



REPORT

# Broadening our horizons: seascape use by coral reef-associated fishes in Kavieng, Papua New Guinea, is common and diverse

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**Abstract** There is increasing evidence that non-reef habitats in the seascape surrounding coral reefs are widely used by reef-associated fishes. However, our understanding of seascape use in the Indo-Pacific region is incomplete due to its large geographical range and as a consequence, considerable environmental variation (e.g. tidal regimes). We used remote video cameras to survey reef-associated fishes within five habitat types (coral reef slope, coral reef flat, macroalgal beds, mangroves and seagrass meadows) around the Tigak Islands, Kavieng, Papua New Guinea. Of the 282 shallow-water reef-associated species observed

across 360 videos, 35% (99 species) were recorded in non-reef habitats, the majority (78 species) on multiple occasions. We found that macroalgal beds dominated by low-complexity algal genera (e.g. *Halimeda*, *Caulerpa*) were used extensively by reef-associated fishes, complementing previous research that has documented the use of canopy-forming macroalgae (e.g. *Sargassum*). Mean species richness and relative abundances (MaxN) of reef-associated fishes were twofold higher in macroalgal beds than mangroves or seagrass. Interestingly, mangroves contained the most distinct fish assemblage of the three non-reef habitats, including several reef-associated species that were not recorded from any other habitat type. This suggests that mangroves possess attributes not shared by other shallow non-reef, or even reef, habitats. Importantly, many of the fish families commonly found in non-reef habitats (i.e. lethrinids, lutjanids) are targeted by local fishers and are thus critical to sustaining local livelihoods. Our study demonstrates that non-reef habitat use is common for many reef-associated fishes and highlights the need to incorporate a range of habitats into study designs to better understand habitat use patterns in the Indo-Pacific. Given the widespread degradation of coral reefs and other shallow-water habitats, we emphasize the need to recognize that reefs are embedded within a mosaic of habitat types that influence patterns and processes and that management strategies should be scaled appropriately.

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## Introduction

The influence of the wider landscape or seascape on patterns and processes observed within a habitat patch remains a long-standing and important question in ecology (Miller-Rushing et al. 2019). It has been proposed that the close proximity of particular kinds of habitat may have a range of effects on community composition, species diversity and ecosystem function (Fahrig et al. 2011). The effects of habitat adjacency on species diversity may occur directly, for example if a species requires resources that are found in both habitat types (e.g. different breeding and foraging habitats); or indirectly, via exchanges of nutrients and other subsidies between adjacent habitats (Alsterberg et al. 2017). Habitat adjacency and complementarity have long been recognized as important drivers of species abundance and distribution patterns in terrestrial systems (Fahrig et al. 2011), and a similar effect is increasingly evident from shallow-water coastal ecosystems (e.g. Dorenbosch et al. 2006; Pittman et al. 2007; Olds et al. 2012; Berkström et al. 2013; Aller et al. 2014).

Many coral reef fish taxa use multiple habitat types throughout their life cycle (Nagelkerken et al. 2000; Adams et al. 2006; Harborne et al. 2008). An understanding of the use of these habitats and the connections between them is critical to predict and manage the likely impacts of local and global disturbances (Berkström et al. 2012; Pittman and Olds 2015). Although numerous studies have documented the effects of coral loss on coral reef fish communities (e.g. Jones et al. 2004; Pratchett et al. 2011; Richardson et al. 2018), far fewer have considered how disturbances in the wider seascape can influence fish communities, despite many reef systems occurring within a mosaic of highly productive (Birkeland 1985) and extensive (Parrish 1989) non-reef habitat types such as mangroves and seagrass meadows. Much like coral reefs, these shallow-water ecosystems are undergoing rapid systemic change with widespread areal losses and degradation in recent decades (Valiela et al. 2001; Waycott et al. 2009; Hamilton and Casey 2016).

The number of coral reef-associated fish species that have been observed in non-reef habitats is substantial. Globally, at least 670 species of coral reef-associated fishes have been recorded in non-reef habitats in addition to reefs, representing approximately 20% of all coral reef fish species (Sambrook et al. 2019). Reef fishes use the wider seascape for a range of reasons including foraging (Beets et al. 2003; Hitt et al. 2011), spawning (Pittman and McAlpine 2003) and as juvenile habitat before migrating to reefs as subadults or adults (Dahlgren and Eggleston 2000; Nagelkerken et al. 2000, 2001; Adams et al. 2006; Jaxion-Harm et al. 2011). As a result, short- and long-term

movements by reef fishes between different components of the seascape can contribute to ecosystem functioning on reefs through nutrient transfer (Meyer and Schultz 1985; Shantz et al. 2015), trophic subsidies and cascades (Heck et al. 2008; Harborne et al. 2016) and population replenishment (Nakamura et al. 2008; McMahon et al. 2012).

Much of our knowledge about seascape use by reef-associated fishes comes from the Caribbean (Nagelkerken et al. 2000; Aguilar-Perera and Appeldoorn 2008; Dorenbosch et al. 2009). Less is known about how, why and which reef fishes use non-reef habitats in the Indo-Pacific (Sambrook et al. 2019). Our limited understanding in the Indo-Pacific is, in part, complicated because of its large spatial extent and biophysical variability. For instance, unlike the Caribbean where shallow-water habitats are permanently accessible to fishes, tidal regimes in the Indo-Pacific range from micro- to macro-tidal (Krumme 2009), affecting the accessibility of non-reef habitats to reef fishes (Igulu et al. 2014). As a consequence, understanding fish-habitat relationships in the Indo-Pacific requires exploration across a wider range of locations and tidal regimes.

Understanding habitat use patterns of coral reef fishes is also highly relevant when addressing concerns around long-term food security in the Indo-Pacific (Foale et al. 2013; Blasiak et al. 2017). This is because many of the coral reef fishes that are known to use non-reef habitats are common fisheries targets (Sambrook et al. 2019) and the Indo-Pacific is home to a multitude of small island communities (Brodie et al. 2013) that rely on coral reef fisheries to satisfy daily nutritional requirements (Béné et al. 2007) and as a primary source of income (Bell et al. 2009). Many of these coastal communities are experiencing rapid population growth (Burke et al. 2011) which places increasing pressure on already stretched natural resources (Bell et al. 2009). By expanding our understanding of broader seascape use by coral reef fishes, we can identify essential fish habitats, combinations of habitats and/or target species that require better management or protection, which could contribute towards longer-term sustainable fisheries goals.

The objective of this study was to describe and compare reef-associated fish communities across five habitat types that are common in coastal tropical marine seascapes (i.e. coral reef flats, coral reef slopes, mangroves, seagrass meadows and macroalgae beds) in the Indo-Pacific. Specifically, we compared reef fish assemblages associated with the five habitat types, quantified overlap in habitat use and identified the frequency of use of non-reef habitats in Kavieng, Papua New Guinea.

## Methods

### Study site

The study was conducted around the Tigak Island Group within the Kavieng lagoon, New Ireland, Papua New Guinea ( $2^{\circ} 34' S$ ,  $150^{\circ} 48' E$ ; Fig. 1). The Kavieng lagoon is  $\sim 380 \text{ km}^2$  and contains a range of habitats. Extensive reef formations around islands are interspersed with seagrass meadows (predominantly *Enhalus* and *Thalassia* spp.), macroalgae beds (predominantly *Halimeda*, *Caulerpa* spp.) and mangrove forests (*Rhizophora* spp.). The annual water temperature ranges between  $28.7^{\circ} \text{C}$  and  $31.6^{\circ} \text{C}$  (NOAA 2019). Tides are mixed microtidal (Krumme 2009), with a maximum tidal range of 1.09 m. As a consequence, nearshore habitats (e.g. mangroves) are generally submerged, although inundation depths can be shallow ( $\sim 30 \text{ cm}$ ).

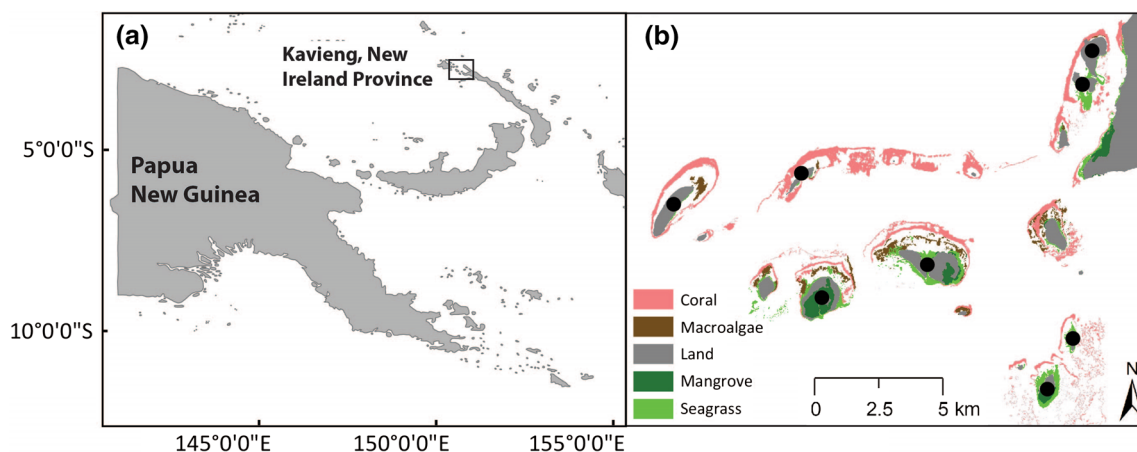
### Data collection

To quantify habitat use by coral reef-associated fishes, we collected data from five common habitat types, specifically: (1) shallow coral reef slopes (3–6 m depth), (2) reef flats containing hard structure (e.g. coral or rock), (3) macroalgal beds, (4) non-estuarine mangroves and (5) seagrass meadows. Data on the use of these habitats by reef fishes were collected between 09:00 and 16:00 during April 2018, using unbaited underwater video cameras. This sampling method was chosen as it reduced any bias due to diver presence (Gotanda et al. 2009; Feary et al. 2011) and also due to the presence of saltwater crocodiles (*Crocodylus porosus*) in the area. The lack of baits on the cameras ensured that observations of habitat use were not influenced by attraction of fishes to bait (Bassett and Montgomery 2011).

Single video cameras (GoPros) mounted on steel frames were lowered to the substratum, and GPS points were recorded for each camera drop. The use of single, as opposed to stereo, video systems precluded the collection of accurate body size data for fishes and prevented the separation of individual fishes into life stages based on body size. For mangrove and reef slope habitats, care was taken to ensure that cameras faced towards the habitat as opposed to adjacent open waters. Replicate camera drops were separated by a minimum of 50 m, both among and between the five habitat types. Each camera was deployed for a minimum of 20 min to enable high replication across broad spatial scales within a relatively short time frame (e.g. Burge et al. 2012; Bradley et al. 2017; Pereira et al. 2017). The depth of the camera drops ranged from 0.3 to 5.5 m. In total, 86 reef slope, 75 reef flat, 41 macroalgae, 58 mangrove and 100 seagrass videos were analysed. This variation was due to differences in the availability of each habitat type and the exclusion of replicates with low video quality (camera fogging and limited underwater visibility).

### Video analysis

For each video, a 15-min segment was analysed by a single observer (KS). Each segment began at least 1 min after the camera had stabilized on the bottom and any sediment disturbed during placement had settled. From each video, we recorded species presence and the maximum number of individuals of a species recorded in a single frame (*MaxN*, sensu Cappo et al. 2004). *MaxN* is a common metric used as a conservative measure of relative abundance (Campbell et al. 2015). Cryptic (e.g. Blenniidae, Gobiidae) and surface-dwelling (e.g. Hemiramphidae) taxa were excluded because they were not able to be consistently counted using video. Individuals were identified to genus or species where possible. We used *FishBase* (Froese and Pauly



**Fig. 1** **a** Map of Papua New Guinea with location of Kavieng, New Ireland Province, and **b** study sites and habitats in the Tigak Island Group, Kavieng. Black circles denote the surveyed islands

2019) to provide an objective assessment of which species were considered reef-associated, hereafter termed “reef fishes”, or not reef-associated (following Sambrook et al. 2019).

### Data analysis

Differences in the composition of fish assemblages between the five habitats were compared with a one-way permutational multivariate analysis of variance (PERMANOVA) using Type III sum of squares and 9999 permutations (Anderson et al. 2008). We used a zero-adjusted Bray–Curtis similarity matrix to account for the high number of zeros present in the MaxN data and applied a fourth-root transformation (Clarke et al. 2006). We used pair-wise tests to examine differences between habitats and visualized the data using non-metric multidimensional scaling (nMDS). The similarity percentages routine (SIMPER) was used to identify characteristic species for each habitat type.

Differences in the mean MaxN (i.e. relative abundance) and species richness between habitats were compared with one-way ANOVAs, followed by Tukey’s HSD post hoc tests using R. In addition, one-way ANOVAs were used to compare differences in mean MaxN for common multi-habitat users to explore whether group sizes might differ between habitat types.

### Results

Across the five habitat types (reef flat, reef slope, macroalgae, mangrove and seagrass), we recorded 15,492 individuals from a total of 319 taxa, of which 288 were identified to species. Across the five habitats surveyed, 282 out of the 288 species (98%) recorded were classed as reef fishes, with only six species observed on the videos considered non-reef associated. These six non-reef-associated fish species were excluded from all further analyses.

In total, 35% of the reef fishes (99 of 282 species) observed in this study were recorded in non-reef habitats, with 20 species recorded in all three non-reef habitats (Fig. 2a; Online Resource 1). Although less speciose compared to the coral reef slope and flat habitats, the total number of reef fish species observed in each non-reef habitat was considerable (Table 1). A total of 53 reef fish species were observed in both seagrass meadows and mangroves and 60 species were observed in macroalgae beds (Fig. 2; Table 1). While the total number of species observed was similar across the three non-reef habitat types, the mean species richness and relative abundance (i.e. mean MaxN) of reef fish per video was approximately twofold higher in macroalgae beds compared to mangroves

or seagrass meadows (Table 1; ANOVA  $F_{2,196} = 15.002$ ,  $p < 0.001$ ). The type and/or combination of non-reef habitats used by each of the 99 reef fish species varied widely. Over half of the species were observed in a single non-reef habitat (Fig. 2), most commonly in macroalgae (22 spp.), followed by mangroves (18 spp.) and seagrass (12 spp.). However, there was also considerable overlap in habitat use with almost half (47 of 99 species) recorded from two or more non-reef habitats (Fig. 2).

### Fish community differences between habitats

Reef fish assemblages differed between the five habitats (PERMANOVA pseudo- $F_{4,355} = 38.926$ ,  $p = 0.0001$ , Fig. 3), with each habitat type containing a distinct assemblage of reef fishes. Macroalgae beds were broadly characterized by several species of *Halichoeres*, the tuskfish *Choerodon anchorago*, the emperor *Lethrinus harak* and the damselfish *Dischistodus chrysopoecilus*. *Lethrinus harak*, *C. anchorago* and *Halichoeres* spp., together with the rabbitfish *Siganus canaliculatus*, were characteristic of seagrass habitats. Mangroves were characterized by a different suite of species including *Gerres oyena*, *Lutjanus ehrenbergii*, *Lutjanus fulviflamma*, the rabbitfish *Siganus lineatus* and the cardinalfish *Sphaeramia orbicularis*.

### Habitat use patterns by reef fish family

Two-thirds of the 41 families recorded during the surveys contained species that used non-reef habitats (27 families). Ten of these reef fish families contained a high proportion ( $\geq 50\%$ ) of species that were recorded in non-reef habitats including jacks (Carangidae), rabbitfishes (Siganidae), snappers (Lutjanidae), emperors (Lethrinidae) and sweetlips (Haemulidae) (Fig. 4a). Patterns of habitat use (i.e. type and number of habitats) varied both among and within families. For example, species of snapper (Lutjanidae) ranged from being only recorded in coral reef habitats to being observed in both coral reef habitats and all three non-reef habitat types. In addition, several families contained species that were not recorded from either of the coral reef habitats (Fig. 4b–d).

### Species-level habitat use patterns

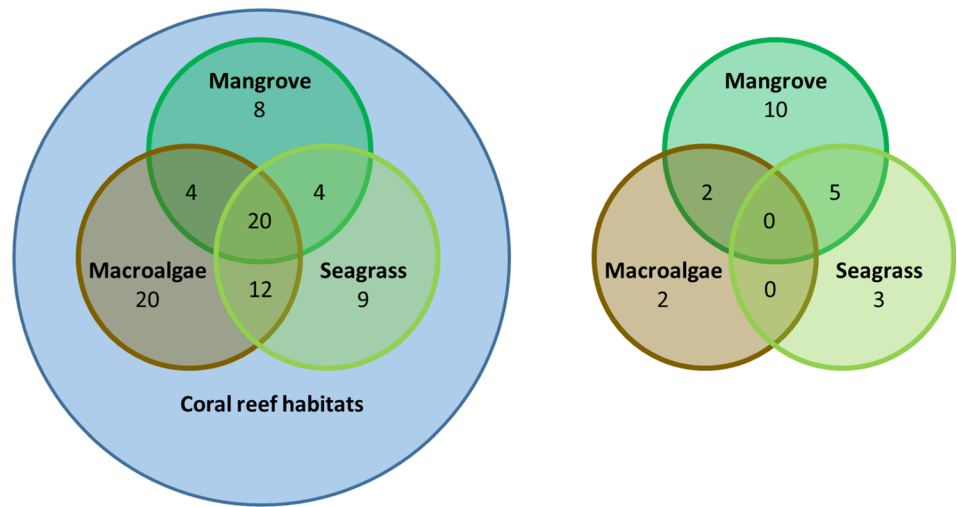
The data revealed a wide variety of habitat usage patterns by the 99 reef fish species that were observed in non-reef habitats. Over three-quarters of the species were recorded on multiple occasions away from coral reef habitats. In addition, over half were observed more frequently in at least one non-reef habitat compared to either of the coral reef habitat types (e.g. Fig. 5a, d, f–h; Online Resource 2), while others occurred in similar frequencies across a range



**Fig. 2 a** Number of reef fish species recorded in reef and non-reef habitats and overlap between non-reef habitats, and **b** the number of species not recorded from coral reef habitats (reef slope and/or reef flat)

**(a)** Number of reef fish species observed in non-reef AND coral reef habitats. 183 species only observed in coral reef habitats.

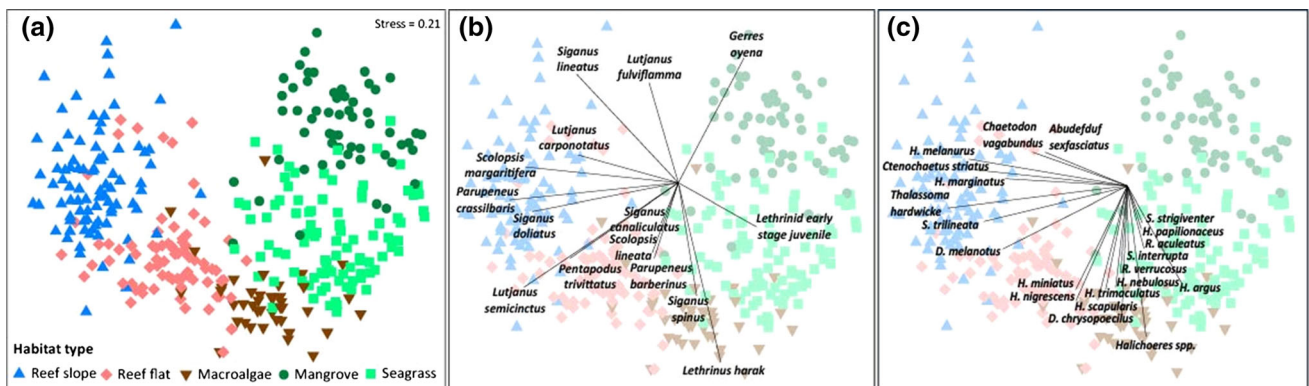
**(b)** Number of reef fish species not recorded from coral reef habitats



**Table 1** The number of replicate video samples (*n*), total number of reef fish species observed across all videos, as well as the mean species richness and relative abundance (i.e. total Max*N*) of reef fish

observed in each habitat type. Total Max*N* calculated by summing the Max*N* of each species recorded per video

	Sample size, <i>n</i>	Total no. of reef fish species observed	Mean species richness per video ± SE (range)	Mean relative abundance (total Max <i>N</i> ) per video ± SE (range)
Reef slope	86	243	35.05 ± 1.19 (14–59)	95.56 ± 7.07 (16–420)
Reef flat	75	155	21.76 ± 0.83 (8–46)	46.20 ± 2.57 (9–143)
Macroalgae	41	60	13.12 ± 0.90 (3–36)	31.24 ± 3.09 (4–70)
Mangrove	58	53	6.84 ± 0.52 (1–19)	16.69 ± 1.78 (1–56)
Seagrass	100	53	5.43 ± 0.39 (0–16)	15.6 ± 1.54 (0–72)

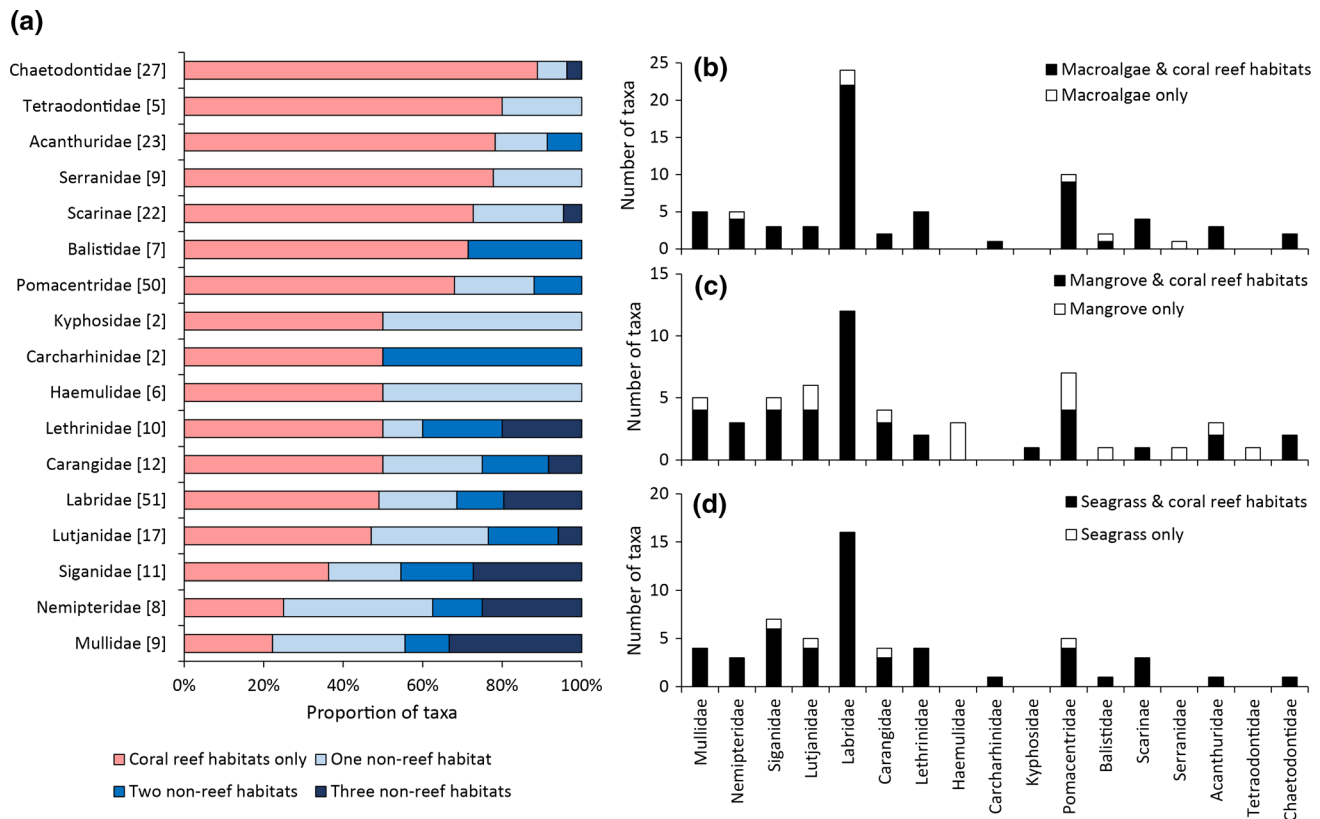


**Fig. 3 a** Non-metric multidimensional scaling plot showing the variation in the community structure of reef fishes recorded from remote underwater video in five habitat types (reef flat, reef slope, macroalgae, mangrove and seagrass). Each point represents a single video based on Max*N* data. Species where adults: **b** ≥ 25 cm max

length and **c** < 25 cm max length recorded on > 10% of videos across all habitats or > 25% of videos in a non-reef habitat type. Abbreviations of genera are *D.* = *Dischistodus*, *H.* = *Halichoeres*, *R.* = *Rhinecanthus*, *S.* = *Stethojulis*

of reef and non-reef habitats (e.g. Fig. 5b–c, e). Eighteen species were identified as widespread multi-habitat users and occurred in all five habitat types (Online Resource 2).

These ranged from larger-bodied species such as the emperor *Lethrinus harak*, the snapper *Lutjanus fulviflamma* and the rabbitfish *Siganus canaliculatus* to smaller-bodied



**Fig. 4** **a** Habitat use patterns of common reef fish families showing proportion of taxa within each family only recorded from coral reefs and those recorded from one, two or three non-reef habitats. [x] denotes the number of species observed in the study, **b** reef fish

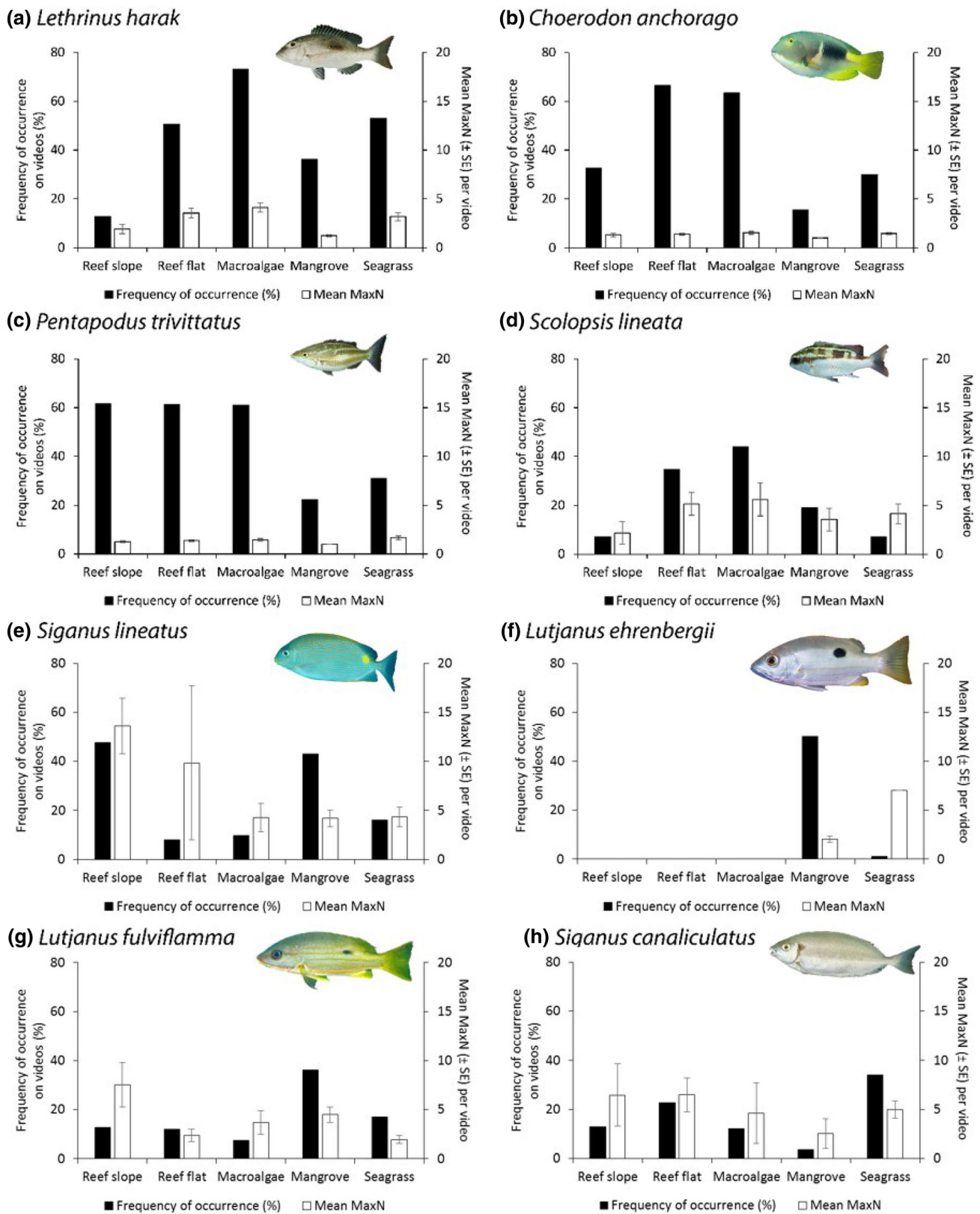
taxa observed in macroalgal beds, **c** mangroves, and, **d** seagrass. Black bars represent species recorded in a non-reef habitat type and in coral reef habitats. White bars show the number of reef fish species that were not observed in coral reef habitats

species such as the butterflyfish *Chaetodon vagabundus*, and the wrasses *Halichoeres scapularis* and *Stethojulis strigiventer*.

Comparing the relative abundance (i.e. MaxN) for some of the most frequently observed and abundant multi-habitat users highlighted potential among habitat differences in group size (Fig. 5). For instance, the mean relative abundance for *Lethrinus harak* was significantly lower in mangroves ( $1.24 \pm 0.10$  SE) compared to reef flat, macroalgae and seagrass habitats (ANOVA  $F_{4,158}=4.68$ ,  $p = 0.01$ ). The mean relative abundance for the rabbitfish *Siganus lineatus* was threefold higher on reef slopes compared to mangroves (ANOVA  $F_{1,64}= 6.39$ ,  $p = 0.01$ ), despite occurring on a similar number of occasions in each habitat, indicating that *S. lineatus* may occur in larger groups on reef slopes. Similarly, the snapper *Lutjanus fulviflamma* had a higher mean relative abundance on reef slopes ( $7.55 \pm 2.26$  SE) compared to all other habitat types, almost double the mean relative abundance in mangroves ( $4.48 \pm 0.79$  SE).

## Discussion

There is increasing evidence of the widespread use of non-reef habitats by reef-associated fishes, with a recent meta-analysis suggesting that  $\sim 20\%$  of reef fish species use non-reef habitats (Sambrook et al. 2019). By comparing fish assemblages across five habitat types in Kavieng, Papua New Guinea, we found that percentage to be even higher, with over a third (35%) of reef-associated fish species recorded in non-reef habitats, many of which occurred in multiple non-reef habitats. In addition, many of the species identified using multiple habitats are ecologically (e.g. the macroalgae browser *Siganus canaliculatus*) or economically important. Our findings thus provide additional support for claims of widespread use of multiple habitat types by reef fishes and for the importance of better understanding habitat complementarity in coral reef ecosystems. Our study also demonstrates the value of examining species distributions across a wider range of habitats at each study location in the Indo-Pacific, as has previously been noted for the Caribbean (Nagelkerken et al. 2000; Harborne et al. 2008). Observed species-



**Fig. 5** Species-specific habitat use patterns for eight common multi-habitat users. Black bars show the frequency of occurrence (%) on videos. White bars show the mean MaxN ( $\pm 1$  SE) calculated from videos where the species was recorded

specific patterns of habitat use would have been incomplete had we sampled a more limited range of habitats.

Macroalgal beds contained, on average, more species and higher relative abundances of reef fish compared to mangroves or seagrass meadows, albeit considerably lower than the two reef habitats. This supports the growing number of studies that have documented high abundances and diversity of coral reef fishes in macroalgae beds (e.g. Rossier and Kulbicki 2000; Wilson et al. 2010; Chaves et al. 2013; Evans et al. 2014; Eggertsen et al. 2017; Tano et al. 2017). The majority of these studies have focused on beds of canopy-forming macroalgae, such as *Sargassum* (but see Rossier and Kulbicki 2000), finding that the structural complexity and canopy height of algae are important factors influencing its use by coral reef fishes, particularly juvenile life stages (Wilson et al. 2014; Fulton et al. 2019, 2020; Tang et al. 2020). In contrast, our macroalgal study sites were predominantly a mixture of *Halimeda* and *Caulerpa*, which are smaller and less structurally complex than *Sargassum*. Despite these differences, we observed a similar suite of families (e.g. Labridae, Lethrinidae, Siganidae) to that reported from *Sargassum*-based studies. This suggests that factors other than structural complexity of the algae, such as the availability of food resources, visibility of predators and proximity to other habitat types (e.g. van Lier et al. 2018), may also influence the suitability of macroalgal beds for coral reef fishes. Although fish assemblages in macroalgal beds were typically more speciose than seagrass meadows or mangroves, there was considerable overlap in species using macroalgal beds and seagrass meadows, indicating that these two habitat types could act as complementary habitats for some fishes (Dunning et al. 1992). Seagrass meadows and macroalgal beds can be structurally similar (Gratwicke and Speight 2005) and contain comparable resources and refugia opportunities (Macreadie et al. 2017) which could drive similarities in habitat use.

In contrast, mangroves contained a distinct assemblage of reef fishes including some species (e.g. *Lutjanus argentimaculatus*) that were exclusive to this habitat. Although we were unable to separate our data into life stages based on body size, we did observe several individuals, particularly snappers (i.e. lutjanids), with juvenile markings within mangrove habitats. These findings are interesting, but require additional research, given the debate about whether mangrove habitats in the Indo-Pacific are as important for coral reef fishes, particularly juveniles, as they are in the Caribbean (Blaber & Milton 1990; Thollot 1992; Dorenbosch et al. 2005; Nakamura et al. 2008; Unsworth et al. 2009; Barnes et al. 2012; Kimirei et al. 2013; Dubuc et al. 2019). Mangrove systems in the Indo-Pacific vary considerably depending on tidal regime (Krumme 2009; Igulu et al. 2014), geomorphological and

spatial context (Blaber 2007; Unsworth et al. 2008; Olds et al. 2013; Bradley et al. 2019), as well as the size, composition and structural complexity of mangrove forests (Laegdsgaard and Johnson 2001; Nanjo et al. 2014), all of which can influence habitat use patterns (Sheaves 2017). Here, we examined non-estuarine mangroves in a microtidal location and suggest that under these conditions, mangroves appear to possess certain attributes (e.g. refuge, food availability) that are not provided by the other shallow non-reef, or even reef, habitats surveyed. Therefore, the impact of mangrove loss or degradation could be greater for coral reef fishes that appear to selectively use mangroves compared to species that appear to use multiple habitats interchangeably.

Importantly, a substantial number (> 50%) of the species using multiple habitat types belong to families (e.g. Carangidae, Lethrinidae, Lutjanidae and Siganidae) caught by small-scale fisheries in the region (Papua New Guinea National Fisheries Authority 2005, 2007). Reef fishes have historically been, and continue to be, an important source of animal protein for Pacific Island communities (Dalzell et al. 1996; Pinca et al. 2012). However, increasing human populations have placed pressure on reefs, and many island nation reef fisheries are considered to be operating at unsustainable levels (Newton et al. 2007). As reefs become more degraded, it has been suggested that the availability of non-reef habitats could play an important role in maintaining the productivity of reef fisheries (Rogers and Mumby 2019). Fishing around the Tigak Islands is largely restricted to inshore waters surrounding the islands, particularly during the monsoon season (Lawless and Frijlink 2016), with the only commercial fishing targeting tuna and other pelagic fishes in offshore waters. Our findings suggest that this dependence on inshore waters for several months each year, combined with growing populations, requires careful management of the entire seascape, not just reefs, by local communities to protect food security into the future.

“Coral reef fishes” is a widely used term to describe fish assemblages that occupy waters in the vicinity of coral reefs, yet over one-third of the fishes recorded from shallow-water habitats in the Kavieng Lagoon were present in one or more non-reef habitat. Many of these species were frequently encountered away from coral reef habitat and could be considered as “seascape users” or “habitat generalists” as opposed to “coral reef fish”. Terminology aside, being flexible in habitat use could be advantageous given the widespread degradation of many shallow-water coastal habitats. As has been demonstrated from terrestrial landscapes (e.g. in birds, Salido et al. 2011), populations of such habitat generalists might be less vulnerable to the degradation of one habitat type. In contrast, species that obtain complementary resources from different habitats



(e.g. food vs. shelter, Ries et al. 2004) may be negatively impacted by habitat disturbance or loss. However, the drivers of multiple habitat use are not well understood for many of the species identified here as multi-habitat users.

It is now widely recognized that coral reefs are moving into uncertain territory. However, efforts to predict how reefs might function in the future rarely consider that many reefs are embedded within, and consequently influenced by, a mosaic of other habitat types. Such connections may become increasingly important in the future both for supporting key ecological functions on reefs and providing food security for nations with strong dependencies on coral reef fisheries.

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#### Compliance with ethical standards

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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