



Habitat specialisation and overlap in coral reef gobies of the genus *Eviota* (Teleostei: Gobiidae)

Peter C. Doll^{1,2,*}, Philip L. Munday², Mary C. Bonin^{2,3}, Geoffrey P. Jones^{1,2}

¹Marine and Aquaculture Science, College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

²Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

³Great Barrier Reef Foundation, Brisbane City, QLD 4000, Australia

ABSTRACT: On coral reefs, many small coral-associated fishes exhibit high levels of habitat specialisation, which can contribute to their susceptibility to habitat loss. However, high levels of habitat partitioning may buffer communities from the loss of particular habitat types. This study provides a quantitative evaluation of habitat specialisation, substratum selectivity and habitat overlap of 9 *Eviota* (Gobiidae) species in Kimbe Bay, Papua New Guinea. All but 1 locally common *Eviota* species were strongly associated with scleractinian coral substrata, and species ranged from habitat generalists to obligate coral specialists with some of the most extreme fine-scale patterns of habitat specialisation known for coral reef fishes. Patterns of substratum selectivity varied greatly within the genus, but many species showed distinct preferences for particular corals, most notably the scleractinian genera *Acropora* and *Porites*. Most species exhibited low habitat overlap and partitioned habitat on a fine spatial scale, but there were notable exceptions. Two *Acropora* coral specialists and some species with strong preference for massive *Porites* coral exhibited high overlap. Overall, the local abundance of *Eviota* species varied in relation to the degree of habitat specialisation, with the most generalised species more abundant than the habitat specialists. Habitat structure and species-specific differences in habitat specialisation, substratum selectivity and habitat overlap are likely to be key drivers explaining the distribution and abundance of *Eviota* species and the local community structure. Most importantly, many coral-dependent and less abundant species of *Eviota* may be vulnerable to habitat loss as a result of the ongoing degradation of coral reefs.

KEY WORDS: Habitat specialisation · Cryptobenthic reef fish · Niche breadth · Live coral · Selectivity · Habitat overlap · Coral reef

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Species across all ecosystems vary in their patterns of habitat versatility, habitat preferences and degree of habitat overlap (MacNally 1995, Krebs 1999, Devictor et al. 2010). Species vary along a continuum from habitat generalists to extreme habitat specialists (Brown 1984), and pairs of species vary from those exhibiting high overlap to those that fully partition habitat resources (Abrams 1980). The environmental variability within and among habitats and the average degree of habitat overlap between pairs of

species within a community may have important ecological implications. Specialisation and overlap may explain the distribution and abundance of a species, how a species performs in different environments within its habitat, the degree to which ecologically similar species interact and how species and communities respond to habitat availability and degradation (Brown 1984, MacNally 1995, Colles et al. 2009, Saito et al. 2018). Habitat generalists may exhibit broad distributions across ecological gradients and reach greater local abundances, while specialists often have narrow distributions, low local abundances and

*Corresponding author: peterchristopher.doll@my.jcu.edu.au

show greater variability in their use of different environments (Gaston et al. 1997, Lawton 1999, Slatyer et al. 2013). While habitat generalists can perform moderately well in habitats with highly variable environments, habitat specialists may exhibit superior performance and outcompete generalists in their preferred habitat types (Futuyma & Moreno 1988, Morris 1996, Kassen 2002). Interspecific competitive interactions can lead to increased habitat specialisation as a result of habitat partitioning, which reduces overlap among species (Colwell & Fuentes 1975, Diamond 1978). Hence, patterns of habitat specialisation and overlap are critical to understanding the distribution and abundance of species, and the local composition of ecological communities.

Quantifying patterns of ecological versatility and overlap is becoming increasingly important to predicting the responses of individual species and communities to habitat loss and assessing local extinction risks (Warren et al. 2001, Fisher et al. 2003, Wilson et al. 2008). Habitat generalists are generally less likely than specialists to decline in response to habitat loss (Brown 1984). Conversely, habitat loss will have a major impact on the structure of communities composed of specialised species (Vázquez & Simberloff 2002, Munday 2004). High levels of habitat partitioning may buffer communities from the loss of particular habitat types, except for the species dependent on those habitat types. However, for communities composed of specialists with a high habitat overlap, the effects of the loss of the preferred habitat type may be devastating. Evaluating the likely impacts of habitat loss therefore requires quantitative descriptions of the degrees of both habitat specialisation and overlap within a particular community of species.

Coral reef habitats are susceptible to a range of anthropogenic and natural disturbances that have resulted in markedly reduced coral cover worldwide (Gardner et al. 2003, Hughes et al. 2018, Wilson et al. 2019, Sheppard et al. 2020). Close relationships between the abundance and diversity of reef fishes and their habitat characteristics, especially coral cover, have been well documented by previous studies (Bell & Galzin 1984, Bouchon-Navaro et al. 1985, Jones et al. 2004). Past declines in coral cover have been shown to lead to dramatic population declines and local extinctions in various reef-fish families (Jones et al. 2004, Graham et al. 2006, Bonin et al. 2009, Pratchett et al. 2012, Cheal et al. 2017). Population declines have been more common and severe in resource-specialised fishes (Munday 2004, Wilson et al. 2008, Pratchett et al. 2012), showing the ecological specialisation of reef fishes to be the principal factor explain-

ing interspecific variation in response to habitat change and loss. In general, reef fish species with a high level of habitat specialisation also tend to exhibit low levels of habitat overlap (Munday et al. 1997). However, there are exceptions. For example, coral reef cardinalfishes (Apogonidae), one of the most specialised coral-reef fish groups, exhibit high degrees of habitat overlap between pairs of species (Gardiner & Jones 2005). In such cases, multi-specific communities of habitat-specialised reef fishes may entirely rely on the fate of a single coral taxon.

To date, the effect of habitat loss has been described for a range of relatively small-bodied, specialised fish taxa including many species of damselfishes, butterflyfishes and gobies (Munday et al. 1997, Syms & Jones 2000, Munday 2004, Bonin et al. 2009). However, patterns of habitat specialisation and overlap are not necessarily consistent across genera within these families. Gobiidae is one of the most diverse families of reef fishes, with species observed in nearly every type of environment on coral reefs (Munday 2004, Syms & Jones 2004, Dirnwöber & Herler 2007, Herler et al. 2009, Schiemer et al. 2009, Bos & Hoeksema 2015). Yet, they also include a large number of species requiring or favouring specific substrata (Munday et al. 1997, Depczynski & Bellwood 2004, Herler 2007, D'Aloia et al. 2011, Majoris et al. 2018). In general, the intra- and intergeneric habitat diversity in Gobiidae is high (Coker et al. 2014). While habitat generalists have wide niche breadths and associate with a range of substrata, extreme specialists can use a single species of coral (Kuwamura et al. 1994, Munday 2002, 2004, Dirnwöber & Herler 2007). Within the family Gobiidae, past research on their habitat ecology on coral reefs mainly focussed on species of the obligate coral-dwelling genera *Gobiodon* and *Paragobiodon* (Munday et al. 1997, 2004, Herler 2007, Pereira 2017). Patterns of habitat specialisation and overlap in more ecologically diverse genera, including *Trimma* or *Eviota*, have received much less attention. *Eviota* species use a wide variety of coral reef substrata, from live branching coral to rubble and sand patches (Herler 2007, Tornabene et al. 2013, Brandl et al. 2018). However, there has been no systematic comparison of niche breadth, patterns of substratum selectivity or habitat overlap within this genus.

The aim of this study was to examine the degree of habitat specialisation, substratum selectivity and habitat overlap of common *Eviota* species in Kimbe Bay, Papua New Guinea. To predict potential consequences of habitat loss on species abundance and community dynamics of *Eviota* species, 4 aspects were considered: (1) whether local *Eviota* assem-

blages consisted of habitat generalists or specialists; (2) the degree of association with different reef substrata, including live branching corals; (3) the degree of habitat overlap between species; and (4) the relationship between the degree of habitat specialisation and the relative local abundance of the species. To test whether the study species varied along the specialist–generalist continuum, niche breadth was calculated based on the frequency of occurrence of a species in different substrata and the frequency of occurrence of the substrata. To examine whether species varied in their patterns of substratum selectivity, we compared substratum occupancy with substratum availability and calculated selectivity indices for the different substratum types. Patterns of habitat overlap were calculated from pairwise comparisons of species' frequency of occurrence on different substrata. On the basis of their small body size and a close association between cryptobenthic reef fishes

and their underlying substrata, we predicted that (1) most species would be associated with scleractinian corals, (2) species would have narrow niche breadths and show high levels of substratum selectivity, (3) pairwise combinations of species would generally exhibit a low level of habitat overlap, and (4) the local abundance of species would decrease in relation to their degree of habitat specialisation.

2. MATERIALS AND METHODS

2.1. Study site and species

This study was undertaken in Kimbe Bay, West New Britain Province, Papua New Guinea ($5^{\circ}17'S$, $150^{\circ}05'E$) in April and May 2018 (Fig. 1a). The water temperature in this sheltered embayment is relatively constant throughout the year, ranging from approxi-

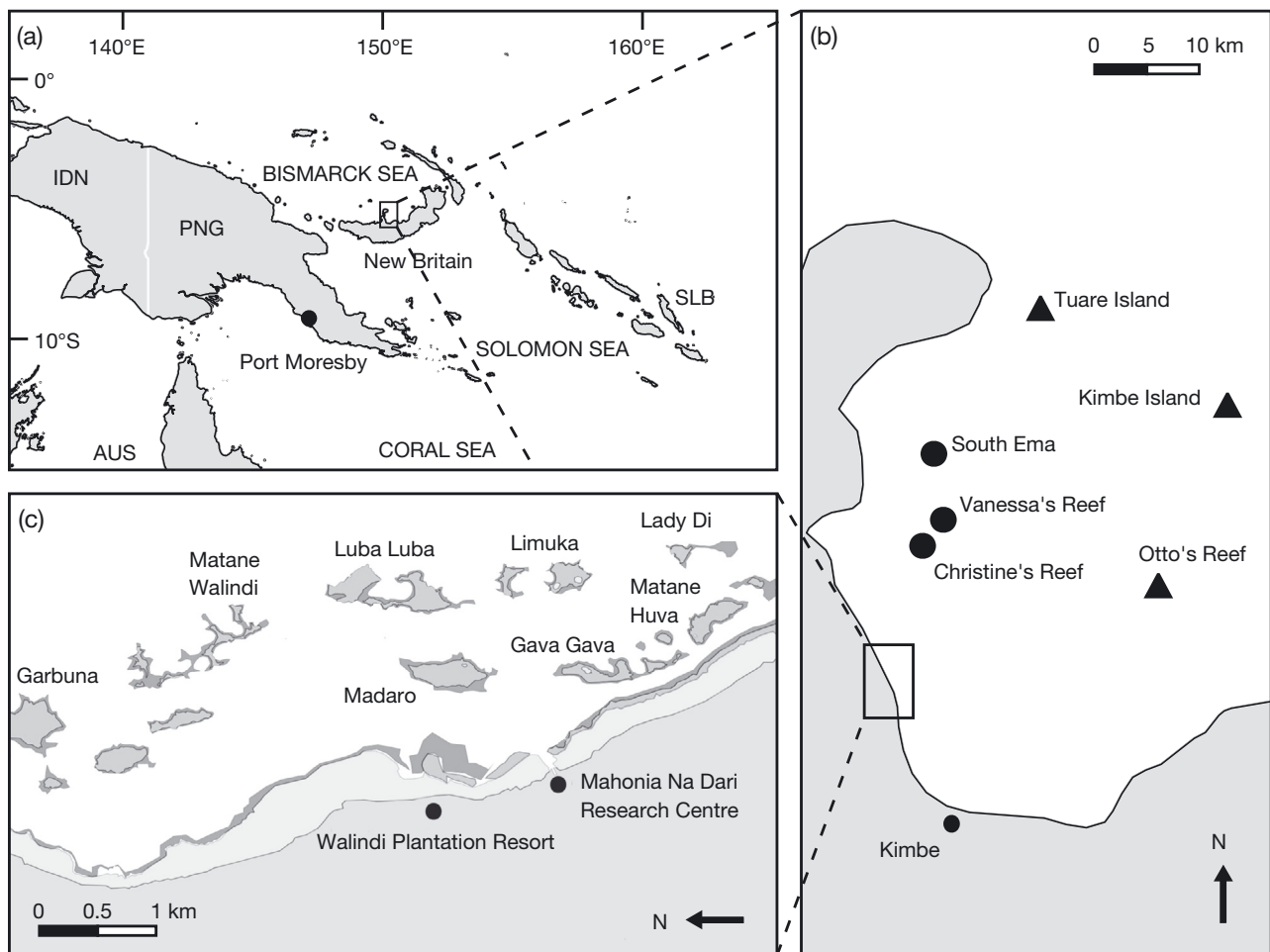


Fig. 1. Locations of (a) Kimbe Bay, New Britain Province, Papua New Guinea (AUS: Australia; IDN: Indonesia; PNG: Papua New Guinea; SLB: Solomon Islands), (b) offshore (triangle) and midshore (circle) sites and (c) 8 inshore sites where reefs were surveyed (grey and surrounding dark grey areas indicate intertidal and subtidal coral reef areas, respectively)

mately 28.5 to 30.0°C. Clusters of discrete coral reefs can be found at different distances from the inner part of Kimbe Bay. Study reefs were selected in 3 zones, categorised in relation to distance offshore: (1) inshore reefs, (2) midshore reefs and (3) offshore reefs, as previously described by Munday (2000) and MacDonald et al. (2016). All selected reefs were emergent at low tide and exhibited steep reef slopes to depths of >100 m, resulting in morphologically similar reefs sampled. This study did not test the potential effects of this gradient, and the occurrence of *Eviota* on different substrata and the frequency of occurrence of these substrata were only quantified at shallow water depths (≤ 10 m). The analyses of this study are therefore limited to the spatial scales of species' habitats and the shallow reef environments within. *Eviota* is one of the most common cryptobenthic reef-fish genera in Kimbe Bay. The 9 most locally abundant *Eviota* species were included in the analyses (Table 1).

2.2. Sampling surveys

Visual censuses were undertaken at 14 sampling sites (Fig. 1) to record the abundance of all species of *Eviota* and their occurrence on different substrata across the study area. In total, 168 visual transects of 50 × 1 m size were surveyed. At each sampling site, 4 replicate transects were surveyed at each of 3 shallow-water depths (2, 6, 10 m). Along each transect, the same diver recorded and identified every individual of *Eviota* that was observed. Individuals re-

corded (approximately 0.5–3.0 cm in total body length) were not distinguished into groups but included both adults and large juveniles. Meticulous examination of all substrata by a single diver minimised potential differences in the detectability of *Eviota* species on different substratum types. *Eviota* species identification was based on Greenfield & Winterbottom (2016). Additionally, the substratum type that each individual of *Eviota* was found on was identified. Association with the underlying substratum was evident, with all individuals recorded either resting or slowly moving on top of the substratum surface or within it. In the case of *E. brahmi*, some individuals were observed hovering directly over *Acropora* colonies at up to 15 cm in height. Coral identification followed Wallace (1999) and Veron (2000). While occupied hard corals were identified at the species level, all other substrata were categorised into the following coarse-scale substratum categories: soft corals, sponges, macroalgae, rubble, sand, and other substrata.

2.3. Occurrence of substratum types

The frequency of occurrence of substratum types was simultaneously measured by a second diver along each transect. The substratum underneath 100 marked points along each transect (2 points per 1 m transect interval) was identified. The same 6 non-scleractinian, coarse-scale substratum categories were used, while hard corals were mostly classified by genus, with some genera subdivided by growth form. To cal-

Table 1. Observed *Eviota* species, number of occurrences of *Eviota* species (n), frequency of occurrence (%) of each *Eviota* species on hard coral substrata (i.e. number of occurrences on all hard coral substrata divided by the total number of occurrences on all coarse-scale substratum types), number of substratum types occupied (i.e. total number of coarse-scale and fine-scale substratum categories) and Hurlbert's standardised niche breadth (B'_A) for *Eviota* species. B'_A ranges between 0 and 1, where lower values indicate a smaller niche breadth and thus greater habitat specialisation; nc: not calculated

Species	Species authors	n	Occurrence on hard coral substrata (%)	Substratum types occupied (no.)	B'_A
<i>Eviota atriventris</i> ^a	Greenfield & Suzuki (2012)	1748	36.4	21	0.383
<i>Eviota rubrisparsa</i> ^a	Greenfield & Randall (2010)	772	88.1	13	0.230
<i>Eviota</i> cf. <i>dorsogilva</i> ^a	Greenfield & Randall (2011) ^b	316	100.0	3	0.006
<i>Eviota seebrei</i> ^a	Jordan & Seale (1906)	155	98.7	7	0.119
<i>Eviota smaragdus</i> ^a	Jordan & Seale (1906)	91	67.0	7	0.256
<i>Eviota prasites</i> ^a	Jordan & Seale (1906)	73	67.1	7	0.310
<i>Eviota brahmi</i> ^a	Greenfield & Tornabene (2014)	68	100.0	2	0.008
<i>Eviota melasma</i> ^a	Lachner & Karnella (1980)	59	100.0	4	0.092
<i>Eviota bifasciata</i> ^a	Lachner & Karnella (1980)	36	100.0	6	0.015
<i>Eviota fasciola</i>	Karnella & Lachner (1981)	4	75.0	3	nc
<i>Eviota lachdeberiei</i>	Giltay (1933)	2	0.0	1	nc

^aThese 9 species were used to calculate niche breadth, substratum selectivity and habitat overlap (study species)
^bSee also Tornabene et al. (2015)

culate niche breadths, selectivity indices and habitat overlaps, the substratum types available and occupied by *Eviota* were defined at the same 2 levels. Firstly, 7 coarse-scale substratum categories (hard corals, soft corals, sponges, macroalgae, rubble, sand, other substrata) were used to describe patterns of selectivity and habitat overlap for all studied species on both live and dead substrata. Secondly, to accurately assess niche breadths, substratum selectivity and habitat overlaps among the coral-dwelling species, hard coral substrata were further subdivided into 30 fine-scale substratum categories: *Anacropora*, *Acropora* corymbose, *Acropora* plate, *Acropora* bottlebrush, *Acropora* staghorn, *Acropora* other, *Isopora*, *Montipora*, Pocilloporidae, *Porites* massive, *Porites* encrusting, other Poritidae, Siderastreidae, *Pavona*, *Pachyseris*, other Agariciidae, *Fungia*, *Galaxea*, *Favia*, *Diploastrea*, other Faviidae, *Oxypora*, *Echinophyllia*, *Lobophyllia*, *Echinopora*, other Merulinidae, *Symphylia*, *Caryophyllidae*, *Turbinaria*, other hard corals.

2.4. Niche breadth

Niche breadth was calculated as a proportional similarity index and weighted by substratum availability as proposed by Hurlbert (1978). Hurlbert's niche breadth was calculated as:

$$B' = \frac{1}{\sum \left(\frac{p_j^2}{a_j} \right)} \quad (1)$$

where B' is the Hurlbert's niche breadth index of a species, p_j is the mean proportion of individuals of this species found using substratum (resource) j ($\sum p_j = 1.0$), and a_j is the mean proportion of the total available substrata consisting of substratum j ($\sum a_j = 1.0$), at the 14 reefs surveyed. In order to compare the niche breadths of species more comprehensively, B' was standardised to a scale of 0 to 1 using the equation:

$$B'_A = \frac{B' - a_{min}}{1 - a_{min}} \quad (2)$$

where B'_A is Hurlbert's standardised niche breadth, B' is Hurlbert's niche breadth, and a_{min} is the smallest observed proportion of all the substrata (min. a_j).

2.5. Substratum selectivity

Substratum (resource) selection ratios were calculated for each species. A measure of selectivity (Manly et al. 2002) was calculated for each substratum type using the equation:

$$w_i = \frac{o_i}{\pi_i} \quad (3)$$

where w_i is the substratum selection probability function for substratum i , o_i is the mean proportion of frequency at which substratum i was occupied, and π_i is the mean proportion of frequency at which substratum i occurred at the 14 reefs surveyed. Bonferroni Z-corrected 95 % confidence intervals (CIs) were calculated using the equation:

$$CI = Z_{\frac{a}{2k}} \sqrt{\left[o_i \frac{(1 - o_i)}{(U_+ \pi_i^2)} \right]} \quad (4)$$

where $Z_{a/2k}$ is the critical value of the standard normal distribution corresponding to the upper tail area of $a/2k$ ($a = 0.05$, $k =$ number of substratum types used), and U_+ is the total number of substratum types used by a species. *Eviota* species were considered to be using a specific substratum type significantly more often than expected if selectivity indices and associated 95 % CIs were >1 . Selection indices ($\pm 95\%$ CI) <1 showed significantly negative substratum selection, and indices encompassing the value of 1 indicated that substratum selection was in proportion to the relative frequency of occurrence of the substratum type.

2.6. Habitat overlap

A measure of percentage niche similarity was used to calculate the habitat overlap between pairs of *Eviota* species on coarse-scale and fine-scale (hard corals) substratum categories. This was calculated as a percentage habitat overlap (Schoener 1970) using the equation:

$$P_{jk} = \left[\sum_{i=1}^n (\text{minimum } p_{ij}, p_{ik}) \right] 100 \quad (5)$$

where P_{jk} is the percentage habitat overlap between species j and species k , n is the total number of substrata, p_{ij} is the proportion that substratum i comprises of all substrata used by species j , and p_{ik} is the proportion that substratum i comprises of all substrata used by species k (Krebs 1999). This method is not sensitive to how substrata are divided up into categories (Abrams 1980). Indices of niche breadth, substratum selectivity and habitat overlap were all calculated using Microsoft Excel (v. 2019).

2.7. Specialisation and abundance relationship

To test whether the local abundance of *Eviota* species is correlated to the degree of habitat specialisa-

tion, a linear regression analysis was conducted between abundance and both the niche breadth and the number of coral species occupied ($\alpha = 0.05$). The relative abundance of each species was log-transformed to meet the assumption of normality of the error distribution. RStudio version 1.2.5033 (RStudio Team 2020) and R version 4.0.3 (R Core Team 2020) were used to conduct this analysis and create all figures.

3. RESULTS

3.1. Niche breadth

Most species exhibited a narrow niche breadth, although there was substantial variation among species (Table 1). Among the 9 species used to calculate niche breadth, substratum selectivity and habitat overlap, the least coral-associated species, *Eviota atriventris*, was observed in the highest number of substratum types (21) and showed the widest niche breadth of all species (Table 1). *E. rubrisparsa*, *E. smaragdus* and *E. prasites* were observed on 13, 7, and 7 substratum types, respectively, and had relatively wide niche breadths (Table 1). In contrast, *E. bifasciata*, *E. cf. dorsogilva* and *E. brahmi* were the most habitat-specialised species, found on 6, 3 and 2 substratum types, respectively, and exhibiting the narrowest niche breadths (Table 1).

3.2. Coarse-scale substratum selectivity

Species of *Eviota* varied greatly in their patterns of coarse-scale substratum selectivity. Four species were found exclusively on scleractinian corals, and 4 species occupied hard coral substrata with a frequency of 67% or greater (Table 2a). These 8 species were never observed on soft corals, sponges or sand patches and were absent or $\leq 10\%$ in relative abundance on macroalgal substrata (Fig. 2, Table 2a). Live hard coral cover made up approximately 40% of the substrata in the study area (Fig. 3a). The substratum occupancy of these 8 species of *Eviota* was therefore not distributed in proportion to substratum availability (Table 2a). While these 8 species used hard coral substrata significantly more than expected, *E. atriventris* displayed hard coral selection in proportion to its availability (Table 2a). Additionally, *E. atriventris* occupied sponges, macroalgae and sand patches in significantly lower proportions than the availability of these substrata (Table 2a). *E. atriventris* was found

to favour rubble habitats, with 46% of individuals found on rubble patches (Table 2a). Preferential utilisation of rubble substrata was also observed in *E. smaragdus* and *E. prasites*. By contrast, *E. seebrei* occupied rubble substrata significantly less than expected (Table 2a). *E. rubrisparsa* and *E. prasites* used macroalgal substrata less than expected.

3.3. Fine-scale substratum selectivity

Although most study species were most frequently observed on scleractinian substratum types, there was a high inter-species variability in selectivity for different hard coral substrata (Table 2b, Fig. 3b). *E. atriventris* was observed on 33 different species of hard coral and showed the least preferential selection of particular coral growth forms or taxa (Table 2b). Specifically, this species favoured the coral genera *Anacropora*, *Acropora*, *Porites* (encrusting), *Pachyseris*, *Fungia*, *Favia*, *Diploastrea*, *Oxypora*, *Echinophyllia*, *Symphyllia* and *Turbinaria* (Table 2b). *E. prasites* and *E. melasma* were found on a much smaller number of coral taxa, and showed strong association with encrusting taxa of the genera *Diploastrea* (Favidae), *Montipora* and *Porites* (Table 2b). *E. rubrisparsa* was observed on a wide range of different coral substrata (Table 2b), though most commonly on massive *Porites* spp. (Fig. 2). *E. smaragdus* and *E. seebrei* were most frequently observed on massive *Porites* coral and some of the same encrusting coral taxa as *E. rubrisparsa* (Table 2b). *E. cf. dorsogilva*, *E. brahmi* and *E. bifasciata*, all of which were found on a small range of hard coral substrata, strongly favoured plate, bottlebrush and corymbose growth forms of *Acropora* (Table 2b, Fig. 4). *E. bifasciata* also used a range of encrusting and massive coral taxa (Fig. 4). In contrast, *E. cf. dorsogilva* and *E. brahmi* displayed strong substratum selectivity at a fine scale, as they were almost exclusively found on few species of plate (*A. caroliniana*, *A. jacquelineae* and *A. paniculata*) and bottlebrush (*A. echinata*, *A. subglabra* and *A. longicyathus*) *Acropora* coral (Fig. 4).

3.4. Habitat overlap

Given the generally high degree of association with hard corals, pairwise overlap between most *Eviota* species was high for the coarse-scale classification of available substrata (Table 3a). Coarse-scale habitat overlap was higher than 53% between all species with the exception of pairs including the rub-

Table 2. Relative occupancy of (a) coarse-scale substratum categories and (b) fine-scale substratum categories (hard coral substrata) by species of *Eviota*. Values are percentage of fish observed on each substratum type. Significance of the association is shown by cell colours using resource selection ratios and Bonferroni Z-corrected 95 % confidence intervals; red: substratum used significantly more than expected; blue: substratum used significantly less than expected; green: substratum used in proportion to availability; grey: substratum not used (Manly et al. 2002)

	<i>E. atriventris</i>	<i>E. bifasciata</i>	<i>E. cf. dorsogilva</i>	<i>E. brahmi</i>	<i>E. rubrisparsa</i>	<i>E. melasma</i>	<i>E. smaragdus</i>	<i>E. prasites</i>	<i>E. seebrei</i>
(a)									
Hard corals	36	100	100	100	88	100	67	67	99
Soft corals	0	0	0	0	0	0	0	0	0
Sponges	<1	0	0	0	0	0	0	0	0
Macroalgae	16	0	0	0	3	0	0	10	0
Rubble	46	0	0	0	9	0	33	23	1
Sand	<1	0	0	0	0	0	0	0	0
Other substrata	0	0	0	0	0	0	0	0	0
(b)									
<i>Anacropora</i>	2	0	0	0	0	0	0	0	0
<i>Acropora</i> (corymbose)	1	8	<1	0	<1	0	0	0	0
<i>Acropora</i> (plate)	1	8	78	56	<1	0	0	0	0
<i>Acropora</i> (bottlebrush)	<1	53	22	44	<1	0	0	3	0
<i>Acropora</i> (staghorn)	0	0	0	0	0	0	0	0	0
<i>Acropora</i> (other)	0	0	0	0	0	0	0	0	0
<i>Isopora</i>	0	0	0	0	0	0	0	0	0
<i>Montipora</i>	6	20	0	0	17	41	10	34	12
Pocilloporidae	0	0	0	0	0	0	0	0	0
<i>Porites</i> (massive)	7	8	0	0	45	5	40	1	68
<i>Porites</i> (encrusting)	9	0	0	0	10	29	10	25	8
Other Poritidae	0	0	0	0	0	0	0	0	0
Siderastreidae	0	0	0	0	0	0	0	0	0
<i>Pavona</i>	2	0	0	0	3	0	0	0	0
<i>Pachyseris</i>	1	0	0	0	<1	0	0	0	0
Other Agariciidae	0	0	0	0	0	0	0	0	0
<i>Fungia</i>	1	0	0	0	0	0	1	0	0
<i>Galaxea</i>	<1	0	0	0	0	0	0	0	0
<i>Favia</i>	1	0	0	0	1	0	4	0	0
<i>Diploastrea</i>	1	3	0	0	10	25	2	4	6
Other Faviidae	0	0	0	0	0	0	0	0	0
<i>Oxypora</i>	<1	0	0	0	0	0	0	0	0
<i>Echinophyllia</i>	<1	0	0	0	0	0	0	0	0
<i>Lobophyllia</i>	0	0	0	0	0	0	0	0	2
<i>Echinopora</i>	0	0	0	0	0	0	0	0	0
Other Merulinidae	0	0	0	0	0	0	0	0	0
<i>Symphyllia</i>	<1	0	0	0	<1	0	0	0	0
Caryophyllidae	0	0	0	0	0	0	0	0	0
<i>Turbinaria</i>	<1	0	0	0	0	0	0	0	2
Other hard corals	0	0	0	0	0	0	0	0	0

ble-dwelling species *E. atriventris* (Table 3a). The hypothesis that *Eviota* species would exhibit a low level of habitat overlap was supported by the finer subdivision of hard coral substrata (Table 3b). With a few exceptions, percentage overlaps were <20%. Low overlap was often observed between *Eviota* species with relatively narrow and wide niche breadths (e.g. 0.3% between *E. brahmi* and *E. rubrisparsa*). In some cases, the habitats of obligate coral-dwellers did not overlap; the *Acropora* specialists *E. cf. dorsogilva* and *E. brahmi* inhabited completely different

coral species than *E. melasma*, *E. smaragdus* and *E. seebrei* (Table 3b). The highest habitat overlaps were revealed between relatively habitat-specialised species of *Eviota*, which used similar substrata, e.g. species that frequently occurred on massive *Porites* corals (*E. seebrei*, *E. smaragdus* and *E. rubrisparsa*). The 2 specialist species *E. cf. dorsogilva* and *E. brahmi* exhibited the highest fine-scale habitat overlap (>53%), almost exclusively living on a limited selection of plate and bottlebrush *Acropora* species (Table 3b). Both species frequently occupied the

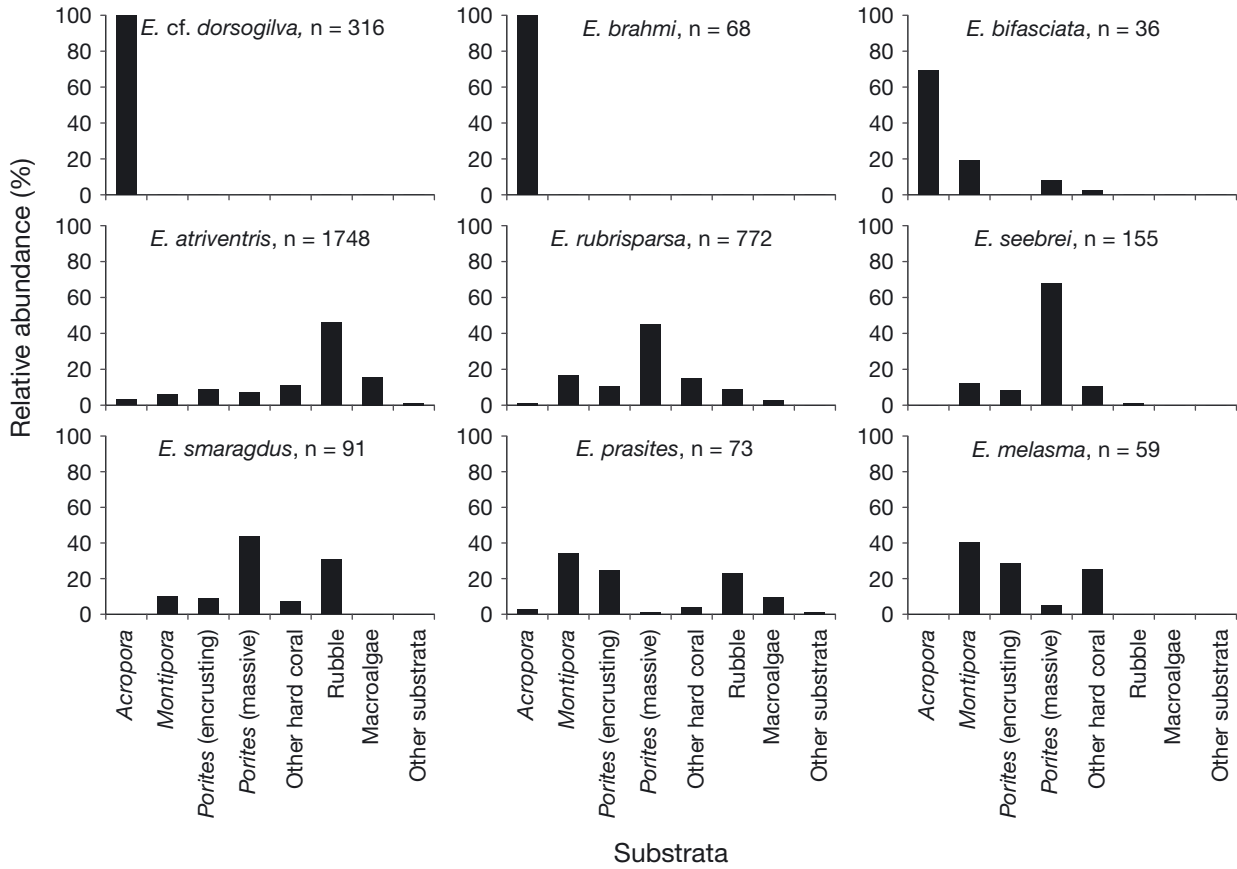


Fig. 2. Relative abundance of 9 common *Eviota* species on key coral and non-coral substrata (i.e. a selection of the defined coarse-scale and fine-scale substratum categories) in Kimbe Bay, Papua New Guinea. n: number of individuals recorded per species

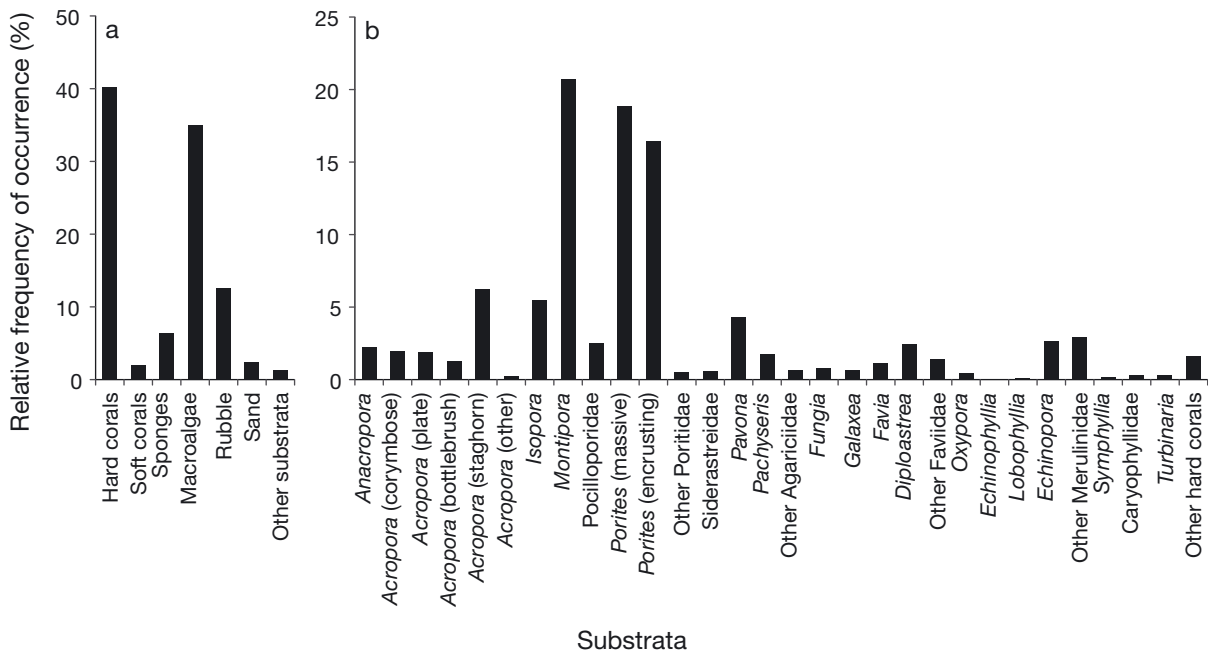


Fig. 3. Relative frequency of occurrence of observed (a) coarse-scale substratum categories and (b) fine-scale substratum categories (hard coral substrata)

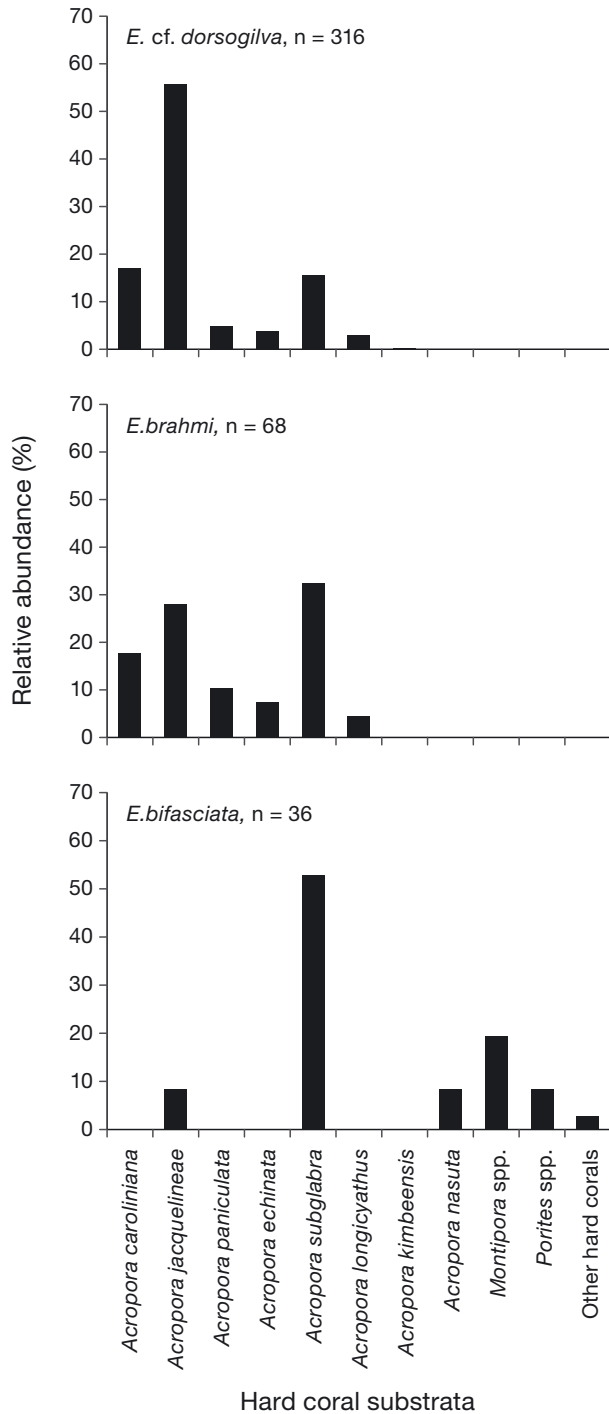


Fig. 4. Relative abundance of 3 obligate coral-associated species of *Eviota* on a selection of hard coral substrata (n = number of individuals recorded per species)

same *Acropora* coral colonies, with *E. brahmi* usually hovering at substantial height above the colony, whereas individuals of *E. cf. dorsogilva* used the space within or directly on the surface of the coral colony.

3.5. Relationship between specialisation and abundance

We found no significant relationship between abundance of *Eviota* species and niche breadth (Fig. 5a, $R^2 = 0.18$, $F_{1,7} = 2.74$, $p = 0.14$), but abundance increased with the number of coral species occupied (Fig. 5b, $R^2 = 0.73$, $F_{1,7} = 22.28$, $p = 0.002$). The 2 most common species, *E. atriventris* and *E. rubrisparsa*, occupied the largest number of coral species. In contrast, all species of *Eviota* with relatively low abundance were found in a small number of coral species.

4. DISCUSSION

We found varying levels of habitat specialisation and overlap within this understudied but ecologically important genus of cryptobenthic reef fishes. The results of this study generally support our hypotheses that *Eviota* species would exhibit a high association with scleractinian corals, narrow niche breadths, high levels of substratum selectivity and low habitat overlaps. There was also support for the hypothesis that more specialised species exhibit lower abundance, suggesting that these species are at particular risk in degrading reef environments. Collectively, these findings may have important implications for the potential influence of declining coral abundance and diversity on these cryptobenthic fish species. Most coral-associated species of *Eviota*, particularly the *Acropora* coral specialists, will likely be increasingly threatened by anthropogenic changes to reefs due to their apparent reliance on these substrata.

Based on their niche breadth and patterns of substratum selectivity, we found some *Eviota* species to be closer to the habitat generalist end of the scale while others appear to be true habitat specialists. This diversity in habitat specialisation within a guild of reef fish is consistent with previous studies in Kimbe Bay, Papua New Guinea, on the genus *Gobiodon* (Munday 2000), triggerfishes (Bean et al. 2002), damselfish recruits (Bonin 2012) and wrasses (Berkström et al. 2012). Previous studies on *Eviota* concluded that the majority of species inhabiting live corals typically occur on many different species of hard coral as well as coral rock (Herler 2007, Tornabene et al. 2013). This suggests that many species of *Eviota* are attracted by a range of 3-dimensional structures of variable complexity (Dirnwöber & Herler 2007, Herler 2007, Tornabene et al. 2013). Our study extends this previous work, showing that the apparent selection for hard coral is very high, with all

Table 3. Habitat overlap using the percentage overlap method (Schoener 1970) on (a) coarse-scale (hard corals, soft corals, sponges, macroalgae, rubble, sand, other substrata) and (b) fine-scale substratum categories (the 30 hard coral substrata in addition to all coarse-scale substratum categories except hard corals)

	<i>E. bifasciata</i>	<i>E. cf. dorsogilva</i>	<i>E. brahmi</i>	<i>E. rubrisparsa</i>	<i>E. melasma</i>	<i>E. smaragdus</i>	<i>E. prasites</i>	<i>E. seebrei</i>
(a)								
<i>E. atriventris</i>	36.7	36.7	36.7	88.0	36.7	39.6	36.9	36.8
<i>E. bifasciata</i>		100	100	88.1	100	69.2	67.1	98.7
<i>E. cf. dorsogilva</i>			100	88.1	100	69.2	67.1	98.7
<i>E. brahmi</i>				88.1	100	69.2	67.1	98.7
<i>E. rubrisparsa</i>					88.1	63.8	61.5	87.1
<i>E. melasma</i>						69.2	67.1	98.7
<i>E. smaragdus</i>							53.6	68.7
<i>E. prasites</i>								66.6
(b)								
<i>E. atriventris</i>	2.5	1.2	1.1	10.2	5.9	18.9	16.8	7.2
<i>E. bifasciata</i>		18.2	27.9	0.2	9.0	5.6	8.3	8.2
<i>E. cf. dorsogilva</i>			53.1	0.4	0.0	0.0	0.6	0.0
<i>E. brahmi</i>				0.3	0.0	0.0	1.2	0.0
<i>E. rubrisparsa</i>					14.5	25.3	11.6	32.0
<i>E. melasma</i>						9.3	22.1	7.5
<i>E. smaragdus</i>							13.4	32.3
<i>E. prasites</i>								7.8

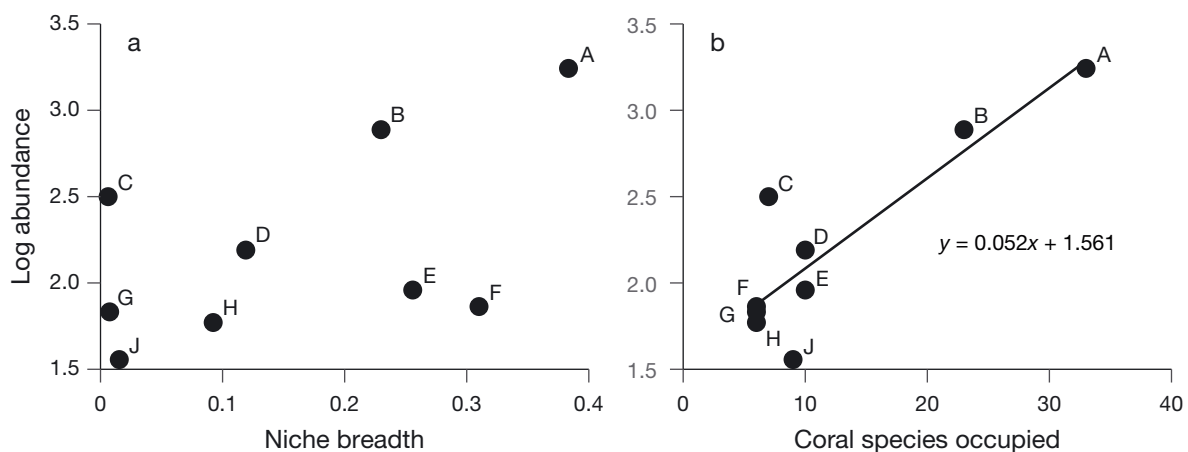


Fig. 5. Relationship between habitat specialisation and the abundance of 9 common species of *Eviota* in Kimbe Bay, Papua New Guinea (A = *E. atriventris*; B = *E. rubrisparsa*; C = *E. cf. dorsogilva*; D = *E. seebrei*; E = *E. smaragdus*; F = *E. prasites*; G = *E. brahmi*; H = *E. melasma*; J = *E. bifasciata*). Habitat specialisation is defined as (a) Hurlbert's standardised niche breadth (Hurlbert 1978) and (b) the number of coral species occupied by each *Eviota* species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m677p081_supp.pdf)

but one locally common *Eviota* species found to primarily live in hard coral substrata. Due to its preferential selection of rubble substrata but wide range of substratum types occupied, *E. atriventris* can be categorised as a rubble-dwelling, relatively habitat-generalised species. Other rubble-dwelling generalists such as *E. queenslandica*, *E. lachdeberae* or *E. spilota* have been the focus of past studies, and their selection of rubble and various other habitat types defined by sand and coral rock has been documented (Depczynski & Bellwood 2003, Bellwood et al. 2006, Hernaman & Probert 2008, Ahmadi et al. 2012,

Tornabene et al. 2013, Brandl et al. 2018). These species of *Eviota* manage to exploit rubble and rubble-sand patches due to their extremely small body size (Tornabene et al. 2013). The exploitation of non-coral environments by *Eviota* species, including *E. atriventris*, provides a potential ecological opportunity, while some other gobiid genera (e.g. *Gobiodon*) are unable to capitalise on the smaller-scale complexity of these alternative environments (Tornabene et al. 2013).

Several species of *Eviota* preferentially select particular hard coral morphologies and species. While *E.*

cf. *dorsogilva*, *E. brahmi* and *E. bifasciata* were strongly associated with particular morphologies of *Acropora* corals, other *Eviota* species selected for a range of massive and encrusting species of the genera *Montipora*, *Porites* and *Diploastrea*. Due to their strong preference of massive *Porites* corals, some rubble-dwelling species cannot be considered extreme habitat generalists. *E. rubrisparsa*, *E. smaragdus* and in particular *E. seebrei* were all found to primarily dwell on massive *Porites* spp., corroborating observations made by Herler (2007). The species with the most distinct coral substratum preferences were *E. cf. dorsogilva*, *E. brahmi* and *E. bifasciata*. High levels of fine-scale habitat specialisation have previously been recorded in genera of obligate branching *Acropora* dwellers such as *Gobiodon* and *Paragobiodon* (Kuwamura et al. 1994, Munday et al. 1997, Herler 2007, Wong 2011). Similar to other specialised groups of coral gobies, the habitat selection of these *Acropora*-specialised *Eviota* species may be linked to the high amount of shelter and refuge spaces offered by branching coral morphologies due to their structural complexity (Richardson et al. 2017). The additional utilisation of other encrusting and massive corals by *E. bifasciata*, however, is possibly driven by interspecific competition with *E. cf. dorsogilva* and *E. brahmi* over preferred *Acropora* colonies (Munday 2001, Munday et al. 2001). Recruits of coral-associated damselfish species have also been observed in the same plate and bottlebrush *Acropora* species (Bonin 2012). While species are generally assumed to select habitats that maximise their survival and reproductive fitness, the proportional use of different habitat types is frequently affected by processes such as competition and density-dependent selection (Rosenzweig 1991, Munday et al. 2001). Competition for shelter in combination with the relatively limited availability of appropriately sized plate and bottlebrush *Acropora* colonies may thus explain the low degree of utilisation of these corals by other species of *Eviota* in Kimbe Bay.

As a result of species-specific associations with different substrata, levels of habitat overlap were generally low among pairs of *Eviota* species, with few exceptions. This generally high level of fine-scale habitat partitioning follows competition theory (Hardin 1960, MacArthur & Levins 1967). However, it is unclear whether low habitat overlap among pairs of *Eviota* species is directly governed by competition for space (i.e. shelter) or indirectly driven by partitioning of other resources (e.g. food). Munday et al. (2001) demonstrated that diverse roles of competition can be expected to regulate habitat overlap in complex

cryptobenthic reef-fish communities. Although likely dependent on species' levels of dietary (Pratchett et al. 2006) and early life-history (Jones et al. 2004) specialisation, the high habitat partitioning among most *Eviota* species may buffer the overall assemblage from the loss of specific habitat types. Conversely, high habitat overlap between the 2 most habitat-specialised species, *E. cf. dorsogilva* and *E. brahmi*, may translate to local extinction of these coral specialists (Munday 2004, Graham et al. 2006) and an increased proportion of habitat generalists within the assemblage following disturbance (Bellwood et al. 2006). Here, *E. cf. dorsogilva* and *E. brahmi* occupy the same few species of plate and bottlebrush *Acropora* coral, frequently hovering together over the same coral colonies. This finding contrasts with recent observations of habitat specialised species of the *E. nigriventris* species complex in Milne Bay, Papua New Guinea (Greenfield & Randall 2011), where groups of *E. brahmi* and *E. dorsopurpurea* live in close proximity, but segregated between different coral species (Greenfield & Randall 2011). A combination of assortative mating and habitat partitioning may be driving and maintaining these clear species boundaries (Greenfield & Randall 2011, Tornabene et al. 2015). In the case of *E. cf. dorsogilva* and *E. brahmi*, we hypothesise that their specialised niches are partitioned on a scale even finer than individual coral species, with the space occupied by each species separated in height above the coral colony surface. This hypothesis may be tested using video observations and removal experiments.

Our findings support previous studies showing that highly habitat-specialised species appear to be less abundant than their more generalist counterparts (Munday 2000, Bean et al. 2002, Gardiner & Jones 2005). The relationship among species' abundances and their degree of resource specialisation is commonly used to assess the vulnerability of species in conservation biology (Brown 1984, Gaston et al. 1997). Here, 2 locally abundant *Eviota* species (*E. atriventris* and *E. rubrisparsa*), which occupied the highest numbers of coral species in addition to non-coral substrata, are predicted to be at least risk of population decline due to disturbance. In contrast, highly specialised species that are locally scarce may be subject to the combination of risk factors associated with small population size and habitat loss (Jones et al. 2002, Munday 2004). Thus, locally scarce *Eviota* species occupying only a few coral species could face a 'double jeopardy' of local extinction in cases where the habitat types they preferentially select are reduced (Gaston 1998, Munday 2004).

Altogether, the findings of this study have implications for predicting the potential consequences of ongoing habitat loss and degradation on coral reefs. Previous studies have supported the hypothesis that habitat specialised gobies (Munday 2004) and other reef fishes (Wilson et al. 2008) are at greater risk of population decline due to disturbance than generalists. This may translate to communities dominated by generalist taxa, which do not rely on specific coral substrata at any stage in their life history (Wilson et al. 2008). Rubble-dwelling species such as *E. atriventris* are not expected to decline in response to coral loss and could even benefit from it, as observed in some generalist coral-reef fishes (Bellwood et al. 2006, Feary et al. 2007). However, the hard-coral associations observed in most of the other study species suggest that many *Eviota* species may be negatively affected by the global decline in coral cover. Similar levels of reliance on hard corals have been linked with declines of other cryptobenthic reef-fish taxa in response to habitat change and loss (Munday 2004, Ahmadi et al. 2012). Reef fish taxa that depend on live coral habitat throughout their adult life (Munday 2004) or during other critical life-history stages (Jones et al. 2004) will likely be negatively impacted by coral loss. Loss of coral cover has been recorded in Kimbe Bay (Jones et al. 2004, Munday 2004, Feary et al. 2007, Bonin et al. 2011). Although the generally low level of habitat overlap may buffer this assemblage from the effects of losing specific habitat types, most coral-associated *Eviota* species could potentially be threatened, especially those that depend on corals susceptible to disturbance, such as *Acropora* corals with complex branching morphologies (Loya et al. 2001). Similar to other coral reef gobies in the past (Munday 2004), populations of *E. cf. dorsogilva* and *E. brahmi* are therefore likely to decline, and could even be locally extirpated in response to coral loss.

Acknowledgements. We are grateful to the traditional owners of the Tamare-Kilu reefs for access to their reefs. Special thanks to the Mahonia Na Dari Research and Conservation Centre and the Walindi Plantation Resort for significant logistical support; Nelson Sikatua and Amy Coppock for assistance in the field; Kai Pacey for statistical advice; and G. Polgar and 2 anonymous reviewers whose comments and edits greatly improved this manuscript. This project was carried out under James Cook University animal ethics approval number A2533, and funding was provided by a research allocation to G.P.J. from the Australian Research Council Centre of Excellence for Coral Reef Studies.

LITERATURE CITED

- Abrams P (1980) Some comments on measuring niche overlap. *Ecology* 61:44–49
- Ahmadi GN, Pezold FL, Smith DJ (2012) Cryptobenthic fish biodiversity and microhabitat use in healthy and degraded coral reefs in SE Sulawesi, Indonesia. *Mar Biodivers* 42:433–442
- Bean K, Jones GP, Caley MJ (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). *Mar Ecol Prog Ser* 233:263–272
- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Mar Ecol Prog Ser* 15:265–274
- Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Glob Change Biol* 12: 1587–1594
- Berkström C, Jones GP, McCormick MI, Srinivasan M (2012) Ecological versatility and its importance for the distribution and abundance of coral reef wrasses. *Mar Ecol Prog Ser* 461:151–163
- Bonin MC (2012) Specializing on vulnerable habitat: *Acropora* selectivity among damselfish recruits and the risk of bleaching-induced habitat loss. *Coral Reefs* 31:287–297
- Bonin MC, Munday PL, McCormick MI, Srinivasan M, Jones GP (2009) Coral-dwelling fishes resistant to bleaching but not to mortality of host corals. *Mar Ecol Prog Ser* 394: 215–222
- Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* 92:1503–1512
- Bos AR, Hoeksema BW (2015) Cryptobenthic fishes and co-inhabiting shrimps associated with the mushroom coral *Heliofungia actiniformis* (Fungiidae) in the Davao Gulf, Philippines. *Environ Biol Fishes* 98:1479–1489
- Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien M (1985) Impact of coral degradation on the chaetodontid fish assemblage (Moorea, French Polynesia). *Proc 5th Int Coral Reef Symp* 5:427–432
- Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol Rev Camb Philos Soc* 93: 1846–1873
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. *Glob Change Biol* 23:1511–1524
- Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. *Rev Fish Biol Fish* 24:89–126
- Colles A, Hsiang Liow L, Prinzing A (2009) Are specialists at risk under environmental change? Neocological, paleoecological and phylogenetic approaches. *Ecol Lett* 12: 849–863
- Colwell RK, Fuentes ER (1975) Experimental studies of the niche. *Annu Rev Ecol Syst* 6:281–310
- D'Aloia CC, Majoris JE, Buston PM (2011) Predictors of the distribution and abundance of a tube sponge and its resident goby. *Coral Reefs* 30:777–786
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Mar Ecol Prog Ser* 256:183–191
- Depczynski M, Bellwood DR (2004) Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Mar Biol* 145:455–463
- Devictor V, Clavel J, Julliard R, Lavergne S and others (2010) Defining and measuring ecological specialization. *J Appl Ecol* 47:15–25

- Diamond JM (1978) Niche shifts and the rediscovery of interspecific competition. *Am Sci* 66:322–331
- ✦ Dirnwöber M, Herler J (2007) Microhabitat specialisation and ecological consequences for coral gobies of the genus *Gobiodon* in the Gulf of Aqaba, northern Red Sea. *Mar Ecol Prog Ser* 342:265–275
- ✦ Feary DA, Almany GR, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153:727–737
- ✦ Fisher DO, Bloomberg SP, Owens IPF (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc R Soc B* 270:1801–1808
- ✦ Futuyma DJ, Moreno G (1988) The evolution of ecological specialisation. *Annu Rev Ecol Syst* 19:207–233
- ✦ Gardiner NM, Jones GP (2005) Habitat specialisation and overlap in a guild of coral reef cardinalfishes (Apogonidae). *Mar Ecol Prog Ser* 305:163–175
- ✦ Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- ✦ Gaston KJ (1998) Rarity as double jeopardy. *Nature* 394:229–230
- ✦ Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *J Anim Ecol* 66:579–601
- Giltay L (1933) Résultats scientifiques du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mém Mus R His Nat Belg* 5:1–129
- ✦ Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci USA* 103:8425–8429
- Greenfield DW, Randall JE (2010) Four new gobiid fishes of the genus *Eviota* from the western Pacific, with clarification of *Eviota guttata* and *Eviota albolineata* (Teleostei: Gobiidae). *Proc Calif Acad Sci* 61:269–289
- ✦ Greenfield DW, Randall JE (2011) Two new Indo-Pacific species in the *Eviota nigriventris* complex (Teleostei: Gobiidae). *Zootaxa* 2997:54–66
- ✦ Greenfield DW, Suzuki T (2012) *Eviota atriventris*, a new goby previously misidentified as *Eviota pellucida* Larson (Teleostei: Gobiidae). *Zootaxa* 3197:55–62
- ✦ Greenfield DW, Tornabene L (2014) *Eviota brahmi* n. sp. from Papua New Guinea, with a redescription of *E. nigriventris* (Teleostei: Gobiidae). *Zootaxa* 3793:133–146
- Greenfield DW, Winterbottom R (2016) A key to the dwarf-goby species (Teleostei: Gobiidae: *Eviota*) described between 1871 and 2016. *J Ocean Sci Found* 24:35–90
- ✦ Hardin G (1960) The competitive exclusion principle. *Science* 131:1292–1297
- ✦ Herler J (2007) Microhabitats and ecomorphology of coral- and coral rock-associated gobiid fish (Teleostei: Gobiidae) in the northern Red Sea. *Mar Ecol* 28:82–94
- ✦ Herler J, Koblmüller S, Sturmbauer C (2009) Phylogenetic relationships of coral-associated gobies (Teleostei, Gobiidae) from the Red Sea based on mitochondrial DNA data. *Mar Biol* 156:725–739
- ✦ Hernaman V, Probert PK (2008) Spatial and temporal patterns of abundance of coral reef gobies (Teleostei: Gobiidae). *J Fish Biol* 72:1589–1606
- ✦ Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. *Nature* 556:492–496
- ✦ Hurlbert SH (1978) The measurement of niche overlap and some relatives. *Ecology* 59:67–77
- Jones GP, Caley MJ, Munday PL (2002) Rarity in coral reef fish communities. In: Sale PF (ed) *Coral reef fishes. Dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, CA, p 81–101
- ✦ Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Jordan DS, Seale A (1906) The fishes of Samoa: description of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. *Fish Bull* 25:173–455
- Karnella SJ, Lachner EA (1981) Three new species of the *Eviota epiphanes* group having vertical trunk bars (Pisces: Gobiidae). *Proc Biol Soc Wash* 94:264–275
- ✦ Kassen R (2002) The experimental evolution of specialists, generalists and the maintenance of diversity. *J Evol Biol* 15:173–190
- Krebs CJ (1999) *Ecological methodology*. Benjamin/Cummings, Menlo Park, CA
- ✦ Kuwamura T, Yogo Y, Nakashima Y (1994) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*. *Mar Ecol Prog Ser* 103:17–23
- Lachner EA, Karnella SJ (1980) Fishes of the Indo-Pacific genus *Eviota* with descriptions of eight new species (Teleostei: Gobiidae). *Smithson Contrib Zool* 315:1–127
- ✦ Lawton JH (1999) Are there general laws in ecology? *Oikos* 84:177–192
- ✦ Loya Y, Sakia K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122–131
- ✦ MacArthur RH, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am Nat* 101:377–385
- ✦ MacDonald C, Bridge TCL, Jones GP (2016) Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge? *Mar Ecol Prog Ser* 561:217–231
- MacNally RC (1995) *Ecological versatility and community ecology*. Cambridge University Press, Cambridge
- ✦ Majoris JE, D'Aloia CC, Francis RK, Buston PM (2018) Differential persistence favors habitat preference that determine the distribution of a reef fish. *Behav Ecol* 29:429–439
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) *Resource selection by animals: statistical design and analysis for field studies*. Kluwer, Dordrecht
- ✦ Morris DW (1996) Coexistence of specialist and generalist rodents via habitat selection. *Ecology* 77:2352–2364
- ✦ Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the genus *Gobiodon*. *Environ Biol Fishes* 58:355–369
- ✦ Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* 128:585–593
- ✦ Munday PL (2002) Does habitat availability determine geographical scale abundances of coral-dwelling fishes? *Coral Reefs* 21:105–116
- ✦ Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Glob Change Biol* 10:1642–1647
- ✦ Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Mar Ecol Prog Ser* 152:227–239
- ✦ Munday PL, Jones GP, Caley MJ (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology* 82:2177–2189

- Munday PL, van Herwerden I, Dudgeon CI (2004) Evidence for sympatric speciation by host shift in the sea. *Curr Biol* 14:1498–1504
- Pereira PHC (2017) Benthic composition influences habitat use and toxicity of coral-dwelling fishes. *Mar Biol* 164: 1–9
- Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of *Chaetodon* butterflyfishes following extensive coral depletion. *J Fish Biol* 69:1269–1280
- Pratchett MS, Coker DJ, Jones GP, Munday PL (2012) Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. *Ecol Evol* 2:2168–2180
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Richardson LE, Graham NAJ, Pratchett MS, Hoey AS (2017) Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environ Biol Fishes* 100:193–207
- Rosenzweig ML (1991) Habitat selection and population interactions: the search for mechanisms. *Am Nat* 137: S5–S28
- RStudio Team (2020) RStudio: integrated development for R. RStudio, PBC, Boston, MA
- Saito VS, Laroche F, Siqueira T, Pavoine S (2018) Ecological versatility and the assembly of multiple competitors: cautionary notes for assembly inferences. *Ecology* 99: 1173–1183
- Schiemer L, Niedermüller S, Herler J (2009) The influence of colony size and coral health on the occupation of coral-associated gobies (Pisces: Gobiidae). *Coral Reefs* 28: 137–142
- Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418
- Sheppard C, Sheppard A, Fenner D (2020) Coral mass mortalities in the Chagos Archipelago over 40 years: regional species and assemblage extinctions and indications of positive feedbacks. *Mar Pollut Bull* 154:111075
- Slatyer RA, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecol Lett* 16:1104–1114
- Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81: 2714–2729
- Syms C, Jones GP (2004) Habitat structure, disturbance and the composition of sand-dwelling goby assemblages in a coral reef lagoon. *Mar Ecol Prog Ser* 268:221–230
- Tornabene L, Ahmadi GN, Berumen ML, Smith DJ, Jompa J, Pezold F (2013) Evolution of microhabitat association and morphology in a diverse group of cryptobenthic coral reef fishes (Teleostei: Gobiidae: *Eviota*). *Mol Phylogenet Evol* 66:391–400
- Tornabene L, Valdez S, Erdmann M, Pezold F (2015) Support for a ‘Center of origin’ in the coral triangle: cryptic diversity, recent speciation, and local endemism in a diverse lineage of reef fishes (Gobiidae: *Eviota*). *Mol Phylogenet Evol* 82:200–210
- Vázquez DP, Simberloff D (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am Nat* 159:606–623
- Veron JEN (2000) Corals of the world, Vol 1–3. Australian Institute of Marine Science, Townsville
- Wallace CC (1999) Staghorn corals of the world. A revision of the genus *Acropora*. CSIRO Publishing, Collingwood
- Warren MS, Hill JK, Thomas JA, Asher J and others (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65–69
- Wilson SK, Burgess SC, Cheal AJ, Emslie M and others (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *J Anim Ecol* 77:220–228
- Wilson SK, Robinson JP, Chong-Seng K, Robinson J, Graham NA (2019) Boom and bust of keystone structure on coral reefs. *Coral Reefs* 38:625–635
- Wong MYL (2011) Group size in animal societies: the potential role of social and ecological limitations in the group-living fish, *Paragobiodon xanthosomus*. *Ethology* 117: 638–644

Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA
Reviewed by: G. Polgar and 2 anonymous referees

Submitted: June 4, 2020
Accepted: August 5, 2021
Proofs received from author(s): October 25, 2021