

Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge?

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ABSTRACT: Increasing disturbance frequency and severity on coral reefs has caused declines in the abundance of structurally complex corals and many fish species that depend on them. However, most studies have focused on the shallowest 10 m, despite coral habitat extending to >30 m in many regions. Reefs in deeper water and offshore locations are less exposed to many stressors associated with coral decline, and may offer a refuge for coral-associated fishes. Understanding how distributions and species-specific fish–habitat relationships vary along depth and distance-from-shore gradients is critical for assessing refuge potential. Here we examined the community structure, distributions and coral habitat associations of 123 reef fish species along a depth gradient from <1 to 40 m, from coastal to offshore reefs in Kimbe Bay, Papua New Guinea. Overall fish density and species richness declined with increasing depth but increased with distance offshore, such that deep offshore assemblages supported similar richness to shallow inshore sites. The most distinctive fish assemblage occurred at depths <1 m and ~25% of species were observed in only the shallowest 5 m. However, ~60% of species occurred at or below 20 m and 24% were broadly distributed from <1 to 30 m, with depth ranges of many species increasing with distance offshore. Strong relationships between fish abundance and coral habitat were observed, and 85% of species that were strongly associated with coral occurred at depths ≥20 m. Our results suggest that while many species are restricted to vulnerable shallow depths, deep offshore reefs provide a potential refuge for a substantial proportion of coral-associated fishes threatened by degradation of shallow coastal reefs, and deep reefs should be afforded greater consideration in conservation planning for coral reef fishes.

KEY WORDS: Reef fishes · Coral habitat availability · Depth distributions · Environmental gradients · Depth refuge · Fish–habitat relationships

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INTRODUCTION

Most species are distributed unevenly along environmental gradients such as latitude, altitude and depth (Schall & Pianka 1978, Gaston 2000, Connolly et al. 2003). These distributions are usually linked to either changes in the physical environment (e.g. temperature, rainfall, light and nutrient availability) or

gradients in biotic habitat structure, such as vegetation type or canopy height (Gaston 2000, Hawkins et al. 2003). The extent to which a species distribution is a response to either physical or biological factors is often unknown (e.g. Karr & Freemark 1983, Martin 2001), but may be elucidated through a detailed analysis of covariance between species, environmental and habitat variables. Species distributions are often

influenced by multiple gradients and may reflect the interactions among them; for example, plants may have extended altitudinal ranges in warmer tropical environments (Cogbill & White 1991). A full understanding of species distributions therefore requires an understanding of responses to gradients in several environmental dimensions. Understanding the influence of these important distribution drivers is becoming increasingly pertinent as species ranges are increasingly impacted by climate change (Parmesan & Yohe 2003, Poloczanska et al. 2013).

In aquatic environments, water depth represents a steep physical gradient that influences the distributions of many taxa. On tropical coral reefs, reef-associated fishes are often restricted to particular depths, and major changes in species composition can occur over narrow depth ranges of just a few meters (McGehee 1994, Nanami et al. 2005). Similar changes can occur along horizontal gradients from coastal to shelf-edge reefs (Williams 1982, Wismer et al. 2009, Emslie et al. 2010). To date, most studies on the factors affecting reef fish distributions have occurred in shallow water, where distributions are strongly influenced by benthic habitat structure and particularly by the availability of live coral habitat (e.g. Bell & Galzin 1984, Syms & Jones 2000, Jones et al. 2004). The diversity (Roberts & Ormond 1987, Messmer et al. 2011), morphology (Nanami et al. 2005) and structural complexity (Luckhurst & Luckhurst 1978, Coker et al. 2012, Noonan et al. 2012) of coral habitats also strongly influence reef fish assemblages in shallow water.

The few studies that have extended into deeper water on coral reefs suggest that both fish density and diversity decline with increasing depth (Bouchon-Navaro 1981, Friedlander & Parrish 1998, Brokovich et al. 2008, Garcia-Sais 2010, Jankowski et al. 2015). However, fish assemblages in depths >15 m remain poorly described in most regions. The extent to which shallow-water fish–habitat associations are maintained at greater depths, and consequently the extent to which species depth ranges are limited by habitat availability, is currently unknown. Coral distributions and benthic habitat structure vary along depth gradients in response to decreasing light, temperature and wave energy (Done 1983, Kleypas et al. 1999, Roberts et al. 2015). In clear tropical waters, many coral species occur to depths of 50 m or more (Jarrett et al. 2005, Bridge et al. 2013, Muir et al. 2015). Greater light penetration and reduced terrestrial influence offshore (Fabricius & De'ath 2001, Fabricius et al. 2016) may enable complex coral habitats to occur at greater depths (e.g. Muir et al. 2015).

If fish distributions are determined by habitat structure, deeper habitats in clear-water offshore locations could be expected to support greater fish diversity and abundance, with species exhibiting greater depth ranges farther offshore.

Understanding the mechanisms underlying cross-shelf and depth distributions is becoming increasingly important as shallow and near-shore reefs become more degraded by climate change impacts and coastal development (e.g. Fabricius et al. 2005, De'ath et al. 2012). Shallow coral reefs have experienced ongoing widespread degradation, including declines in coral cover and structural complexity, and changes in benthic composition (Hughes et al. 2003, Wilkinson 2004, McWilliams et al. 2005). These habitat shifts have resulted in large-scale, long-term, multi-taxon declines in reef fish abundances (Jones et al. 2004, Wilson et al. 2006, 2008), temporally stable shifts in fish communities (Bellwood et al. 2012) and local extinction of highly specialized coral-dependent species on shallow near-shore reefs (Munday 2004, Wilson et al. 2006). Disturbances such as coral bleaching and storm damage can attenuate relatively quickly with increasing depth (Bridge et al. 2014, Smith et al. 2014, Roberts et al. 2015), and depth range is identified as a key factor both for mitigating extinction risk in corals and coral reef fishes (Carpenter et al. 2008, Graham et al. 2011), and for predicting recovery of reefs following disturbance (Graham et al. 2015). However, understanding species potential for utilizing deep-reef refuges requires accurate information on how species distributions, abundances and fish–habitat associations change along both depth and inshore–offshore gradients.

Here we characterized changes in coral reef fish distributions and their relationship with habitat structure along depth and inshore–offshore gradients in Kimbe Bay, Papua New Guinea. Kimbe Bay is a low-latitude reef system with abundant spread across a gradient from fringing reefs heavily influenced by terrestrial inputs through to offshore reefs in clear water with hard coral growth in depths >60 m. The occurrence of reefs with similar geomorphology across the bay provided an ideal location to examine changes in fish distributions across environmental gradients. Specifically, we tested whether (1) reef fish abundance and diversity decline with depth and increases away from the shore, particularly at depths >10 m; (2) individual species exhibit depth preferences within their overall depth range that result in distinct assemblages between depth strata, and whether these also extend deeper offshore; (3) coral habitat cover declines and structural

characteristics change with increasing depth and distance from shore, with greater availability of deep complex coral habitat farther offshore; (4) depth-related distributions of overall fish density and of coral-associated species are limited by the availability of complex coral habitat; and (5) coral–fish associations decline with increasing depth.

MATERIALS AND METHODS

Study site

The study was undertaken in Kimbe Bay, Papua New Guinea (5° 30' S, 150° 05' E) during April and May 2013, and June 2014. A total of 10 reefs were surveyed from 3 positions across the bay ('bay position'): 3 inshore, 4 mid-bay and 3 offshore reefs (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m561p217_supp.pdf). Inshore reefs were <1 km from the coast, while mid-bay and offshore reefs experience progressively clearer water with less terrestrial influence. Inshore reefs in Kimbe Bay experienced high coral loss a decade previously (see Jones et al. 2004, Munday 2004, Gardiner & Jones 2005) and are currently in the advanced stages of recovery but experience ongoing low-level pulse perturbances. All reefs in the region consist of continuous reef substratum with abundant hard coral growth well beyond the maximum study depth, and therefore present no physical barriers to fish migration among depths. The maximum depth of scleractinian coral growth on Kimbe Bay reefs is unknown, but extends to >60 m in some cases (authors' pers. obs.).

Data collection

At each reef, divers recorded high-definition digital video transects both for fishes (30 × 4 m) and benthic data (30 × 1 m) at each of 5 depths: <1, 5, 10, 20 and 30 m. Transects were also recorded at 40 m on 2 outer bay reefs. A total of 4 to 6 replicates were recorded for each depth at each reef (Table S1 in the Supplement). Cameras faced forward for fish transects and directly into the reef for benthic transects. Transect widths were determined by pre-filming metric grids laid along the benthos. The use of video lights, a cyan balancing light filter, high definition (1400 pixels) and high frame rates (60 frames per second) allowed on-screen identification of targeted taxa at all depths.

Reef fishes from 4 non-cryptic, speciose and ecologically varied families (Pomacentridae, Chaetodontidae, Pomacanthidae and Acanthuridae) were identified to species level based on Allen et al. (2003) and counted within a standardized lower section of the screen. Slower playback speeds and repeat viewings were used where species identification was not initially clear or large aggregations occurred. In the latter instance, counts were repeated and consensus or mean abundance was used. If fishes left the frame partially or entirely and re-entered immediately in the same position they were not counted again; otherwise, all fishes entering the frame were considered new individuals. Species richness was recorded as the total number of species observed within the 4 fish families in each transect.

The proportional cover of 10 benthic groups (massive coral, encrusting coral, laminar coral, complex coral, turf algae, crustose calcareous algae, sponges, coral rubble, sand and silt, and reef matrix) was recorded using Coral Point Count with Excel extensions (Kohler & Gill 2006). Complex corals were defined as those considered to be the most suitable complex habitat for the sheltering of small reef fishes. This included all branching, corymbose, hispidose, digitate, foliose and tabulate forms, but not laminar, massive, sub-massive or encrusting corals. For each transect, 60 random points were generated (6 random points assigned within 10 video frames extracted using a stratified random design—equivalent to ten 1 m² quadrats per transect, spaced approximately 3 linear meters apart) and the benthic component directly under each point was recorded.

Data analysis

Influences of depth and bay position on reef fish density and species richness

The total abundance and species richness of reef fishes were tested for unequal distribution between depths (fixed factor) and bay positions (fixed factor), after accounting for differences between reefs (random factor nested within bay position) using log₁₀ transformed data using linear mixed-effects models (lme) and ANOVA with the 'nlme' package in R (Pinheiro et al. 2014). Type III sums of squares were used due to unbalanced sample design, and effect size of each model component (R²) was calculated by isolating variance components (Model 1; Table 1). To assess whether offshore sites supported higher fish densities than inshore sites at each depth, fish den-

Table 1. Summary statistics for 3 models testing the relationship between fish assemblages and explanatory variables depth, bay position and availability of complex coral habitat. Model 1: distributions of reef fish across 5 depths and 3 bay positions; Model 2: relationships between reef fish and complex coral distributions; Model 3: combined effects of depth and complex coral cover on reef fish distributions. All model results show the influence of explanatory variables after first accounting for natural variation between reefs by incorporating reefs as a random factor. R^2 values represent the proportion of variation accounted for by the individual main effects, and interaction terms in each model (sub models a, b, c). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS = not significant ($\alpha = 0.05$); CV: estimates of components of variance; F_{perm} : pseudo- F -statistics based on permutation in PERMANOVA

Model set	Explanatory variables	Reef fishes												
		Abundance (\log_{10})					Species richness (\log_{10})				Community composition			
		df	F	p	R^2	AICc	df	F	p	R^2	df	F_{perm}	p	CV
1a	Depth	4,231	79.92	***	0.498	114.33	4,231	55.25	***	0.402	4,251	25.12	***	31.1
1b	Position	2,7	4.48	NS	0.048	286.49	2,7	6.95	*	0.074	2,251	15.9	***	15.9
1c	Depth × Position	8,231	4.917	***	0.595	117.48	8,231	3.41	***	0.518	2,251	15.7	***	15.7
2	Complex coral	1,242	94.50	***	0.282	215.85	1,242	23.64	***	0.089	–	–	–	–
3	Depth + Complex coral	1,234	3624.74	***	0.555	100.52	1,234	3859.1	***	0.397	–	–	–	–

sity data were grouped within depths and *a priori* contrasts were made between bay positions (with reef as a random nested factor) via ANOVA of lme models. Tukey's post-hoc pairwise comparisons of levels within significant factors were made using the 'lsmeans' package (Lenth & Hervé 2014).

Influences of depth and bay position on species distributions and community structure

The densities of a subset of 51 abundant species were assessed for uneven distributions between depths and bay positions using non-parametric, permutation-based ANOVA in the multivariate statistical program PERMANOVA, from the PRIMER package for ecological statistics (Clarke & Gorley 2006). The 51 'top ranked' species consisted of the 20 most abundant species from each depth, with some species being among the most abundant at multiple depths. Species depth ranges were determined using presence/absence data from each depth.

Changes in fish assemblage structure were analyzed in PRIMER using Bray-Curtis dissimilarity matrices of square root transformed data. Very rare species (present <5% of all transects) were excluded, leaving 114 of 123 species. CLUSTER identified assemblage groupings with averaged linkages, which were visualized on a MDS plot. Formal analyses of changes in community composition were undertaken using 3-factor MANOVA in PERMANOVA (depth, position[reef]). Fish species characteristic of communities at each depth and their proportional contribution to community were identified using SIMPER.

Habitat variation along the depth gradient

ANOVAs of lme models (built as per Model 1 above) were used to test for uneven cover of hard coral, complex coral and laminar coral between depths and bay positions using square root transformed data.

Relative influence of depth and habitat on reef fish distributions

We assessed the comparative influence of depth and habitat availability on total fish abundance (\log_{10}) and species richness (\log_{10}) by testing the level of fit of 3 lme models: depth (Model 1a), complex coral cover (square root transformed; sqrt) (Model 2), and depth and complex coral cover combined (Model 3). The best-fit model had the lowest corrected Akaike's information criterion (AICc) score, provided no model with fewer factors fell within 2 points of the best AICc score. Values of R^2 were used to represent the amount of variation in fish density explained by each model (Demidenko 2013).

Fish-habitat relationships along the depth gradient

The strength of correlation between overall fish density (\log_{10}) and cover of complex coral habitat (sqrt) was assessed at each depth and across all depths using linear models in R. We tested for correlation between abundances of the 123 fish species and the cover of benthic components within each

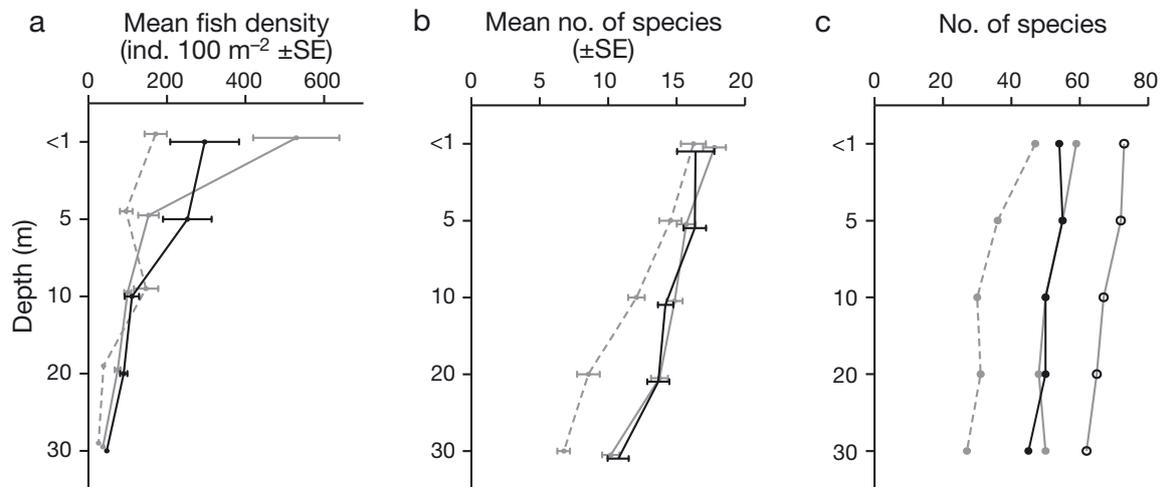


Fig. 1. (a) Mean total fish density, (b) mean species richness per transect and (c) total species richness at each of 5 depth and 3 bay positions. Dashed lines represent the inner bay, solid grey lines the mid-bay and black lines the outer bay. Total species count at each depth is shown (o) in (c)

depth stratum and across all depths using 'cortest' in R using a Dunn-Sidak adjusted $\alpha = 0.0073$ based on the number of benthic components. Relationships between the compositions of the fish benthic assemblages were assessed using Spearman's rank correlations of Bray-Curtis dissimilarity matrices in RELATE (PRIMER). Data from 40 m depth were included in exploratory analyses but excluded from all formal analyses because 40 m transects were recorded only for offshore reefs.

RESULTS

Influences of depth and bay position on reef fish density and species richness

Overall fish density declined by ~40% between each successive depth stratum, resulting in a 10-fold decrease from a peak of ~350 ind. per 100 m² at <1 m to ~35 ind. per 100 m² at 30 m (Fig. 1a). This depth-

associated decline alone accounted for ~50% of variation in fish abundance (Table 1, Model set 1a). The mean number of species present per transect within the 4 fish families also declined with increasing depth below 5 m, from 17 ± 0.58 (SE) and 15.5 ± 0.45 species 120 m⁻² at <1 m and 5 m to 9.3 ± 0.53 species at 30 m (Table 1, Fig. 1b). However, the total number of species declined by only ~15% along the depth gradient, from 72 species at <1 m to 61 species at the 2 deepest depths (Fig. 1c).

The mean number of fish species was significantly lower overall at inshore sites compared to mid-bay (Tukey's $p = 0.0038$) and offshore sites (Tukey's $p = 0.0132$) (Table 1, Fig. 1b). Mid-bay and offshore sites also housed 25 to 30% more species in total than inshore sites (99, 93 and 70 species, respectively).

Reef fish density and species richness on deep reefs (20 to 30 m) were both significantly higher away from inshore sites (Tables 1 & 2, Model set 1c). Overall densities at 20 and 30 m depths were significantly higher offshore (~90 and ~47 ind. 100 m⁻², res-

Table 2. Summary of pre-planned within-depth contrasts of fish abundance between bay positions at each depth. Contrasts: significant contrasts (Tukey's adjusted α); I: inshore; M: mid-bay; O: offshore

Depth	Reef fish abundance (log ₁₀)				Reef fish species richness (log ₁₀)				Complex coral cover (sqrt)			
	df	F	p	Contrasts	df	F	p	Contrasts	df	F	p	Contrasts
1	2,7	4.33	0.064	-	2,7	0.423	0.670	-	2,7	6.97	0.022	I < M
5	2,7	2.72	0.144	-	2,53	1.278	0.287	-	2,7	3.6	0.082	-
10	2,7	0.91	0.449	-	2,7	2.683	0.138	-	2,7	0.59	0.57	-
20	2,7	12.09	<0.001	I < M, I < O	2,45	14.5	<0.001	I < M, I < O	2,7	0.756	0.50	-
30	2,7	6.61	0.032	I < M, I < O	2,7	5.449	0.041	I < M, I < O	2,7	0.267	0.70	-

pectively) than at equivalent depths on inshore reefs (~39 and ~26 ind. 100 m⁻², respectively), and densities at 20 m sites offshore were equivalent to shallow sites (<1 to 10 m) inshore (all Tukey's comparisons $p > 0.1$; Fig. 1a, Table S2 in the Supplement at www.int-res.com/articles/suppl/m561p217_supp.pdf). Likewise, the mean number of species per transect at 20 m (8.6 ± 0.84 species 120 m⁻²) and 30 m (6.75 ± 0.46 species 120 m⁻²) on inshore reefs was lower than at equivalent depths on mid-bay (13.8 ± 0.61 and 10.2 ± 0.64 species 120 m⁻², respectively) and offshore reefs (13.6 ± 0.8 and 10.7 ± 0.8 species 120 m⁻², respectively) (Fig. 1b, Table 2), which also had ~40% more species in total at these depths (Fig. 1c). In addition, total species numbers were higher at the deepest depths offshore than at the shallowest depths inshore (Fig. 1c). Differences in overall fish density between bay positions were more prominent but also more variable in shallow water. As a result, mean densities at <1 m were much higher on mid-bay reefs than on inshore and offshore reefs, but differences were not statistically significant (Table 2, Fig. 1a).

Influences of depth and bay position on species distributions and community structure

The abundances of 41 of the 51 'top-ranked' fish species (see 'Materials and methods: Influences of depth and bay position on species distributions and community structure') (81%) varied significantly with depth, and distribution patterns of 23 species (45%) varied with depth but not bay position (Table 3). Depth ranges varied greatly among all species surveyed, with 36 of the 123 species (29%) pres-

ent at only 1 depth (Fig. 2a), 29 (24%) present at all depths to 30 m and a further 16 species (12%) recorded at all depths to 40 m on outer-bay reefs (e.g. *Chaetodon baronessa*, *Ctenochaetus tominiensis*). At least 1 species was uniquely observed at each study depth; however, the greatest proportion of 'single-depth' species occurred at <1 m (Fig. 2b). A total of 29 species (24%) occurred only at depths ≤5 m (e.g. *Chrysiptera cyanea*, *Chromis viridis*), while 77 species (62%) occurred at depths ≥20 m (Fig. 2c).

Depth patterns in species distributions resulted in significant differences in community composition between all depths (Table 1) (all comparisons; $p < 0.001$) and 3 major depth-related clusters were identified. The fish community at <1 m depth was best characterised by 14 species (Fig. 3) and was <30% similar to a second community cluster that incorporated all other depths (Fig. 4). Of the 14 species characteristic of <1 m, only 4 were also characteristic of the assemblage at 5 m, and none were characteristic of assemblages below 10 m. The next split in the fish community separated assemblages at 5 to 10 m from those at 20 to 30 m, with <40% similarity between the 2 groups. Fewer species characterised the deeper assemblage and those that did were mostly a subset of species characteristic of the assemblage at 5 m (Fig. 3).

The distributions of 18 'top-ranked' species (40%) varied among bay positions (e.g. *Chaetodon lunulatus*, *Chaetodon ornatissimus*), and while the community was similar between mid-bay and offshore positions within the same depths ($p = 0.232$), inshore assemblages differed from both mid-bay and offshore assemblages ($p < 0.001$, $p = 0.019$, respectively).

Approximately half of the 'top-ranked' species were recorded at greater depths or in greater abundance at deeper depths offshore than on inshore

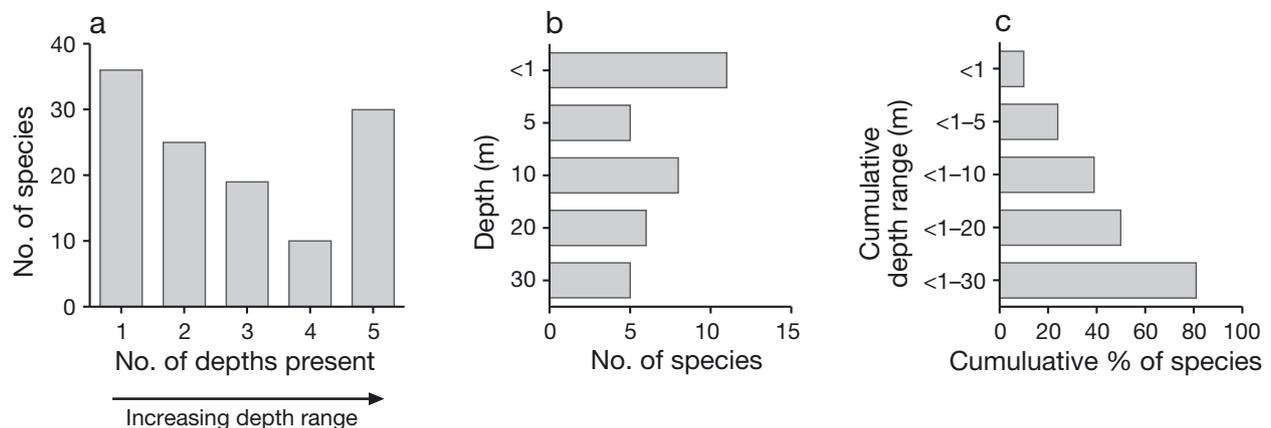


Fig. 2. Frequency histograms showing (a) number of species observed at an increasing number of study depths from only 1 depth up to all 5 depths, (b) number of fish species occurring uniquely within each study depth and (c) percentage of species with occurrence restricted to each cumulative depth bracket

Table 3. Mean density of 51 'top-rank' species at each depth, factors of spatial organization and their correlations to complex coral habitat. **Bold:** depths within which a species is among the top 20 most abundant species; Pos.: bay position; *p < 0.05, **p < 0.01, ***p < 0.001; NS: not significant ($\alpha = 0.05$) from PERMANOVA. Significant correlations to complex coral; $\alpha = 0.0073$

Species	Mean density (ind. 100 m ⁻²)						Spatial organisation (PERMANOVA)				Sig. cor. complex coral (r) All depths
	<1 m	5 m	10 m	20 m	30 m	40 m	Depth	Pos.	Depth x Pos.	Reef	
<i>Chromis ternatensis</i>	151.08	49.87	38.92	6.82	0.74	0.00	***	*	***	***	0.515
<i>Chromis lineata</i>	64.40	26.44	0.00	0.00	0.00	0.00	***	**	**	***	-
<i>Pomacentrus moluccensis</i>	38.09	13.63	4.67	1.69	1.28	0.00	***	NS	*	***	0.426
<i>Chrysiptera arnazae</i>	0.00	3.68	23.39	11.31	3.72	3.31	**	NS	NS	***	-
<i>Acanthochromis polyacanthus</i>	14.25	8.04	8.77	4.26	1.31	0.11	***	*	NS	NS	0.252
<i>Chromis amboinensis</i>	0.15	5.26	4.69	7.15	4.80	11.77	***	NS	NS	***	-
<i>Pomacentrus nigromanus</i>	0.39	5.28	4.00	8.08	5.03	0.00	***	*	*	***	-
<i>Chromis atripectoralis/viridis</i>	9.23	9.47	0.00	0.00	0.00	0.00	*	**	**	*	0.221
<i>Ctenochaetus striatus</i>	14.90	2.27	0.42	0.28	0.11	0.00	***	*	NS	NS	0.250
<i>Chromis retrofasciata</i>	0.09	2.05	5.25	6.02	3.65	6.86	***	NS	*	***	-
<i>Ctenochaetus tominiensis</i>	0.01	2.79	4.39	4.25	3.00	3.09	***	***	**	NS	-
<i>Amblyglyphidodon leucogaster</i>	0.40	3.89	4.96	3.65	1.38	2.29	***	***	***	***	0.292
<i>Chrysiptera cyanea</i>	13.41	0.00	0.00	0.00	0.00	0.00	**	NS	*	***	-
<i>Neoglyphidodon nigrurus</i>	0.62	6.75	4.30	1.35	0.06	0.00	***	NS	NS	***	0.293
<i>Amblyglyphidodon curacao</i>	11.14	0.46	0.24	0.00	0.00	0.00	***	NS	NS	***	0.196
<i>Chrysiptera rollandi</i>	0.16	2.20	0.94	1.48	3.38	0.46	***	**	**	**	-
<i>Zebrasoma scopas</i>	2.86	1.09	1.18	0.48	0.17	0.00	***	***	NS	NS	0.320
<i>Acanthurus thompsoni</i>	0.01	0.49	0.89	2.48	1.78	0.57	*	NS	NS	***	-
<i>Pomacentrus aurifrons</i>	0.00	2.26	2.70	0.14	0.00	0.00	*	NS	**	*	-
<i>Amblyglyphidodon aureus</i>	0.22	1.22	0.82	1.48	1.20	0.69	**	NS	NS	***	-
<i>Plectroglyphidodon lacrymatus</i>	4.61	0.20	0.00	0.00	0.00	0.00	***	*	***	***	-
<i>Acanthurus lineatus</i>	4.42	0.04	0.00	0.00	0.00	0.00	***	NS	NS	***	0.206
<i>Pomacentrus bankanensis</i>	4.19	0.13	0.05	0.00	0.00	0.00	***	NS	NS	**	-
<i>Abudefduf vigiensis</i>	2.28	1.43	0.00	0.00	0.00	0.00	**	NS	NS	***	-
<i>Chrysiptera talboti</i>	0.00	1.60	0.80	0.80	0.00	0.00	**	NS	NS	NS	-
<i>Chaetodon lunulatus</i>	0.68	0.44	0.60	0.45	0.22	0.00	NS	*	NS	*	0.200
<i>Chromis margaritifer</i>	1.17	0.74	0.00	0.00	0.00	0.00	***	*	*	***	-
<i>Chaetodon baronessa</i>	1.13	0.46	0.14	0.12	0.02	0.11	***	NS	NS	NS	0.288
<i>Naso hexacanthus</i>	0.00	0.22	0.00	0.09	0.17	10.29	NS	NS	NS	NS	-
<i>Chromis xanthura</i>	0.34	1.39	0.00	0.00	0.00	0.00	**	***	**	NS	-
<i>Zanclus cornutus</i>	0.46	0.29	0.78	0.23	0.08	0.00	**	NS	NS	**	-
<i>Pygoplites diacanthus</i>	0.56	0.49	0.25	0.26	0.20	0.23	NS	***	*	NS	-
<i>Heniochus varius</i>	0.41	0.62	0.27	0.25	0.15	0.11	*	***	NS	NS	-
<i>Forcipiger flavissimus</i>	0.07	0.25	0.47	0.54	0.17	0.23	*	***	NS	NS	-
<i>Neopomacentrus azysron</i>	1.33	0.08	0.00	0.00	0.00	0.00	***	NS	***	NS	-
<i>Pomacentrus adelus</i>	1.39	0.00	0.00	0.00	0.00	0.00	**	**	***	**	-
<i>Acanthurus pyroferus</i>	0.43	0.53	0.14	0.09	0.08	0.11	NS	**	NS	NS	-
<i>Chromis delta</i>	0.00	0.00	0.05	0.51	0.74	0.11	**	NS	NS	***	-
<i>Pomacentrus lepidogenys</i>	1.23	0.03	0.00	0.00	0.00	0.00	**	NS	NS	***	-
<i>Centropyge vroliki</i>	0.93	0.17	0.09	0.00	0.02	0.00	***	*	NS	***	-
<i>Chaetodon octofasciatus</i>	0.00	0.08	0.30	0.51	0.28	0.00	*	NS	NS	NS	-
<i>Chaetodon ornatissimus</i>	0.21	0.27	0.20	0.17	0.18	0.34	NS	***	NS	NS	-
<i>Centropyge nox</i>	0.04	0.07	0.16	0.43	0.28	0.11	***	NS	NS	NS	-
<i>Pomacentrus reidi</i>	0.00	0.06	0.02	0.35	0.46	0.00	**	NS	NS	***	-
<i>Naso literatus</i>	0.09	0.11	0.13	0.09	0.06	0.34	NS	NS	*	NS	-
<i>Neoglyphidodon thoracotaeniatus</i>	0.00	0.01	0.05	0.18	0.14	0.23	*	NS	NS	*	-
<i>Pomacentrus nigromarginatus</i>	0.00	0.00	0.02	0.55	0.11	0.00	NS	NS	NS	NS	-
<i>Dascyllus flavicaudis</i>	0.00	0.00	0.00	0.00	0.00	1.83	***	NS	NS	NS	-
<i>Heniochus monoceros</i>	0.01	0.01	0.00	0.03	0.11	0.11	NS	NS	NS	NS	-

reefs (25 species), and 18 species distributions were significantly influenced by the interaction of depth and bay position (Table 3). Of these interactions

between depth and bay position, 11 (60%) occurred in species distributed in the shallowest 5 m, where small damselfish species had high peak densities in

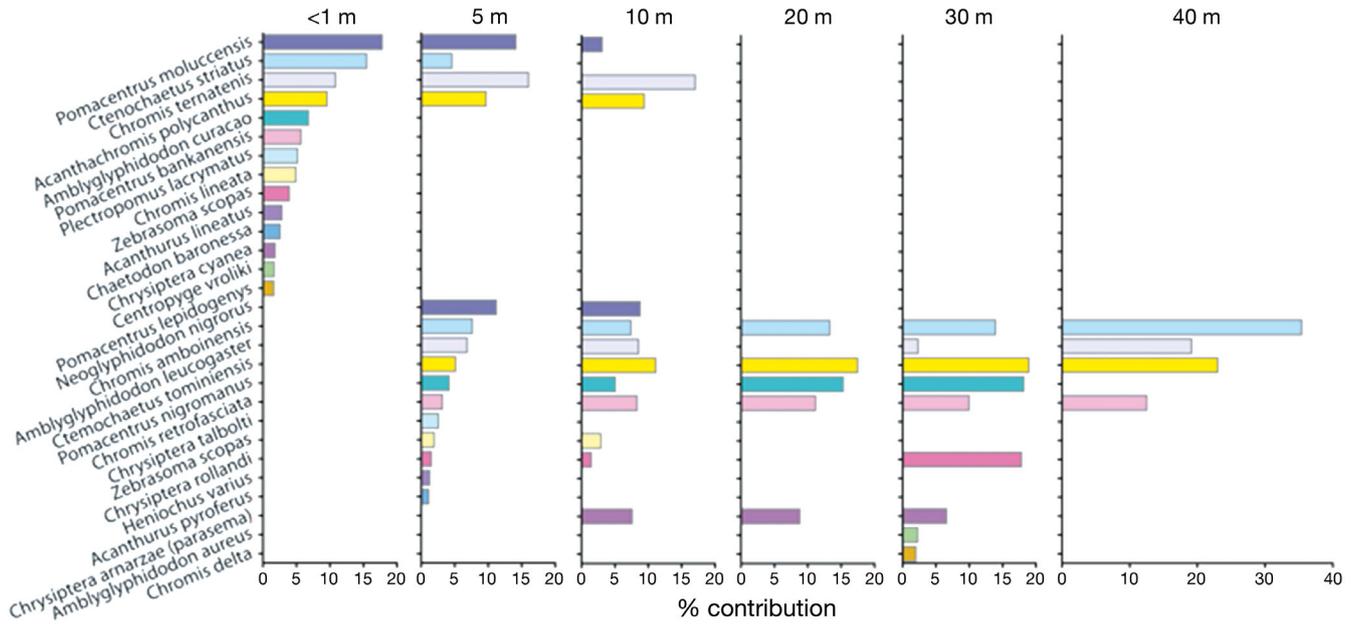


Fig. 3. Species most characteristic of the assemblage at each depth, and their proportional contribution to within-depth similarities

only 1 or 2 bay positions. Some characteristic deep-water species increased in density toward the outer bay (e.g. *Chromis amboinensis*, *Chromis delta*, *Chromis retrofasciata* and *Ctenochaetus tominiensis*), whereas others were more numerous in the inner bay (e.g. *Chaetodon octofasciatus*, *Chrysiptera rollandi* and *Pomacentrus nigromanus*). In one example, the coral-feeding butterflyfish *Chaetodon lunulatus* was very rare below 10 m at inshore sites, but equally abundant at all depths to 30 m in the mid-bay and offshore reefs. These species patterns resulted in the depth-related separation of the fish assemblage being strongest inshore, with the deep assemblages (20 to 30 m) in the mid-bay and offshore positions being more similar to the mid-water (5 to 10 m) assemblages (Fig. 4).

Habitat variation along the depth gradient

Total hard coral cover was relatively high (48 to 60%) at all sites (Fig. 5a), although small (<12% cover) significant changes did occur among depths and bay positions, with no significant interaction between the 2 (Table 4, Fig. 5a). Total coral cover was significantly higher at 5 and 10 m than at 30 m (Tukey’s $p = 0.008$ and $p = 0.001$), and was generally ~12% higher in the mid-bay than the outer bay (Tukey’s $p = 0.025$). The functional composition of coral growth forms changed more substantially over

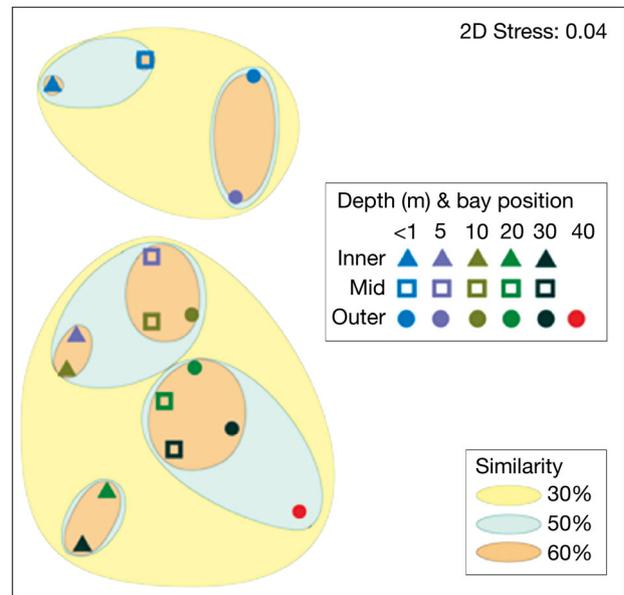


Fig. 4. MDS plot showing similarities and differences in the composition of the reef fish community at each combination of depth and bay position. Similarity groupings are calculated via cluster analysis

the depth gradient. For example, where complex coral cover declined overall below 10 m (Fig. 5b, Table 4), laminar corals increased with depth at all bay positions (Fig. 5c, Table 4), with depth accounting for ~20% of variation in complex coral cover ($R^2 =$

Table 4. Summary statistics tests for spatial organisation in the distributions of coral habitat across 5 depths and 3 bay positions. R^2 values represent the proportion of variation accounted for by the individual main effects (sub models a, b, c), and interaction terms in each model. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS: not significant ($\alpha = 0.05$)

Model set	Explanatory variables	Coral cover											
		Hard coral cover				Complex coral cover				Laminar coral cover			
		df	F	p	R^2	df	F	p	R^2	df	F	p	R^2
1a	Depth	4,231	4.79	*	0.018	4,231	22.61	***	0.189	4,231	16.27	***	0.159
1b	Position	2,7	15.25	**	0.101	2,7	7.25	*	0.113	2,7	0.225	NS	0.011
1c	Depth \times Position	8,231	1.65	NS	0.120	8,231	3.89	*	0.383	8,231	0.893	NS	0.188

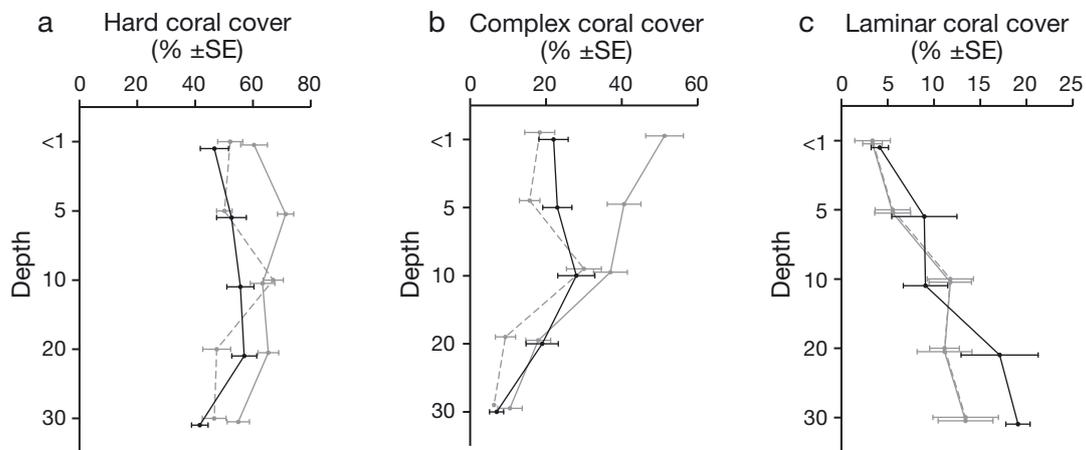


Fig. 5. Mean percent cover of (a) all hard corals, (b) complex corals and (c) laminar and tiered corals, at each of 5 study depths and 3 bay positions. Dashed grey lines denote the inner bay, solid grey lines the mid-bay and black lines the outer bay

0.189; Table 4). The highest cover of complex coral habitat was in shallow water (≤ 10 m) on mid-bay reefs ($\sim 51\%$), (all Tukey's comparisons < 1 to 10 m, $p > 0.9$; all comparisons < 10 m against > 10 m, $p < 0.05$), and varied substantially in the shallowest 1 m (Table 2). Although complex coral cover was twice as high at 20 m on mid-bay ($\sim 17\%$) and offshore reefs ($\sim 19\%$) than inshore reefs ($\sim 9\%$), cover was not significantly different between bay positions at depths below 5 m (Table 2).

Relative influence of depth and habitat on reef fish distributions

Depth distributions were not strongly habitat limited. After accounting for between-reef differences, the combined influences of depth and complex coral cover explained 55% of the variation in overall fish density and was the best-fit model (Table 1, Model set 3). However, depth alone explained a similarly high proportion of variation (50%) (Table 1, Model set 1a), which was almost twice that explained by

complex coral cover alone (28%) (Table 1, Model set 2). Similarly, more than double the number of density distributions in the 51 'top-ranked' species varied with depth (41 species, 80%) than with complex coral cover (13 species, 25%) (Table 3). In addition, 11 of the 13 top-ranked species (85%) with correlations to complex coral cover were broadly distributed to 20 m or deeper, with the other 2 species limited to the shallowest 5 m.

Fish-habitat relationships along the depth gradient

Fish-habitat relationships were not strongly depth dependent. The strength of relationships between total fish density and the availability of complex coral cover did not decline uniformly with depth (Fig. 6, Table 5). Positive correlations between the 2 occurred at < 1 m and at 20 m, but not at other depths. Overall, 18% of all species distributions (22 of 123 species) were positively correlated to the availability of complex coral habitat when considered across all depths (Fig. 7a), and 36% (44 species) were corre-

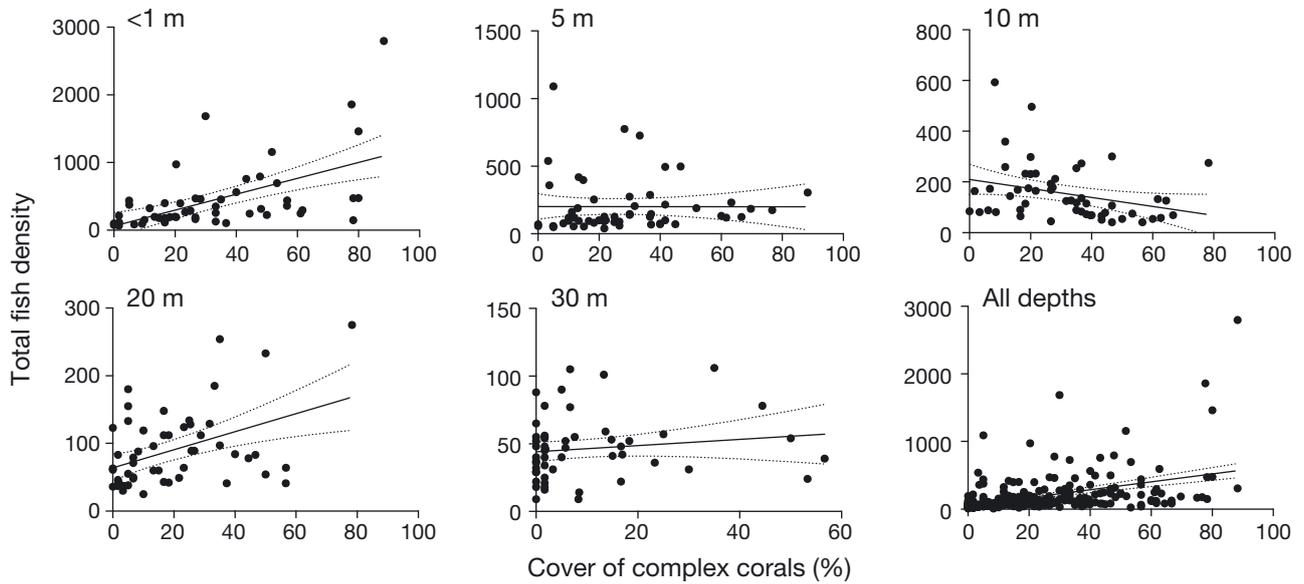


Fig. 6. Correlations between total fish density and cover of complex corals at 5 depths along a gradient from <1 to 30 m, and across all depths. Regressions at <1, 10, 20 m and across all depths are significant. Dotted lines represent 95% confidence intervals of the mean

lated to at least 1 benthic habitat category (Fig. 7b). Again, there was no uniform decline with increasing depth in the number of species distributions correlated to the cover of complex coral habitat or other

benthic habitats (Fig. 6). However, association with complex coral habitat was stronger among fish species characteristic of shallow-water assemblages than characteristically deep-water species. The distributions of 8 of the 14 (57%) species most characteristic of the fish assemblages between <1 and 5 m (see Fig. 4) were correlated to the availability of complex coral habitat when habitat availability was considered across all depths, and 71% (10 species) were negatively correlated to laminar coral cover. In contrast, the densities of 55% of fish species characteristic of assemblages below 10 m (5 of 9 species) were

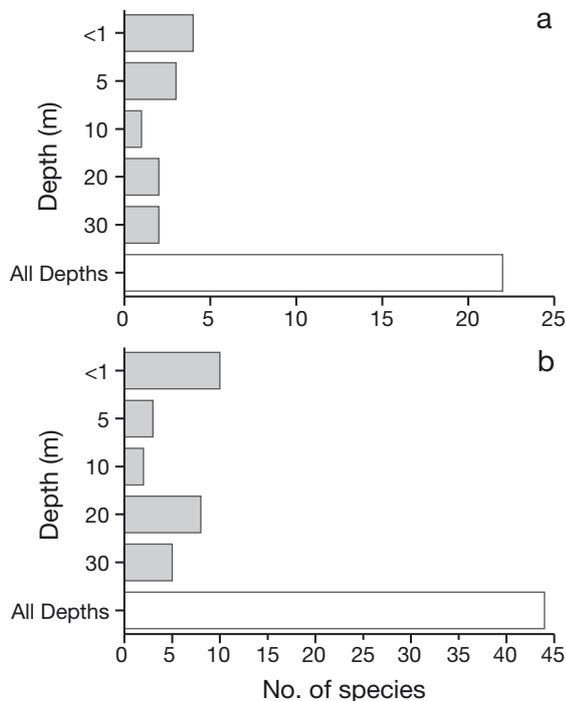


Fig. 7. Number of species with distributions that have a significant positive correlation ($\alpha = 0.0031$ with Bonferroni adjustment) within each depth, and across all depths, to (a) complex coral cover and (b) one or more benthic habitat types at each depth

Table 5. Summary statistics for relationships between fish and coral habitat distributions at various depths. NS: not significant ($\alpha = 0.05$)

Depth (m)	Correlation (R^2)	Regression (Rho)	p-value
Fish density & complex coral cover			
<1–30	0.179		<0.001
<1	0.365		<0.001
5	-		NS
10	0.115		0.023
20	0.146		0.007
30	-		NS
Composition of fish & benthic communities			
<1–30		0.231	0.01
<1		0.285	0.01
5		-	NS
10		-	NS
20		0.154	0.03
30		0.203	0.01

positively correlated with laminar coral cover, and 3 species were negatively related to the availability of complex coral habitat. Only 2 characteristically deep-water species were correlated strongly with complex coral habitat cover.

A total of 23% of overall variation in the composition of the fish community was explained by changes in the benthic structure, and the structures of fish and benthic communities were significantly correlated within 3 of the 5 depth strata (Table 5). Again, however, there was no linear trend through the depth gradient. While the strongest correlations were in the shallowest water (<1 m), there was no correlation at either 5 or 10 m, and significant correlations occurred at 20 and 30 m.

DISCUSSION

The presence of contiguous reef habitat to depths ≥ 40 m in Kimbe Bay allowed us to address a number of questions concerning depth distributions of reef fishes and the extent to which depth ranges are influenced by habitat availability and bay position across a wide depth range, from the surface to upper mesophotic depths. Overall, our results suggest that a considerable proportion of fish species can occur across a broad depth range, and may be capable of utilising deep refuges if habitat degradation is depth-dependent. Furthermore, depth ranges and/or abundances at greater depths increased with distance offshore for many species, suggesting that deep habitats on clear-water, offshore reefs may be particularly important refuges. However, approximately 25% of all species were restricted to shallow depths (<5 m), suggesting some species are unlikely to benefit from potential depth refuges unless their depth ranges shift.

As expected, the overall abundance and mean species richness of reef fishes per unit area declined significantly with increasing depth, while the total number of species declined by only 15% between <1 and 30 m. The abundance of the majority of individual fish species also varied with depth, with the greatest changes in community composition occurring between the shallowest depth (<1 m) and all other depths. While some species were restricted to a narrow depth range, others were broadly distributed throughout the depth gradient, particularly on offshore reefs. At greater depths (20 to 30 m), more fish species and higher abundances occurred on offshore reefs. This resulted in similar total fish abundance and species richness between deep offshore and shallow inshore reefs.

Although depth was the most important single factor influencing fish distributions, some species were also strongly associated with habitat structure. Despite high hard coral cover at all depths and bay positions, the functional composition of coral habitat varied with depth, which facilitated deep distributions of some fish species, including some coral specialists, but not others. The strength of association between fishes and complex corals did not decline uniformly with depth, with some of the strongest correlations occurring at 20 m.

Fish distributions along the depth gradient

The general depth-related declines in abundance and species richness observed in Kimbe Bay are consistent with previous studies (e.g. Bouchon-Navaro 1981, Nagelkerken et al. 2001, Brokovich et al. 2008, Kahng et al. 2010). Species depth distributions varied substantially, and species with narrow depth ranges occurred most often in shallow depths, which is consistent with previous observations and experiments showing narrower distributions in shallow-water specialists versus deep-water specialists (Bean et al. 2002, Srinivasan 2003, Jankowski et al. 2015).

The average depth distributions in Kimbe Bay were narrower than those reported for a comparable, but deeper gradient in Puerto Rico. In the present study, 25% of all species occurred only in the shallowest 5 m, a further 25% of species occurred from <1 to 30 m, and more than half of all recorded species occurred at depths ≥ 20 m, with a further 10% distributed from <1 to 40 m on offshore reefs. Garcia-Sais (2010) surveyed at 30 and 40 m, and from 15 to 50 m in 2 different Puerto Rican locations, and reported species assemblages similar to nearby shallow reefs, with three-quarters of all species observed deeper than 30 m, and two-thirds observed at all depths. Similarly, ~80% of species surveyed from 32 to 78 m at Johnstone Atoll in the central Pacific are also known from shallow-water surveys (Wagner et al. 2014). The inclusion of the more unique fish assemblage in shallower water in the present study, as well as regional differences in fish biodiversity and the differing taxonomic breadth of the studies, may account for some of these differences. The inclusion of more fish families, particularly larger bodied species and some planktivores (e.g. Anthiinae) that tend to have broader and deeper depth ranges (e.g. Kulbicki et al. 2015, Bridge et al. 2016) would likely increase proportional species richness at deeper depths in Kimbe Bay.

Influence of bay position on depth distributions

Our study confirmed that both depth and bay position influenced the composition of fish communities in Kimbe Bay. The effects of bay position, including changes in species richness and composition offshore, were similar to previous studies along cross-shelf gradients in other regions (e.g. Williams 1982, Malcolm et al. 2010), with differences generally separating inshore reefs from those farther offshore. The simultaneous assessment of both depth and bay position here enabled us to provide the first analysis of the interaction between these 2 factors. Half of the species distributions that varied by depth also varied among bay positions. Many species had broader depth ranges on offshore reefs, where community assemblages were more similar between depths. Importantly, deep offshore reefs in this study showed substantial ecological value, supporting high fish diversity and densities equivalent to shallow inshore reefs.

Depth influences on habitat availability and fish–habitat relationships

Hard coral cover was prominent throughout the depth gradient and was high at 30 m compared to most contemporary shallow reef systems (Gardner et al. 2003, Bellwood et al. 2004, Wilson et al. 2009, Chong-Seng et al. 2012, De'ath et al. 2012). The cover of habitat-forming complex coral declined with increasing depth in Kimbe Bay, but at 20 and 30 m was comparable to or higher than on shallow reefs that have 'recovered' from severe disturbances in other regions (e.g. Wilson et al. 2009, Chong-Seng et al. 2012). Bay position exerted less influence on coral cover and habitat structure than expected, and was most prominent in shallow mid-bay habitats, where complex coral cover was twice as high compared to equivalent depths both inshore and offshore. This potentially results from mid-bay reefs being less exposed to storms than offshore reefs (*sensu* Roberts et al. 2015) and less influenced by anthropogenic and terrestrial pressures than reefs inshore (Jones et al. 2004). There was some evidence to suggest deeper extensions of complex coral habitat availability on offshore reefs, where cover at 20 m was generally ~50% higher than on inshore reefs, although there was some variability among reefs.

The strength of relationships between reef fish distributions and benthic habitat structure overall was similar to other studies from shallow depths (e.g. Wil-

son et al. 2008), with the strongest relationships observed at the shallowest depth (<1 m). Surprisingly, however, the strength of relationships did not decline uniformly with depth; instead, fish–habitat relationships were weak or non-existent at 5 and 10 m, but strong at 20 m. Jankowski et al. (2015) recently reported an increasing strength of fish–coral habitat relationships with depth to 20 m on the Great Barrier Reef, suggesting general depth patterns may differ from expectations of a general decline in fish–coral associations with increasing depth.

The relatively weak fish–habitat relationships at 5 to 10 m were surprising, given that some species observed at these depths are known to associate strongly with live coral (Srinivasan 2006, Bonin 2012, Boström-Einarsson et al. 2013). Potentially, variation in microhabitat structure among depths may account for this observation and further, more detailed analysis within depths may be warranted to further elucidate fine-scale patterns of microhabitat use.

The distributions of characteristic shallow-water species tended to correlate positively with complex coral habitat availability and/or negatively with laminar coral cover, whereas the distributions of characteristic deep-water species were more often positively correlated with laminar coral cover. However, the distributions of some deep-water species were related to the continued presence of complex corals to at least 30 m. For example, *Chrysiptera arnazae* (formerly *C. parasema*) associates strongly with complex coral habitat in waters ≤10 m deep (Srinivasan 2006, Bonin 2012, Boström-Einarsson et al. 2013), and is considered highly vulnerable to coral habitat loss in shallow water (Bonin 2012). The relationships in deeper water recorded here may therefore reduce the vulnerability of this and similar species from shallow-water coral loss.

Comparing the influences of depth and habitat availability

Depth-related changes in habitat structure significantly influenced overall reef fish abundance and many species distributions along the depth gradient. However, depth alone explained more variation in overall fish abundance and influenced more species distributions than did depth-related variation in habitat availability. Although finer-scale surveys of micro-habitat association may reveal more about the importance of fish–habitat relationships at deeper depths, it is probable that depth influences other important ecological processes than habitat composi-

tion alone, as suggested by experimental studies (Srinivasan 2006).

It is unclear why some coral-associated species did not occur in deep water even where suitable habitat was available, while others did. Depth preferences may be related to other ecological processes that control species niches such as differences in settlement depth of juveniles (Leis 1986, 1991, Srinivasan 2003), adult dispersal capacity (e.g. Frederick 1997), interspecific competition (e.g. Boström-Einarsson et al. 2013), or predation pressure (e.g. Beukers & Jones 1998). Likewise, subtle physiological differences may also influence the success of species or individuals on deep reef habitat (e.g. Brokovich et al. 2010). It is not clearly understood if deeper habitat use incurs higher energetic costs, though some shallow-water species experience a greater cost of being outside their preferred depth range than deeper species (Srinivasan 2003), while 1 species of rubble-dwelling damselfish is known to alter energy allocation according to depth (Hoey et al. 2007).

Are deep reefs a potential refuge?

Shallow coastal reefs are often more vulnerable to degradation and are likely to be at greater risk from disturbances such as storms, bleaching and sedimentation than reefs in deeper water and farther offshore (Bridge et al. 2013). Consequently, fish species restricted to shallow, inshore habitats and that are strongly dependent on live coral are most at risk from habitat degradation (e.g. Munday 2004, Wilson et al. 2008, Graham et al. 2011). Deep, offshore reefs may help mitigate disturbance-associated declines at local to regional scales by providing a refuge for species with more general habitat requirements, or coral-associated species with broad depth distributions. Approximately a quarter of our study species occurred exclusively in the shallowest 5 m and the fish community at <1 m depth was more abundant, more diverse and had stronger relationships to complex coral habitat at both community and species levels than at deeper depths. This suggests that a considerable proportion of species are likely to be substantially affected by reef degradation (Jones et al. 2004, Munday 2004, Wilson et al. 2008, Graham et al. 2011) and are unlikely to benefit from a depth refuge. However, the majority of species in Kimbe Bay can occur in relatively deep water, and may be capable of persisting through disturbance events in deep, offshore habitats. Deep offshore sites supported a high abundance of complex coral habitat, and were occupied by

many fish species with both general and highly specialized habitat requirements. Many species were highly flexible in their spatial distribution and/or habitat requirements, with as many as half extending into deeper water farther offshore. A quarter of all species were broadly distributed from <1 to 30 m, and half were present at 20 m. In addition, more than half of the most abundant species were distributed independently of complex coral habitat availability. Surprisingly, a high proportion of the abundant species with distributions correlated to complex coral availability were present to at least 20 m, and in most cases 30 m, suggesting that depth offers a potential refuge even for some coral specialists.

Our study contributes to an emerging body of work that suggests deep reefs may act as a refuge for reef fishes if they are less exposed to disturbances. A more complete understanding of the refuge potential will require further detailed assessments of the ecological and physiological processes that control species niches and depth ranges along extended depth gradients. Tests for the detrimental impacts and sub-lethal effects of changes in micro-habitat use, diet, prey quality, movement ecology and competitor densities are well established along horizontal ecological gradients for many reef fish species, and should be easily adapted to studies along depth gradients.

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LITERATURE CITED

- Allen GR, Steene R, Humann P, Deloach N (2003) Reef fish identification: tropical Pacific. New World Publications, Jacksonville, FL
- ✦ Bean K, Jones GP, Caley M (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, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- ✦ Bellwood DR, Baird AH, Depczynski M, González-Cabello A, Hoey AS, Lefèvre CD, Tanner JK (2012) Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* 170:567–573
- ✦ Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- ✦ 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

- Boström-Einarsson L, Bonin MC, Munday PL, Jones GP (2013) Strong intraspecific competition and habitat selectivity influence abundance of a coral-dwelling damselfish. *J Exp Mar Biol Ecol* 448:85–92
- Bouchon-Navaro Y (1981) Quantitative distribution of the Chaetodontidae on a reef of Moorea Island (French Polynesia). *J Exp Mar Biol Ecol* 55:145–157
- Bridge TCL, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. *Nat Clim Change* 3: 528–530
- Bridge T, Hoey A, Campbell S, Muttaqin E, Rudi E, Fadli N, Baird AH (2014) Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000 Res* 2:187
- Bridge TC, Luiz OJ, Coleman RR, Kane CN, Kosaki RK (2016) Ecological and morphological traits predict depth-generalist fishes on coral reefs. *Proc R Soc B* 283: 20152332
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Mar Ecol Prog Ser* 371:253–262
- Brokovich E, Ben-Ari T, Kark S, Kiflawi M, Dishon G, Iluz D, Shashar N (2010) Functional changes of the visual system of the damselfish *Dascyllus marginatus* along its bathymetric range. *Physiol Behav* 101:413–421
- Carpenter KE, Abrar M, Aeby G, Aronson RB and others (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–563
- Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The influence of coral reef benthic condition on associated fish assemblages. *PLOS ONE* 7:e42167
- Clarke KR, Gorley RN (2006) User manual/tutorial. Primer-E, Plymouth
- Cogbill CV, White PS (1991) The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. *Vegetatio* 94:153–175
- Coker DJ, Graham NAJ, Pratchett MS (2012) Interactive effects of live coral and structural complexity on the recruitment of reef fishes. *Coral Reefs* 31:919–927
- Connolly SR, Bellwood DR, Hughes TP (2003) Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology* 84:2178–2190
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27 year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci USA* 109: 17995–17999
- Demidenko E (2013) Mixed models: theory and applications with R. John Wiley & Sons, Hoboken, NJ
- Done TJ (1983) Coral zonation: its nature and significance. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, p 107–147
- Emslie MJ, Pratchett MS, Cheal AJ, Osborne K (2010) Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs* 29:705–715
- Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19: 303–309
- Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Mar Pollut Bull* 51:384–398
- Fabricius KE, Logan M, Weeks SJ, Lewis SE, Brodie J (2016) Changes in water clarity in response to river discharges on the Great Barrier Reef continental shelf: 2002–2013. *Estuar Coast Shelf Sci* 173:A1–A15
- Frederick JL (1997) Post-settlement movement of coral reef fishes and bias in survival estimates. *Mar Ecol Prog Ser* 150:65–74
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Garcia-Sais J (2010) Reef habitats and associated sessile-benthic and fish assemblages across a euphotic-mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs* 29:277–288
- 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 (2000) Global patterns in biodiversity. *Nature* 405:220–227
- Graham NA, Chabanet P, Evans RD, Jennings S and others (2011) Extinction vulnerability of coral reef fishes. *Ecol Lett* 14:341–348
- Graham NA, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97
- Hawkins BA, Field R, Cornell HV, Currie DJ and others (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Hoey J, McCormick MI, Hoey AS (2007) Influence of depth on sex-specific energy allocation patterns in a tropical reef fish. *Coral Reefs* 26:603–613
- Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Jankowski MW, Graham NAJ, Jones GP (2015) Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth-refuge hypothesis. *Mar Ecol Prog Ser* 540:203–215
- Jarrett B, Hine A, Halley R, Naar D and others (2005) Strange bedfellows: deep-water hermatypic coral reef superimposed on a drowned barrier island, southern Pulley Ridge, SW Florida platform margin. *Mar Geol* 214: 295–307
- Jones GP, McCormick MI, Srinivasan M, Eagle JV, Paine RT (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Kahng S, Garcia-Sais J, Spalding H, Brokovich E and others (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29:255–275
- Karr JR, Freemark KE (1983) Habitat selection and environmental gradients: dynamics in the “stable” tropics. *Ecology* 64:1481–1494
- Kleypas JA, McManus JW, Meuz LAB (1999) Environmental limits to coral reef development: where do we draw the line? *Am Zool* 39:146–159
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32: 1259–1269

- Kulbicki M, Parravicini V, Mouillot D (2015) Patterns and processes in reef fish body size. In: Mora C (ed) Ecology of fishes on coral reefs. Cambridge University Press, Cambridge, p 104–115
- ✦ Leis JM (1986) Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Mar Biol* 90:505–516
- ✦ Leis JM (1991) Vertical distribution of fish larvae in the Great Barrier Reef Lagoon, Australia. *Mar Biol* 109:157–166
- ✦ Lenth RV, Hervé M (2014) lsmeans: least-squares means. R package version 2.11. CRAN.R-project.org/package=lsmeans
- ✦ Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- ✦ Malcolm HA, Jordan A, Smith SD (2010) Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. *Mar Biodivers* 40:181–193
- ✦ Martin TE (2001) Abiotic vs biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* 82:175–188
- ✦ McGehee MA (1994) Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105:243–255
- ✦ McWilliams JP, Côté IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature induced coral bleaching in the Caribbean. *Ecology* 86:2055–2060
- ✦ Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks J (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* 92:2285–2298
- ✦ Muir PR, Wallace CC, Done T, Aguirre JD (2015) Limited scope for latitudinal extension of reef corals. *Science* 348:1135–1138
- ✦ Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Glob Change Biol* 10:1642–1647
- ✦ Nagelkerken I, van der Velde G, Cocheret de la Morinière E (2001) Fish feeding guilds along a gradient of bay biotopes and coral reef depth zones. *Aquat Ecol* 35:73–86
- ✦ Nanami A, Nishihira M, Suzuki T, Yokochi H (2005) Species-specific habitat distribution of coral reef fish assemblages in relation to habitat characteristics in an Okinawan coral reef. *Environ Biol Fishes* 72:55–65
- ✦ Noonan SHC, Jones GP, Pratchett MS (2012) Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish. *Mar Ecol Prog Ser* 456:127–137
- ✦ Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. CRAN.R-project.org/package=nlme
- ✦ Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W and others (2013) Global imprint of climate change on marine life. *Nat Clim Change* 3:919–925
- ✦ Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- ✦ Roberts TE, Moloney JM, Sweatman HPA, Bridge TCL (2015) Benthic community composition on submerged reefs in the central Great Barrier Reef. *Coral Reefs* 34:569–580
- ✦ Schall JJ, Pianka ER (1978) Geographical trends in numbers of species. *Science* 201:679–686
- ✦ Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J (2014) A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology* 95:1663–1673
- ✦ Srinivasan M (2003) Depth distributions of coral reef fishes: the influence of microhabitat structure, settlement, and post-settlement processes. *Oecologia* 137:76–84
- Srinivasan M (2006) Recruitment in time and space: the dynamics and distributions of reef fish populations on a low latitude coral reef. PhD dissertation, James Cook University, Townsville
- ✦ Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81:2714–2729
- ✦ Wagner D, Kosaki RK, Spalding HL, Whitton RK and others (2014) Mesophotic surveys of the flora and fauna at Johnston Atoll, Central Pacific Ocean. *Mar Biodivers Rec* 7:e68
- Wilkinson C (ed) (2004) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville
- ✦ Williams DM (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1:35–43
- ✦ Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Glob Change Biol* 12:2220–2234
- ✦ 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 S, Dolman A, Cheal A, Emslie M, Pratchett MS, Sweatman HP (2009) Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* 28:3–14
- ✦ Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Mar Ecol Prog Ser* 376:45–54

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