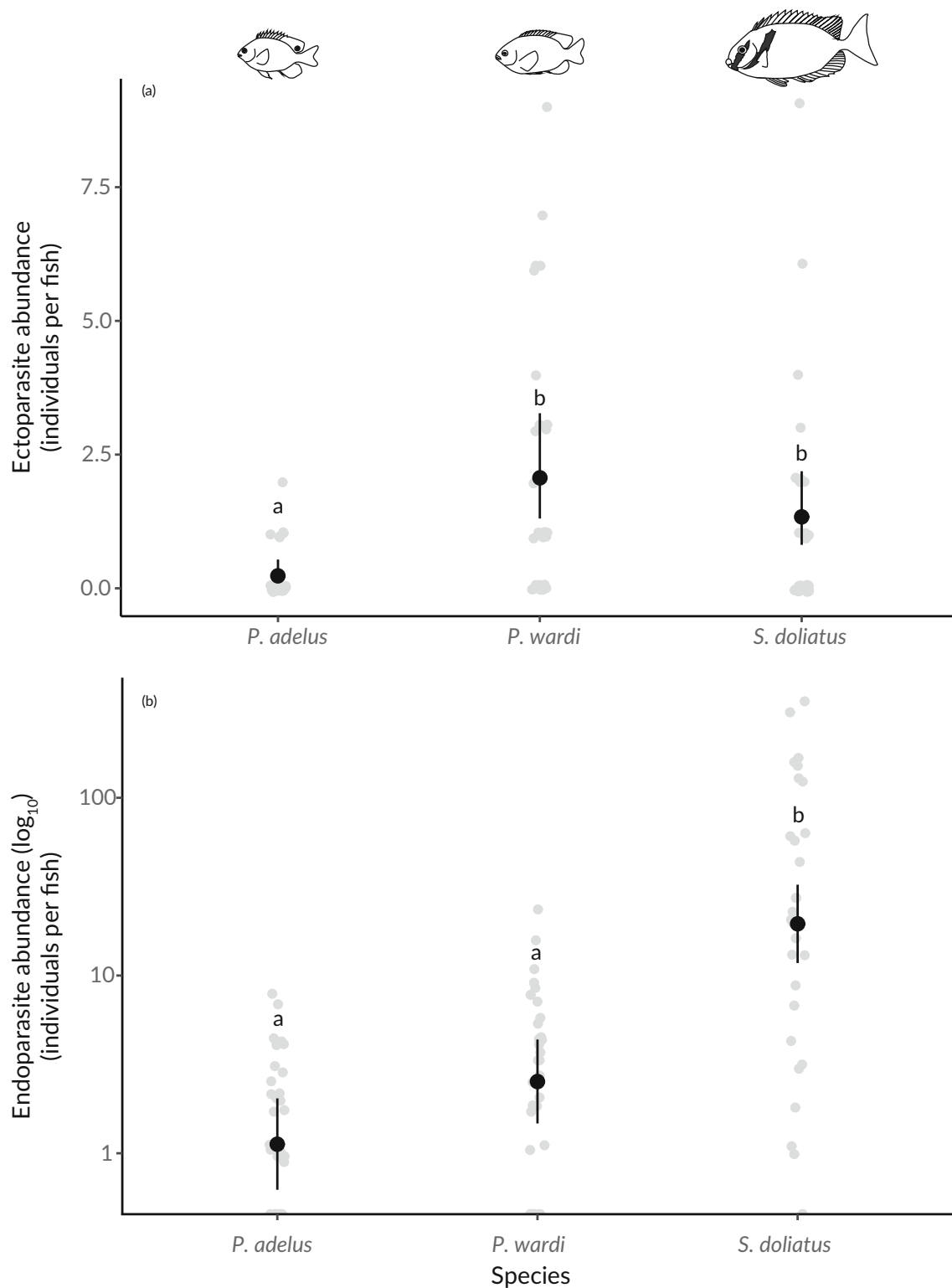
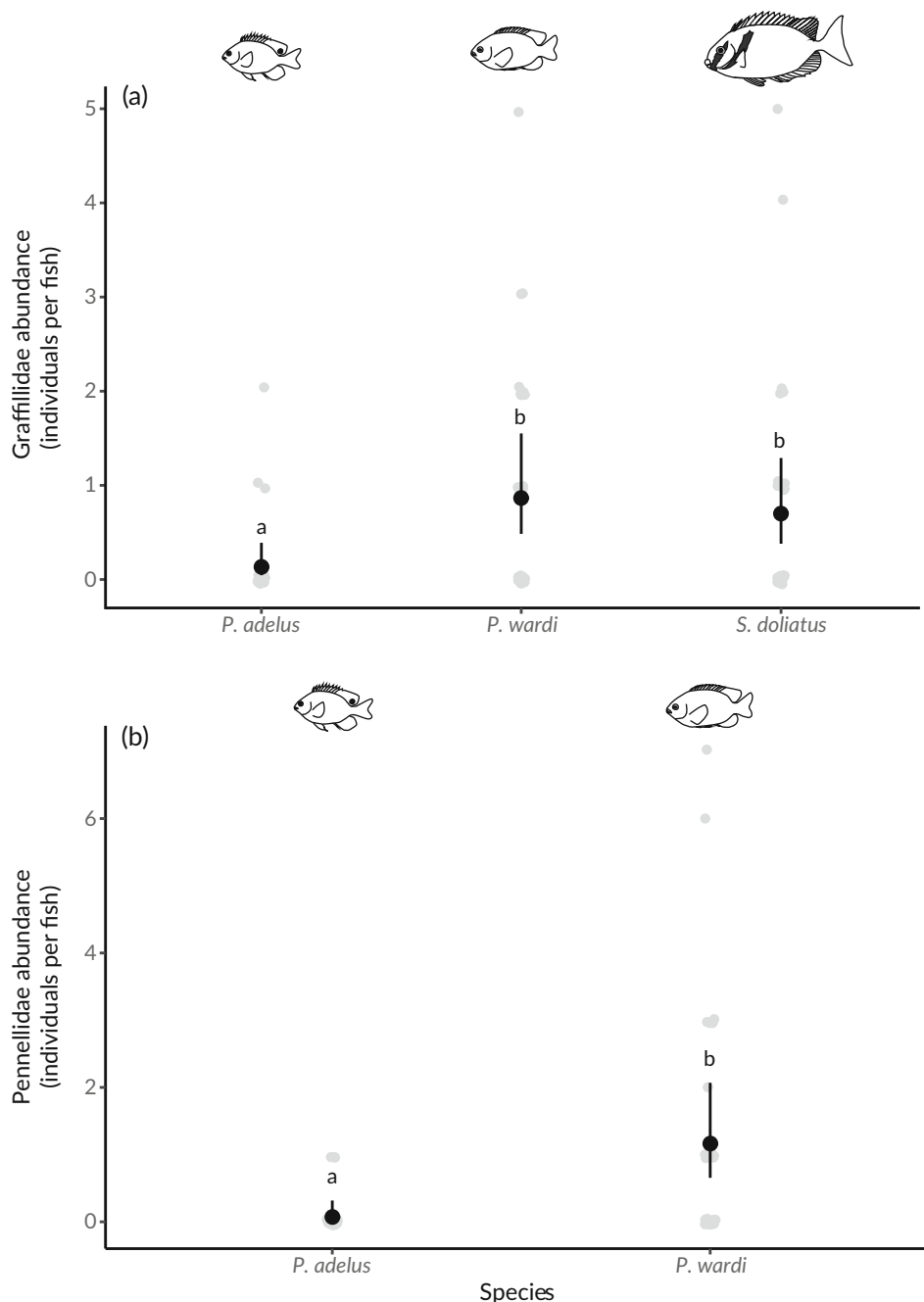


FIGURE 4 Differences in the abundance of (a) ectoparasites and (b) endoparasites infecting three co-occurring herbivorous fishes, *Pomacentrus adelus*, *Pomacentrus wardi* and *Siganus doliatus*, from Pioneer Bay, Orpheus Island, central Great Barrier Reef. Lines represent 95% C. I.; black points represent adjusted means; grey points represent raw data. Letters indicate significant differences between species (Tukey's *post hoc* test, $P < 0.05$)

the intestines of both *P. wardi* and *P. adelus*. Novel records of 6 parasite families and at least 16 species were recorded for *S. doliatus*, as well as new records of 6 families and at least 6 species were

documented for *P. wardi*. The parasite community of *P. adelus*, including 8 families and at least 10 species, is documented for the first time (Table 1).

FIGURE 5 Differences in the abundance of (a) graffillid turbellarians (Graffillidae) and (b) pennellid copepods (Pennellidae) infecting three species of co-occurring herbivorous fish, *Pomacentrus adelus*, *Pomacentrus wardi* and *Siganus doliatus*, from Pioneer Bay, Orpheus Island, central Great Barrier Reef. No pennellid copepods were recorded from *S. doliatus*. Lines represent 95% C.I.; black points represent adjusted means; grey points represent raw data. Letters represent significant differences between species [Tukey's honestly significant difference (HSD), $P < 0.05$]



4 | DISCUSSION

Characterising the parasite communities of coral reef fishes is important to understand coral reef biodiversity, ecology and interspecific interactions. This study found significant differences in the abundance, richness and composition of parasites infecting three co-occurring herbivorous fishes (*S. doliatus*, *P. wardi* and *P. adelus*) from an inshore reef in the central GBR. The parasite communities of the two territorial pomacentrids were broadly similar but distinct from those of the larger-bodied and more mobile rabbitfish, *S. doliatus*. Further, the larger-bodied *S. doliatus* (22.3 ± 2.8 cm s.e.) was infected with the

greatest abundance and richness of parasite taxa relative to the smaller-bodied *P. wardi* and *P. adelus* (mean TL: 7.3 ± 1.7 cm s.e. and 6.9 ± 1.5 cm s.e., respectively). These patterns were largely driven by differences in the abundance and richness of endoparasites among the three fish species. Despite the similarity in their parasite community composition, there were differences in the abundance and richness of parasites infecting the two pomacentrid species. In general, *P. wardi* had a greater abundance and richness of parasites overall and a greater abundance of ectoparasites than *P. adelus*. Differences in the parasite communities among the three fish species investigated may be related to differences in their diet, phylogeny, behaviour and/or body size.

4.1 | Diet

The observed differences in the endoparasite communities of *S. doliatus* and the two pomacentrids may be attributed to differences in their diet and/or feeding ecology (Campbell *et al.*, 1980; Rohde, 2005). *Pomacentrus wardi* and *P. adelus* are territorial, or farming, damselfishes that cultivate and feed predominantly on filamentous and finely branched algae (e.g., *Polysiphonia* spp., *Jania* spp. and *Galaxaura* spp., and the foliose *Lobophora* spp.), together with detritus and invertebrates within their territories (Ceccarelli, 2007; Kramer *et al.*, 2013). Three of the most abundant endoparasites infecting both *P. adelus* and *P. wardi* (i.e., the bivesiculid *Bivesicula claviformis*, derogenid and lecithasterid digeneans) infect fish through the consumption of either a first-intermediate gastropod or a second-intermediate crustacean host infected with the parasite larvae (cercariae or metacercariae, respectively; Cribb *et al.*, 1998; K ie & Gibson, 1991; Rohde, 2005). Although invertebrates represent only a very small proportion of the material ingested by *P. wardi* and *P. adelus*, it seems likely that their direct or incidental consumption may be a likely source of infection for these parasites. In contrast, *S. doliatus* typically feeds on red and brown thallate and red and green filamentous algae (e.g., *Hypnea* spp., *Gracilaria* spp. and *Padina* spp.; Fox *et al.*, 2009; Hoey *et al.*, 2013). Species of Atractotrematidae, Gyliachenidae and Microscaphidiidae, the dominant endoparasites infecting *S. doliatus* in the present study, also use a molluscan first-intermediate host, from which cercariae (larval digeneans) emerge and encyst on aquatic vegetation. These species thereby infect their herbivorous fish host through its consumption of specific algal taxa, a trait typical of digeneans infecting herbivorous fishes (Al-Jahdali & Hassanine, 2012; Hassanine *et al.*, 2016; Huston *et al.*, 2018). Although further research is required to determine the infection pathways of these endoparasites, and whether these, or similar parasite assemblages, are shared by other fish species with similar feeding ecologies, differences in diet may have contributed to the observed differences in endoparasite communities of these three species.

4.2 | Host–parasite interactions

The greater abundance of endoparasites in *S. doliatus* was largely attributed to gyliachenid digeneans (f. Gyliachenidae) that were found to infect 73% of the *S. doliatus* individuals examined, with up to 1916 specimens found to infect a single fish. Gyliachenids are digenetic trematodes found exclusively in herbivorous coral reef fishes (Hall & Cribb, 2005). Within the Indo-West Pacific, the rabbitfishes (f. Siganidae) are host to up to 52% of described gyliachenid species (Hall, 2004). Gyliachenid digeneans feed on host gut contents and may be particularly prevalent and in high abundance in the digestive tract of herbivorous fishes with a fermentative gut (i.e., *S. doliatus*, Clements & Choat, 1995; Hall & Cribb, 2005). They have been hypothesised to benefit the host by assisting in the digestion of macroalgae (Hughes-Stamm *et al.*, 1999; Jones *et al.*, 2000). Further, host mortality rate associated with gyliachenid infections is considered to be negligible, with a few known incidences of pathogenesis, as

these worms are mobile, creating little site-specific damage (Rohde, 2005). The relationship between gyliachenid digeneans and *S. doliatus* may therefore be more mutualistic than parasitic, allowing a single *S. doliatus* to harbour significant numbers with little or no adverse effects. In contrast, most digenean families, such as those found to infect *P. adelus* and *P. wardi* (Bivesiculidae, Derogenidae, Lecithasteridae and Faustulidae), are generally considered more damaging to the host, feeding on mucus, epithelial cells and sometimes blood, often leading to significant pathogenesis (Rohde, 2005).

4.3 | Body size and mobility

The abundance and richness of ectoparasites infecting coral reef fish and other animal taxa have previously been linked to differences in body size, with larger-bodied animals providing an increased surface area, a greater resource volume and a potentially greater number of niches (D attilo *et al.*, 2020; Lo *et al.*, 1998; Mu oz *et al.*, 2007; Poulin, 1995). Of the three fish species studied, *S. doliatus* is the largest and was infected with the greatest abundance of parasites overall, largely driven by its high abundance of endoparasites (discussed earlier). Nonetheless, no difference in ectoparasite abundance was observed between *P. wardi* and *S. doliatus* despite substantial differences in body size and mobility. Moreover, *P. wardi* (mean TL = 7.3 cm) was infected by a significantly greater abundance and richness of ectoparasites than *P. adelus* (mean TL = 6.9 cm), despite a minimal difference in mean body size between them (i.e., 0.4 cm). It appears unlikely that such a small difference in body size would contribute to the difference in ectoparasite infection between these two pomacentrid species. Similarly, Caro *et al.* (1997) found differences in the parasite richness of confamilial fish species (f. Mugilidae and Sparidae) of similar size and ecology. The differences in parasitism of *P. wardi* and *P. adelus* may therefore be due to differences in their ecology, demography (e.g., age; Lo *et al.*, 1998), immunity and infection history (Sol *et al.*, 2003), host and parasite behaviours (Bush & Clayton, 2018; Strohm *et al.*, 2001) and host densities (Arneberg, 2002; Arneberg *et al.*, 1998). Differences in farmed algal communities may also affect the abundance and richness of parasites infecting *P. wardi* relative to *P. adelus*. The algae within the territories of *P. wardi* are typically dominated by *Polysiphonia*, *Lobophora* and *Jania*, whereas territories of *P. adelus* are typically dominated by *Polysiphonia* and *Galaxaura*, although the composition can vary geographically (Ceccarelli, 2007). These differences in farmed algal communities may provide alternate attachment structures for parasite species, different habitats for parasite intermediate hosts and free-living stages and thus potentially influence the abundance and richness of parasites infecting these two species.

4.4 | Geographic variation in parasite communities

This study is the first to characterise the metazoan parasite communities of *S. doliatus*, *P. wardi* and *P. adelus*. Comparisons to existing host–parasite records for *S. doliatus* and *P. wardi* within the broader

GBR (see Table 1), and for *S. doliatus* and other siganids in other regions (*Siganus sutor* in Kenya: Martens & Moens, 1995; *Siganus argenteus*, *Siganus luridus* and *S. rivulatus* from the Red Sea: Diamant & Paperna, 1986; Dzikowski et al., 2003; Hassanine & Al-Jahdali, 2007), provide insights into the potential influence of host-parasite co-evolution and geography to the parasite communities of these fish species. For example, abundant parasite taxa infecting *P. wardi* (penellid copepods and derogenid digeneans) and *S. doliatus* (*Pseudohaliotrema* sp.) at Orpheus Island have not been recorded to infect these species on mid-shelf reefs of the GBR (i.e., Lizard or Heron Island; see Table 1). Conversely, parasites recorded to infect *P. wardi* (*Spirocamalanus* sp., Lester & Sewell, 1989; *Lepotrema* sp., Bray & Cribb, 1998) and *S. doliatus* (*Phthinomita* sp., Nolan & Cribb, 2006; *Lepeophtheirus* sp., Grutter, 1994) at other GBR locations were not recorded to infect these species within the present study at Orpheus Island. These apparent differences in the parasite communities of *S. doliatus* and *P. wardi* add to a growing body of research documenting geographic variation in the parasite communities of reef fish within the GBR (Cribb et al., 2014; Grutter, 1994; Trieu et al., 2015). Some parasite taxa appeared to be common across greater geographic distances, with several parasite families and genera found to infect *S. doliatus* across the Pacific Ocean (e.g., *Gyiliauchen* sp. at Heron, Lizard and Orpheus Island, Noumea and New Caledonia, Hall, 2004; Hall & Cribb, 2004, 2008; Hughes-Stamm et al., 1999; *Phthinomita* sp. at Heron Island, Lizard Island and Palau, Nolan & Cribb, 2006). Moreover, these parasites are conserved in congeneric species, with *S. argenteus*, *S. rivulatus* and *S. luridus* from the Red Sea reported to be infected with *Ceratomyxa* sp., gyliuchenid digeneans and *Gnathia piscivora* (Diamant & Paperna, 1986). Similarly, *S. sutor* from the Indian Ocean shares infections of *Tetrancistrum* sp., *Pseudohaliotrema* sp., *Caligus* sp., *Gnathia* sp., *Hexangium sigani* and gyliuchenid digeneans with *S. doliatus* from the GBR (Martens & Moens, 1995). These parasite species that are shared among congeneric hosts may potentially be more resilient to disturbances and habitat loss. Nonetheless, with coral reefs experiencing increasingly frequent climatic and anthropogenic stressors, the potential loss and fragmentation of these habitats may reduce populations of coral reef parasites, particularly those species with smaller distributions, found in specific regions of the GBR.

4.5 | Summary

This study was the first to document the complete parasite communities of *S. doliatus*, *P. wardi* and *P. adelus*, expanding on our understanding of parasite species' associations of these fishes. In doing so it has identified two potentially new species and provided several novel host-parasite records and the first parasite records for *P. adelus*. Baseline data on the parasite communities of these three common herbivorous fish species can facilitate future comparisons to understand how parasite communities vary with environmental degradation and change. This is particularly relevant for coral reefs given the current and predicted future disturbances to which they are exposed (Hughes et al., 2017; Vercelloni et al., 2020). Although phylogeny and

geography are major determinants of fish parasite communities, differences in parasitism and parasite communities observed among the three species are also likely related to differences in their diet, mobility and habitat use. Further comparisons of the parasite communities of multiple reef fishes from within and across functional and trophic groups, fish families and locations are required to evaluate the role and interplay of these ecological, geographic and phylogenetic variables in determining parasite community composition and parasitism in coral reef fishes.

AUTHOR CONTRIBUTIONS

K.M. conducted data collection, performed statistical analyses with guidance from A.S.H. and prepared the manuscript. A.S.H. and K.S.H. assisted with experimental design, manuscript preparation, editing and funding. K.S.H. provided laboratory facilities and training and assisted with fish dissections and parasite identification. All authors revised previous versions of the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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