

# Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific

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**ABSTRACT:** We conducted *in situ* diver surveys describing the spatial structure of reef fish assemblages at Kingman Reef, an unexploited and remote atoll in the central North Pacific. Structural patterns reflect natural ecological processes that are not influenced by fishing or other anthropogenic factors. The most striking feature of this assemblage is an inverted biomass pyramid dominated by apex predators, primarily sharks and large snappers, across all depth and habitat strata examined. This pattern is most pronounced at greater depths (20 m) on the fore reef. Apex predators dominated to lesser extents in back-reef, patch-reef, and shallow fore-reef habitats. Prey assemblage size spectra showed fewer large prey and greater numbers of prey from small size classes at locations with greater piscivore biomass. Other patterns of prey abundance generally conformed to those previously observed at more commonly encountered, human-altered reefs (e.g. highest herbivore abundance on back reefs and shallower depths on the fore reefs; greater planktivore prevalence deeper on the fore reef). The latter patterns, however, inadvertently miss the less obvious differences in assemblage dynamics that result from alterations in the size structures of prey fish populations where apex predators have been heavily exploited or extirpated. The present study of a fully intact coral reef suggests that (1) piscivores are common across all habitats and depths, (2) the presence of predators does not lead to appreciable reductions in the biomass of other guilds, and (3) predators alter the size structure and therefore the potential productivity and energy flow of the ecosystem.

**KEY WORDS:** Predator-dominated ecosystem · Pristine atoll · Fish assemblage structure · Kingman Reef · Zonation

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## INTRODUCTION

Our understanding of what is natural in the marine environment is becoming increasingly compromised by the absence of locations that are unimpacted by human activities. Nowhere is this more evident than in coral reef ecosystems, where overexploitation and severe depletion are occurring on a global scale (Bellwood et al. 2004, Birkeland 2004, Pandolfi et al. 2005). Pollution, coastal development, and invasive species

all impact coral reefs locally, and climate change now is having a global effect on corals and reef ecosystems as a whole. Fishing, however, has historically exerted the most direct and pervasive influence on most reefs and other marine ecosystems (Jennings & Kaiser 1998, Jackson et al. 2001). Fisheries on coral reefs tend to first remove large long-lived and slow-growing predators and progressively shift towards smaller, less desirable species as resources decline (Jennings & Polunin 1996, Russ & Alcala 1996, Pauly et al. 1998). Predator-

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dominated coral reef ecosystems may well be the natural state, but they contain the species that are most rapidly removed by human activities, thus making the natural state difficult to observe in most cases.

Protected, remote locations are some of the few remaining examples of coral reefs without major anthropogenic influence. Ecological descriptions of the structure and functioning of ecosystems in the absence of human impacts, so-called ecological baselines, provide fundamental insights needed for conservation and restoration efforts (Knowlton & Jackson 2008, Sandin et al. 2008). Surveys of the fishes of uninhabited, remote sites in the northwestern Hawaiian Islands and the northern Line Islands (Friedlander & DeMartini 2002, DeMartini et al. 2008, Sandin et al. 2008) strongly support historical reports of great fish abundance and predator domination that characterized coral reefs before extensive fishing efforts occurred. Kingman Atoll in the northern Line Islands has been found to have greater total fish biomass and a greater proportion of apex predators (DeMartini et al. 2008, Sandin et al. 2008) than previously described for any coral reef ecosystem to date (McClanahan et al. 2007, Stevenson et al. 2007). Only surveys from Jarvis Island, also in the Line Islands, report larger fish biomass than Kingman (Sandin et al. 2008).

The surveys from Kingman and the other Line Islands have been limited to a narrow depth range on the fore reef (8 to 12 m depth; DeMartini et al. 2008, Sandin et al. 2008). Variation in lagoonal physiography precludes clear comparisons of back-reef and patch-reef habitats across these islands, and logistical constraints in accessing these remote locations have limited the number of fore-reef depth strata sampled to date. The objective of the present work was to describe the fish assemblage of pristine Kingman Atoll more extensively across habitat types and over a range of depths in order to develop a more detailed understanding of the structure of unaltered reef fish assemblages and provide a rare baseline for a coral reef atoll in the central Pacific.

## MATERIALS AND METHODS

**Site and sampling design.** Kingman Atoll is located at 6.4° N, 162.4° W and is the northern-most reef in the Line Island chain (Fig. 1). Kingman lies in the region of the eastward-flowing North Equatorial Countercurrent, which is typified by surrounding waters that are warmer and more oligotrophic than the more equatorial Line Islands to the south (Charles & Sandin 2009). No correlation between fish assemblage structure and oceanographic conditions, however, was observed in a previous study of the northern Line Islands (Sandin et

al. 2008). All resource extraction has been formally prohibited since 2000 when Kingman Atoll became a US National Wildlife Refuge. Prior to 2000, fish extraction is thought to have been generally low at Kingman because of its remote location and lack of emergent land (Maragos et al. 2008). Kingman is currently protected (since January 2009) as part of the Pacific Remote Islands Marine National Monument.

Kingman is a triangular atoll, with shallow (<2 m) reefs along the southern and northern sides that are connected by a deeper (>20 m) reef along the western terrace (Fig. 1). The atoll lacks permanent emergent land, although 2 small rubble islands lie near the eastern ends of the shallow reefs. The lagoon is generally deep (>30 m) with numerous large patch reefs, ranging from 50 to 200 m in diameter and extending to within 2 to 10 m from the surface. The lagoon side of the reef crest has a steeply sloped (30 to 50° inclination) back-reef habitat. The fore-reef habitat is fairly consistent along the northern and southern coasts, beginning with a gradually sloping terrace extending 30 to 60 m from the reef crest with a drop-off beginning at ~20 m depth. The benthos of each habitat is dominated largely by reef-building corals and crustose coralline algae (J. E. Smith et al. unpubl.).

Surveys were conducted using SCUBA around the entire atoll except for the western terrace, where it was too deep (>30 m on average) to conduct comprehensive surveys on SCUBA. Sampling locations were stratified by habitat type (i.e. fore reef, back reef, and patch reefs) at 10 m depth and by depth strata (5, 10, and 20 m) on the fore reef. Surveys were conducted by teams of paired divers swimming apace, with the 4 authors rotating between teams to distribute individual biases (DeMartini et al. 2008). Teams enumerated all fishes encountered within fixed-length (25 m) strip transects whose widths differed depending on fish body size (8 m wide for fishes  $\geq 20$  cm and 4 m for fishes <20 cm). While laying the transect line during the 'swim-out', divers surveyed adjacent and non-overlapping 4 m wide lanes for larger fish, focusing observations ahead in a 5 m long moving window. The swim-out tally was completed within 3 to 4 min. During the 'swim-back', divers quantified the smaller-bodied fish in adjacent 2 m wide lanes. These transect dimensions were selected to optimize data precision and accuracy, while maximizing cost efficiency of field effort (see Mapstone & Ayling 1998 for detailed exploration of survey methodology). The species identity and visually estimated length (in 5 cm increments of total length [TL]) were recorded for each individual fish. Cryptic species and individuals <3 cm TL were not tallied. A constant 3 transects were completed by each diver pair at each station, and a total of 14 to 16 stations were surveyed in each stratum (Fig. 1).

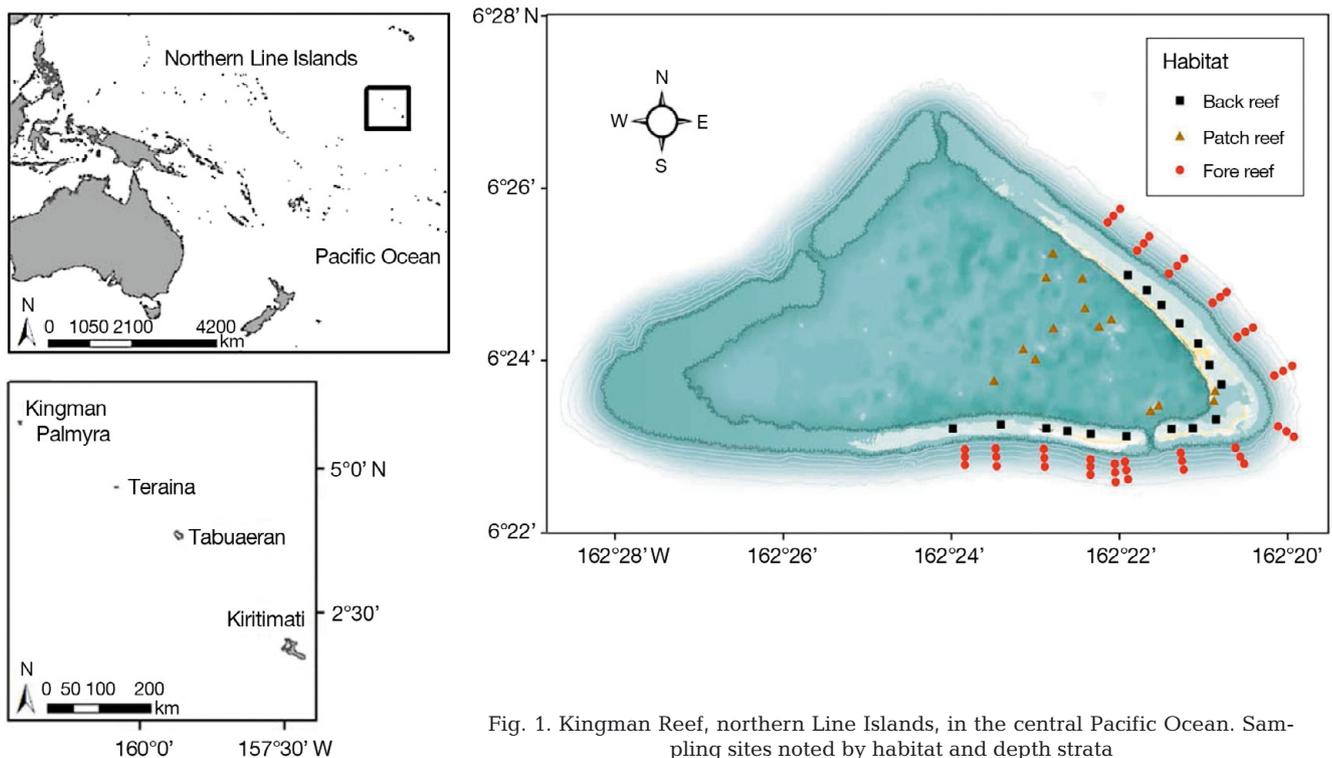


Fig. 1. Kingman Reef, northern Line Islands, in the central Pacific Ocean. Sampling sites noted by habitat and depth strata

The survey methodology was designed to minimize bias associated with *in situ* underwater visual censuses (Mapstone & Ayling 1998). Constraints on the focal window size and survey duration for the swim-out limited problems of over-counting large-bodied, vagile species. Use of 2 transect areas (4 m vs. 2 m lanes) compensates for some of the size-specific differences in density, namely that larger-bodied fish are typically less abundant than their smaller-bodied counterparts, addressing some concerns of differing patterns of variance across size classes. Further, by maintaining regular in-water and post-dive communication, the divers minimized potential issues of double counting and observer drift.

**Data types and statistical analyses.** Nonmetric multidimensional scaling (nMDS) and analysis of similarity (ANOSIM; Clarke & Gorley 2006) were used to evaluate spatial variation in numerical structure of the assemblages among habitat types at 10 m and among depth strata on the fore reef. A Bray-Curtis similarity matrix was created from the square-root-transformed mean fish numerical density matrix prior to conducting the nMDS. The ANOSIM R statistic represents pairs of strata that are either well separated ( $R > 0.75$ ), overlapping but clearly different ( $R > 0.5$ ), or barely separable at all ( $R < 0.25$ ).

Transects provided the input to generate estimates of species richness, diversity, and numerical and biomass densities. Richness was estimated as the total number

of species observed per station by the pair of divers. Species diversity was calculated using the Shannon index (Ludwig & Reynolds 1988):  $H' = -\sum_{i=1}^S (p_i \ln p_i)$ , where  $p_i$  is the proportion of all individuals counted that were of species  $i$ . Fish were tallied by length class, and individual-specific lengths were converted to body weights. In order to maximize comparability with existing studies, numerical density (abundance) was expressed as number of individuals per  $m^2$  and biomass was expressed as tonnes (t) per hectare (ha). The biomass of individual fish was estimated using the allometric length-weight conversion:  $W = aTL^b$ , where parameters  $a$  and  $b$  are species-specific constants,  $TL$  is total length in mm, and  $W$  is weight in grams. Length-weight fitting parameters were obtained from FishBase ([www.fishbase.org](http://www.fishbase.org)) and other published sources (Lettourneur 1998, Kulbicki et al. 2005) and the cross-product of individual weights and numerical densities was used to estimate biomass by species. Fishes were categorized into 4 functional trophic groups: primary consumers (herbivores, detritivores); secondary consumers—planktivores; secondary consumers—benthivores (benthic carnivores); and tertiary consumers (apex predators and other piscivores). Because diets of species change ontogenetically and with environment, we limited trophic categorization to these broad and robust groupings (Harmelin-Vivien 2002).

In order to isolate individual habitat effects on fish assemblage characteristics (i.e. species richness, abundance, biomass, and diversity), two 1-way ANOVAs were performed. Controlling for depth (10 m), we compared the assemblages across habitat types (3 levels: patch reef, back reef, and fore reef). Controlling for habitat type (fore reef), we compared assemblages across depths (3 levels: 5, 10, and 20 m). Stations were used as a blocking factor in the fore reef depth comparisons. Note that the data from the 10 m fore-reef habitat are used in both comparisons. Unplanned comparisons between pairs were examined using the Tukey-Kramer honestly significant difference (HSD) test for ANOVAs ( $\alpha = 0.05$ ). Numerical and biomass abundances were  $\ln(x + 1)$ -transformed prior to statistical analysis to conform to the assumptions of normality and homogeneity of variance (Zar 1999). We thereby tested the null hypotheses that fish assemblage characteristics differed neither among habitats at 10 m depth nor among depths in the fore-reef habitat. For reasons explained in the discussion, our predictions were that these metrics should generally increase from lagoonal patch reef to fore reef and with depth on the fore reef. There was no correlation between rugosity and numerical abundance (Spearman  $\rho = 0.15$ ,  $p = 0.47$ ) or biomass (Spearman  $\rho = 0.17$ ,  $p = 0.40$ ) and therefore habitat covariates were not used. Assemblage characteristics did not differ between windward and leeward locations on the fore reef (all  $p > 0.05$ ) and all stations in each habitat and depth stratum provided the basis for comparison with other habitat and depth strata.

Abundance and biomass of trophic groups were tested for differences among habitats at 10 m and among depths on the fore reef using multivariate analysis of variance (MANOVA). The multivariate test statistic Pillai's trace was used because it is robust to heterogeneity of variance and is less likely to involve type I errors than are comparable tests (Green 1979). We performed univariate ANOVAs when MANOVAs were significant. Canonical discriminant analysis was used to identify and display the nature of the significant differences among treatments found by the MANOVA. Trends in the trophic groups are represented as vectors given by correlations of these variables with the canonical variates. These vectors are plotted on the first 2 canonical axes, together with the treatment centroids and 95% confidence clouds. The strength of each variable in discriminating among groups is displayed graphically as the length of these vectors. The assumption of multivariate normality was validated prior to analysis.

Prey fish size spectra (Rochet & Trenkel 2003, Graham et al. 2005) were described for each habitat stratum by using least-squares regression to relate  $\log_{10}$ -

transformed numerical densities to body length. Lengths (5 cm size classes) were first standardized to the midpoint of the size distribution at the respective stratum to remove the correlation between slope and intercept (Dulvy et al. 2004, Graham et al. 2005). Size spectra were compared among reefs using least-squares analysis of covariance (ANCOVA). Pairwise comparisons of slopes were made using Student's  $t$ , computed as the difference between the 2 slopes divided by the pooled standard error of the difference between the slopes (Kleinbaum & Kupper 1978).

## RESULTS

### Comparisons among habitats at 10 m

The assemblage structure of fishes, based on abundance, formed distinct clusters in ordination space among habitats at 10 m (Global  $R = 0.77$ , Stress = 0.12; Fig. 2A). Samples within the fore-reef habitat were highly concordant and were well separated from both the back-reef (ANOSIM  $R = 0.91$ ) and patch-reef (ANOSIM  $R = 0.96$ ) habitats. The patch-reef samples

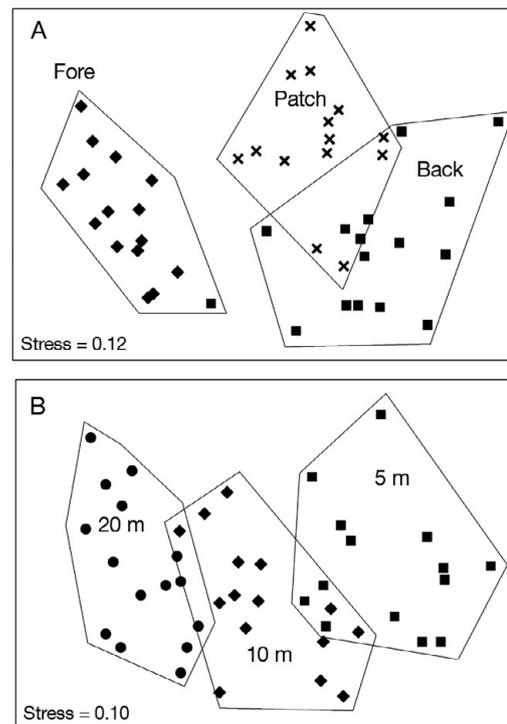


Fig. 2. Non-metric multidimensional scaling plots based on Bray-Curtis similarities of square-root transformed abundance of all fishes among (A) habitat strata at 10 m and (B) among depth strata on the fore reef. Minimum convex polygons drawn around each stratum

showed higher within-habitat concordance than the back reef but these 2 habitats were not well separated from one another in ordination space (ANOSIM  $R = 0.35$ ).

Species richness differed significantly among the 3 habitats at 10 m ( $F_{2,44} = 5.69$ ,  $p = 0.006$ ; Fig. 3A). The fore reef at 10 m averaged 32.2 species (1.6 SE) per transect and differed significantly from the patch reefs. The back reef was intermediate and did not differ significantly from the other 2 habitats. The number of individuals per  $m^2$  was nearly twice as high at 10 m on the fore reef compared to either the back-reef or patch-reef habitats ( $F_{2,44} = 15.3$ ,  $p < 0.001$ ; Fig. 3B). Fish biomass was 2.4 times higher on the fore reef at 10 m compared to patch reefs, with the back reef intermediate to the other 2 ( $F_{2,44} = 4.02$ ,  $p = 0.02$ ; Fig. 3C). Species diversity differed significantly among the 3 habitat types ( $F_{2,44} = 5.90$ ,  $p = 0.005$ ; Fig. 3D), with patch reefs having significantly lower diversity than the fore-reef and back-reef habitats.

Habitat types differed significantly in their trophic composition using MANOVA based on number of individuals (Pillai's trace,  $F_{8,80} = 9.3$ ,  $p < 0.001$ ; Fig. 4A). Planktivores dominated all 3 habitat types in numbers, followed by benthic carnivores, primary consumers, and tertiary consumers (Fig. 3B). The abundance of

planktivores on the fore reef was greater than the back-reef and patch-reef habitats ( $F_{2,44} = 8.4$ ,  $p < 0.001$ , fore > back, patch). Abundance of benthic carnivores was significantly higher on the fore reef compared to the back reef and patch reefs ( $F_{2,44} = 36.2$ ,  $p < 0.001$ , fore > back, patch). The back-reef habitat had significantly more primary consumers than the patch reefs; estimates on the fore reef were intermediate ( $F_{2,44} = 4.42$ ,  $p = 0.021$ , back > patch). The percentage abundance of tertiary consumers (apex predators) was low overall (range: 2.4 to 4.3%), but abundance was twice as high on the fore reef and back reef compared to patch-reef habitats ( $F_{2,44} = 3.17$ ,  $p = 0.05$ ; fore, back > patch).

Habitat types did not differ significantly in their trophic biomass composition (Pillai's trace,  $F_{8,80} = 1.6$ ,  $p = 0.128$ ). Manta rays *Manta birostris*, however, accounted for 91% of the planktivore biomass on the back reef while present at only 25% of back-reef stations and were not encountered in the other habitats. If manta rays are excluded from the analysis, trophic biomass is significantly different among habitats (Pillai's trace,  $F_{8,80} = 2.7$ ,  $p = 0.011$ ; Fig. 4B). Tertiary consumers accounted for 65% of total biomass on the fore reef, 44% on the back reef, and 42% on patch reefs. Biomass of tertiary consumers was 3.7 times

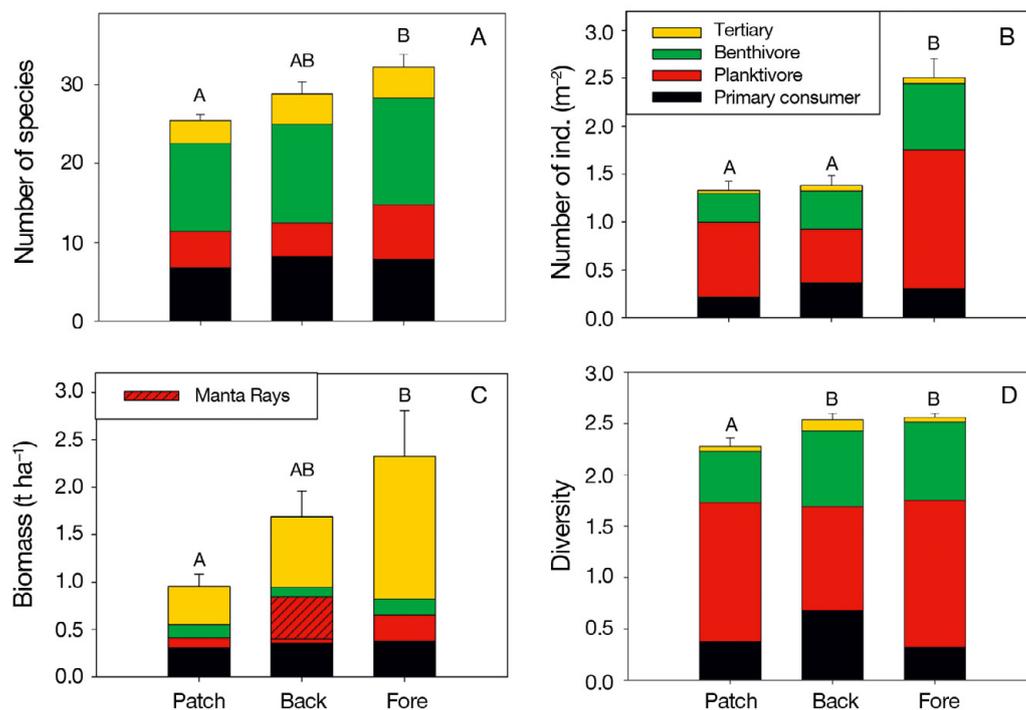


Fig. 3. Comparisons of fish assemblage characteristics (A: species, B: abundance, C: biomass, D: diversity) among habitat strata at 10 m. Letters above bars indicate results of unplanned multiple comparisons among habitat strata tested using Tukey's HSD tests ( $\alpha = 0.05$ ). Strata with the same letter are not significantly different. Values are means + SE. See 'Results' for ANOVA results

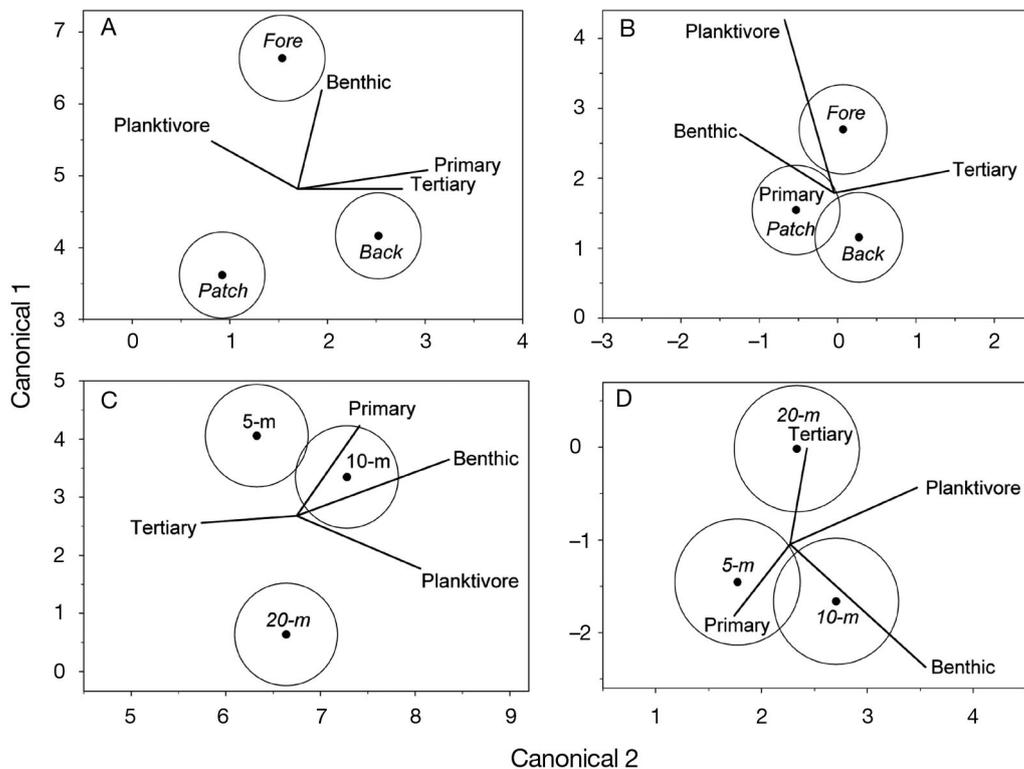


Fig. 4. Canonical discriminant analysis of the difference in trophic groups among habitat types and by depth on the fore reef. Treatment (habitat and depth) centroids and 95% confidence clouds are plotted together with the direction and importance of trends in trophic group. (A) Numerical abundance and (B) biomass (manta rays excluded) by habitat at 10 m, and (C) numerical abundance and (D) biomass by depth on the fore reef

higher on the fore reef compared to patch reefs and 2 times higher than on the back reef ( $F_{2,44} = 3.6$ ,  $p = 0.04$ ). Shark biomass alone showed a similar pattern ( $F_{2,44} = 5.4$ ,  $p = 0.011$ ; 20 m > 5 m). Primary consumers represented 32% of the biomass on patch reefs, 21% on the back reef, and 16% on the fore reef ( $F_{2,44} = 0.38$ ,  $p = 0.68$ ). Nearly 29% of the biomass on the back reef consisted of planktivores, while this trophic group accounted for only 12% of the biomass on the fore reef and 10% on patch reefs. With manta rays excluded, biomass of planktivores was significantly lower on the back reef than the fore reef, with patch-reef biomass of planktivores intermediate ( $F_{2,44} = 6.7$ ,  $p = 0.003$ , fore > back). Benthic carnivores were most prevalent on patch reefs, comprising 15% of total biomass there but only 6 and 7% on the back reef and fore reef, respectively ( $F_{2,44} = 2.28$ ,  $p = 0.11$ ).

A planktivorous damselfish, the bicolor chromis *Chromis margaritifer*, accounted for 17% of total abundance on the back reef, followed by the neon damselfish *Pomacentrus coelestis* (11%) and the striated surgeonfish *Ctenochaetus striatus* (10%; Table 1). Patch reefs were also dominated by bicolor chromis (30%) and neon chromis (11%), with the yellowfin

damselfish *Dascyllus auripinnis* contributing an additional 9% by number. By contrast, the 10 m fore-reef habitat assemblage was dominated numerically (15%) by the olive basslet *Pseudanthias olivaceus*, a regional endemic. The blacktail chromis *Chromis vanderbilti* was second in abundance (12%), followed by the midget chromis *Chromis acares* (12%).

The grey reef shark *Carcharhinus amblyrhynchos* was the largest contributor to overall biomass among all habitats pooled at 10 m (Table 2). This species accounted for 38% of the biomass on the fore reef, 13% on the patch reefs, and 13% on the back reef. The twinspot red snapper *Lutjanus bohar* ranked second in total biomass on the fore reef (14%), followed by the whitetip reef shark *Triaenodon obesus*, which contributed an additional 9%. *Manta birostris* ranked first in total biomass on the back reef (26%) but were encountered infrequently (see 2 paragraphs above). If manta rays are excluded, red snapper comprised 23% of all fish biomass on the back reef, followed by grey reef sharks (18%). The steephead parrotfish *Chlorurus microrhinos* was the most dominant species by weight on the patch reefs (16%), followed by grey reef shark (13%) and red snapper (12%).

### Comparisons among depths on the fore reef

The assemblage structure of fishes based on abundance formed distinct clusters in ordination space among depth strata on the fore reef (Global R = 0.61, Stress = 0.10; Fig. 2B). The 5 m and 20 m depth strata formed distinct clusters that were well separated in ordination space (ANOSIM R = 0.94). The fish assemblage at 10 m overlapped with both the 5 m assemblage (ANOSIM R = 0.43) and the 20 m assemblage (ANOSIM R = 0.50).

Species richness differed among the 3 fore-reef depth strata ( $F_{2,44} = 10.6$ ,  $p < 0.001$ ; Fig. 5A). The lowest species richness was found at the 5 m stratum (27.7 [0.8 SE]), followed by the 10 m (32.2 [0.8 SE]) and 20 m strata (34.4 [1.0 SE]). Numbers per  $m^2$  at 20 m were more than twice as high as those at 5 m and 1.5 times higher than at 10 m ( $F_{2,44} = 29.5$ ,  $p < 0.001$ ; Fig. 5B). Fish biomass at 20 m on the fore reef was 1.8 times higher than the 5 m depth stratum and 1.3 times greater than the 10 m stratum. Biomass at 20 m was significantly greater than at 5 m, with 10 m being intermediate ( $F_{2,44} = 3.6$ ,  $p = 0.04$ ; Fig. 5C). Diversity was highest at the 10 m depth, followed by the 5 m stratum, with diversity in the 20 m stratum significantly lower than the other 2 ( $F_{2,44} = 10.3$ ,  $p < 0.001$ ; Fig. 5D).

Depth strata differed significantly in their trophic composition using MANOVA based on number of individuals (Pillai's trace,  $F_{8,80} = 7.3$ ,  $p < 0.001$ ; Fig. 4C). Plankti-

vores accounted for 43% of numerical abundance at 5 m, 58% at 10 m, and 81% at 20 m. These fishes were 4.0 times and 2.2 times more numerous at 20 m versus 5 m and 10 m, respectively ( $F_{2,44} = 40.0$ ,  $p < 0.001$ ,  $20\text{ m} > 10\text{ m} > 5\text{ m}$ ). Benthic carnivores were the next most numerous trophic group and were statistically indistinguishable between 5 and 10 m, each of which was significantly higher than at 20 m ( $F_{2,44} = 15.9$ ,  $p < 0.001$ ,  $20\text{ m} > 10\text{ m}$ ,  $5\text{ m}$ ). The percentage abundance of primary consumers ranged from 5% at 20 m to 18% at 5 m and was significantly lower at 20 m compared to the 2 shallower depth strata ( $F_{2,44} = 14.6$ ,  $p < 0.001$ ,  $20\text{ m} > 10\text{ m}$ ,  $5\text{ m}$ ). Tertiary consumer abundance did not significantly differ among depths ( $F_{2,44} = 2.4$ ,  $p = 0.11$ ) and ranged from 2% at 20 m to 3% at 5 m (Fig. 5B).

Trophic composition differed significantly among depth strata based on biomass (Pillai's trace,  $F_{8,80} = 3.3$ ,  $p = 0.002$ ; Fig. 4D). Tertiary consumer biomass, as a percentage of the total, ranged from 61% at 5 m to 77% at 20 m (Fig. 5C). Biomass of tertiary consumers was 2.2 times higher at 20 m compared to 5 m and 1.5 times higher than at 10 m ( $F_{2,44} = 4.17$ ,  $p = 0.03$ ;  $20\text{ m} > 5\text{ m}$ ). This pattern also held true when only sharks were considered ( $F_{2,44} = 3.9$ ,  $p = 0.027$ ;  $20\text{ m} > 5\text{ m}$ ). Primary consumer biomass ranged from 8% of total biomass at 20 m to 24% at 5 m ( $F_{2,44} = 3.3$ ,  $p = 0.05$ ;  $5\text{ m} = 10\text{ m} > 20\text{ m}$ ). Benthic carnivores comprised 4% of total biomass at 20 m, 7% at 10 m, and 8% at 5 m, with biomass at 10 m significantly higher than the 20 m stratum

Table 1. Numerical abundance of top 10 species in each habitat at 10 m. Species ordered by overall percentage representation in habitats (Rep., %). Abundance = ind.  $m^{-2}$ , mean  $\pm$  SE

| Patch reef                       |                 |      | Back reef                        |                 |      | Fore reef                               |                 |      |
|----------------------------------|-----------------|------|----------------------------------|-----------------|------|---|-----------------|------|
| Species                          | Abundance       | Rep. | Species                          | Abundance       | Rep. | Species                                 | Abundance       | Rep. |
| <i>Chromis margaritifer</i>      | 0.40 $\pm$ 0.07 | 30.1 | <i>Chromis margaritifer</i>      | 0.23 $\pm$ 0.05 | 16.9 | <i>Pseudanthias olivaceus</i>           | 0.37 $\pm$ 0.11 | 14.7 |
| <i>Pomacentrus coelestis</i>     | 0.15 $\pm$ 0.09 | 11.4 | <i>Pomacentrus coelestis</i>     | 0.15 $\pm$ 0.05 | 11.0 | <i>Chromis vanderbilti</i>              | 0.30 $\pm$ 0.06 | 12.1 |
| <i>Dascyllus auripinnis</i>      | 0.11 $\pm$ 0.02 | 8.6  | <i>Ctenochaetus striatus</i>     | 0.14 $\pm$ 0.03 | 10.2 | <i>Chromis acares</i>                   | 0.30 $\pm$ 0.07 | 12.0 |
| <i>Caesio teres</i>              | 0.05 $\pm$ 0.02 | 3.6  | <i>Siphamia versicolor</i>       | 0.08 $\pm$ 0.09 | 5.6  | <i>Chromis margaritifer</i>             | 0.23 $\pm$ 0.04 | 9.1  |
| <i>Acanthurus nigricans</i>      | 0.05 $\pm$ 0.01 | 3.6  | <i>Acanthurus nigricans</i>      | 0.07 $\pm$ 0.01 | 4.8  | <i>Thalassoma quinquevittatum</i>       | 0.16 $\pm$ 0.03 | 6.4  |
| <i>Ctenochaetus striatus</i>     | 0.05 $\pm$ 0.01 | 3.5  | <i>Dascyllus auripinnis</i>      | 0.07 $\pm$ 0.02 | 4.7  | <i>Plectroglyphidodon johnstonianus</i> | 0.10 $\pm$ 0.01 | 4.0  |
| <i>Ctenochaetus cyanocheilus</i> | 0.05 $\pm$ 0.01 | 3.4  | <i>Eviota albolineata</i>        | 0.06 $\pm$ 0.02 | 4.5  | <i>Acanthurus nigricans</i>             | 0.10 $\pm$ 0.01 | 3.9  |
| <i>Eviota albolineata</i>        | 0.04 $\pm$ 0.02 | 3.2  | <i>Chromis xanthura</i>          | 0.06 $\pm$ 0.01 | 4.0  | <i>Paracirrhites arcatus</i>            | 0.09 $\pm$ 0.01 | 3.5  |
| <i>Thalassoma lutescens</i>      | 0.03 $\pm$ 0.01 | 2.0  | <i>Ctenochaetus cyanocheilus</i> | 0.04 $\pm$ 0.01 | 3.0  | <i>Ctenochaetus cyanocheilus</i>        | 0.08 $\pm$ 0.01 | 3.4  |
| <i>Gomphosus varius</i>          | 0.03 $\pm$ 0.01 | 2.0  | <i>Thalassoma lutescens</i>      | 0.03 $\pm$ 0.01 | 2.5  | <i>Cirrhilabrus exquisitus</i>          | 0.08 $\pm$ 0.05 | 3.3  |

Table 2. Biomass of top 10 species in each habitat at 10 m. Species ordered by overall percentage representation in habitats (Rep., %). Biomass =  $t\ ha^{-1}$ , mean  $\pm$  SE

| Patch reef                        |                 |      | Back reef                         |                 |      | Fore reef                         |                 |      |
|-----------------------------------|-----------------|------|-----------------------------------|-----------------|------|-----------------------------------|-----------------|------|
| Species                           | Biomass         | Rep. | Species                           | Biomass         | Rep. | Species                           | Biomass         | Rep. |
| <i>Chlorurus microrhinos</i>      | 0.15 $\pm$ 0.03 | 16.2 | <i>Manta birostris</i>            | 0.45 $\pm$ 0.21 | 26.4 | <i>Carcharhinus amblyrhynchos</i> | 0.88 $\pm$ 0.37 | 37.8 |
| <i>Carcharhinus amblyrhynchos</i> | 0.12 $\pm$ 0.09 | 12.7 | <i>Lutjanus bohar</i>             | 0.29 $\pm$ 0.06 | 17.0 | <i>Lutjanus bohar</i>             | 0.32 $\pm$ 0.08 | 13.9 |
| <i>Lutjanus bohar</i>             | 0.11 $\pm$ 0.02 | 11.6 | <i>Carcharhinus amblyrhynchos</i> | 0.22 $\pm$ 0.09 | 12.7 | <i>Triaenodon obesus</i>          | 0.22 $\pm$ 0.11 | 9.5  |
| <i>Triaenodon obesus</i>          | 0.10 $\pm$ 0.03 | 10.8 | <i>Triaenodon obesus</i>          | 0.10 $\pm$ 0.05 | 6.2  | <i>Caesio teres</i>               | 0.11 $\pm$ 0.08 | 4.8  |
| <i>Monotaxis grandoculis</i>      | 0.07 $\pm$ 0.03 | 7.8  | <i>Ctenochaetus striatus</i>      | 0.09 $\pm$ 0.02 | 5.5  | <i>Chlorurus microrhinos</i>      | 0.09 $\pm$ 0.02 | 3.9  |
| <i>Caesio teres</i>               | 0.05 $\pm$ 0.02 | 5.6  | <i>Chlorurus microrhinos</i>      | 0.08 $\pm$ 0.02 | 4.6  | <i>Acanthurus nigricans</i>       | 0.09 $\pm$ 0.01 | 3.8  |
| <i>Ctenochaetus striatus</i>      | 0.03 $\pm$ 0.01 | 3.7  | <i>Acanthurus nigricans</i>       | 0.05 $\pm$ 0.01 | 3.1  | <i>Ctenochaetus cyanocheilus</i>  | 0.08 $\pm$ 0.01 | 3.5  |
| <i>Acanthurus nigricans</i>       | 0.03 $\pm$ 0.01 | 3.0  | <i>Lutjanus gibbus</i>            | 0.04 $\pm$ 0.03 | 2.5  | <i>Monotaxis grandoculis</i>      | 0.05 $\pm$ 0.02 | 2.3  |
| <i>Ctenochaetus cyanocheilus</i>  | 0.02 $\pm$ 0.01 | 2.3  | <i>Caranx melampygus</i>          | 0.03 $\pm$ 0.02 | 1.8  | <i>Melichthys niger</i>           | 0.05 $\pm$ 0.02 | 2.0  |
| <i>Lutjanus gibbus</i>            | 0.02 $\pm$ 0.01 | 2.2  | <i>Cephalopholis argus</i>        | 0.03 $\pm$ 0.01 | 1.7  | <i>Cephalopholis argus</i>        | 0.03 $\pm$ 0.01 | 1.4  |

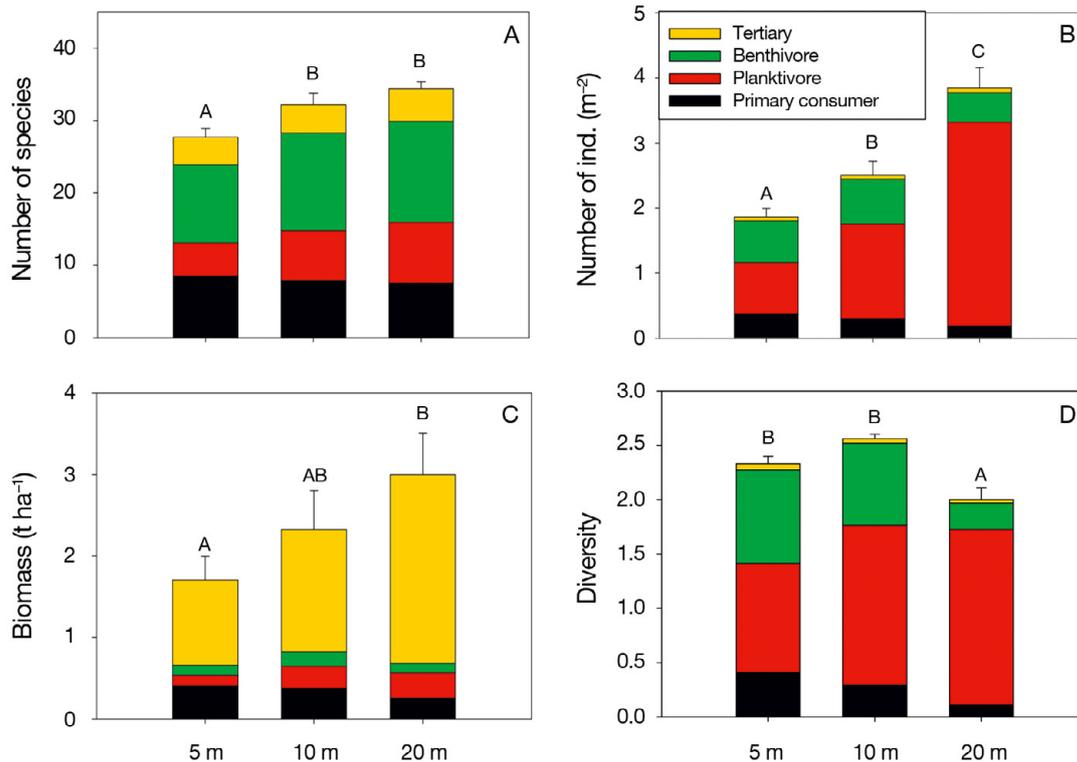


Fig. 5. Comparisons of fish assemblage characteristics (A: species, B: abundance, C: biomass, D: diversity) among depth strata on the fore reef. Letters above bars indicate results of unplanned multiple comparisons among depth strata tested using Tukey's HSD tests ( $\alpha = 0.05$ ). Strata with the same letter are not significantly different. Values are means  $\pm$  SE. See 'Results' for ANOVA results

and the 5 m stratum being intermediate ( $F_{2,44} = 3.9$ ,  $p = 0.03$ ). Planktivore biomass increased monotonically with depth, although these differences were not statistically significant ( $F_{2,44} = 2.5$ ,  $p = 0.09$ ).

At 10 and 20 m, the olive basslet was the most important species by number, accounting for 15% and 39% of total abundance in these fore-reef depth strata, respectively (Table 3). This species occurred in low abundance at 5 m fore-reef sites and only accounted for 0.02% of total numbers at this depth. The bicolor chromis ranked second in overall numbers at 20 m and fourth at 10 m, accounting for 22% and 9% of the total at these depths, respectively. At 5 m, the blacktail chromis was numerically dominant and accounted for 31% of the total by number at this depth, followed by the fivestripe wrasse *Thalassoma quinquevittatum* with 17% and the herbivorous damselfish *Plectroglyphidodon dickii* with 5%.

Grey reef shark and red snapper were the first- and second-ranked species by weight, respectively, among all 3 depth strata on the fore reef (Table 4). The contribution of *Carcharhinus amblyrhynchos* ranged from 38% at 5 m and 10 m to 56% at 20 m. *Lutjanus bohar* biomass ranged from 10% at 20 m to 16% at 5 m. At both 10 and 20 m, *Triaenodon obesus* was third in total biomass with contributions of 9% at each, respectively. At 5 m depth, a triggerfish, the omnivorous black durgon *Melichthys niger*, ranked third and represented 5% of total fish biomass.

### Prey size structure

Regressions of size-specific numerical densities of all prey taxa on body length class showed an interaction between size class and habitat type (ANCOVA  $F_{2,29} = 4.38$ ,  $p = 0.02$ ; Fig. 6A). The slope of the patch-reef regression was significantly different (less negative) than the slopes of the back-reef and fore-reef regressions (both  $p < 0.05$ ). Slopes among habitats became increasingly more negative from patch reef (-0.054) to back reef (-0.064) to fore reef (-0.066,  $p < 0.05$ ). On the fore reef, there was an interaction between size class and depth (ANCOVA  $F_{2,29} = 3.2$ ,  $p = 0.05$ ; Fig. 6B). The slope of the 20 m regression was the most negative and differed significantly from the 10 m regression (10 m [-0.062] < 20 m [-0.070],  $p < 0.05$ ). The 5 m (-0.066) and 20 m slopes did not differ significantly, nor did the 10 m and 5 m slopes (both  $p > 0.05$ ).

### DISCUSSION

Structural patterns of the undisturbed fish assemblage at Kingman are a baseline that reflects natural ecological processes that are not influenced by fishing or other anthropogenic factors.

The most striking feature of this assemblage is the inverted biomass pyramid (with more predator than prey biomass, sensu DeMartini et al. 2008 and Sandin et al.

Table 3. Numerical abundance of top 10 species in each depth stratum on the fore reef. Species ordered by overall percentage representation in habitats (Rep., %). Abundance = ind. m<sup>-2</sup>, mean ± SE

| 5 m                                     |             |      | 10 m                                    |             |      | 20 m                                    |             |      |
|---|-------------|------|---|-------------|------|---|-------------|------|
| Species                                 | Abundance   | Rep. | Species                                 | Abundance   | Rep. | Species                                 | Abundance   | Rep. |
| <i>Chromis vanderbilti</i>              | 0.59 ± 0.09 | 31.5 | <i>Pseudanthias olivaceus</i>           | 0.37 ± 0.11 | 14.7 | <i>Pseudanthias olivaceus</i>           | 1.52 ± 0.32 | 39.5 |
| <i>Thalassoma quinquevittatum</i>       | 0.32 ± 0.03 | 17.0 | <i>Chromis vanderbilti</i>              | 0.30 ± 0.06 | 12.1 | <i>Chromis margaritifer</i>             | 0.86 ± 0.14 | 22.3 |
| <i>Plectroglyphidodon dickii</i>        | 0.09 ± 0.01 | 4.6  | <i>Chromis acares</i>                   | 0.30 ± 0.07 | 12.0 | <i>Chromis acares</i>                   | 0.42 ± 0.10 | 10.8 |
| <i>Stegastes aureus</i>                 | 0.08 ± 0.01 | 4.1  | <i>Chromis margaritifer</i>             | 0.23 ± 0.04 | 9.1  | <i>Chromis xanthura</i>                 | 0.06 ± 0.02 | 1.7  |
| <i>Acanthurus nigricans</i>             | 0.07 ± 0.02 | 3.9  | <i>Thalassoma quinquevittatum</i>       | 0.16 ± 0.03 | 6.4  | <i>Ctenochaetus cyanocheilus</i>        | 0.06 ± 0.01 | 1.5  |
| <i>Chromis margaritifer</i>             | 0.07 ± 0.03 | 3.8  | <i>Plectroglyphidodon johnstonianus</i> | 0.10 ± 0.01 | 4.0  | <i>Labroides dimidiatus</i>             | 0.06 ± 0.01 | 1.5  |
| <i>Ctenochaetus marginatus</i>          | 0.06 ± 0.03 | 3.2  | <i>Acanthurus nigricans</i>             | 0.10 ± 0.01 | 3.9  | <i>Halichoeres ornatissimus</i>         | 0.06 ± 0.01 | 1.4  |
| <i>Plectroglyphidodon johnstonianus</i> | 0.05 ± 0.02 | 3.1  | <i>Paracirrhites arcatus</i>            | 0.09 ± 0.01 | 3.5  | <i>Cirrhilabrus exquisitus</i>          | 0.05 ± 0.02 | 1.4  |
| <i>Ctenochaetus cyanocheilus</i>        | 0.04 ± 0.01 | 2.4  | <i>Ctenochaetus cyanocheilus</i>        | 0.09 ± 0.04 | 3.4  | <i>Paracirrhites arcatus</i>            | 0.05 ± 0.01 | 1.4  |
| <i>Melichthys niger</i>                 | 0.04 ± 0.01 | 2.0  | <i>Cirrhilabrus exquisitus</i>          | 0.08 ± 0.05 | 3.3  | <i>Plectroglyphidodon johnstonianus</i> | 0.05 ± 0.01 | 1.3  |

Table 4. Biomass of top 10 species in each depth stratum on the fore reef. Species ordered by overall percentage representation in habitats (Rep., %). Biomass = t ha<sup>-1</sup>, mean ± SE

| 5 m                               |             |      | 10 m                              |             |      | 20 m                              |             |      |
|-----------------------------------|-------------|------|-----------------------------------|-------------|------|-----------------------------------|-------------|------|
| Species                           | Biomass     | Rep. | Species                           | Biomass     | Rep. | Species                           | Biomass     | Rep. |
| <i>Carcharhinus amblyrhynchos</i> | 0.65 ± 0.24 | 37.8 | <i>Carcharhinus amblyrhynchos</i> | 0.88 ± 0.37 | 37.8 | <i>Carcharhinus amblyrhynchos</i> | 1.68 ± 0.49 | 56.0 |
| <i>Lutjanus bohar</i>             | 0.21 ± 0.05 | 15.8 | <i>Lutjanus bohar</i>             | 0.32 ± 0.08 | 13.9 | <i>Lutjanus bohar</i>             | 0.31 ± 0.04 | 10.3 |
| <i>Melichthys niger</i>           | 0.09 ± 0.03 | 5.5  | <i>Triaenodon obesus</i>          | 0.22 ± 0.11 | 9.5  | <i>Triaenodon obesus</i>          | 0.26 ± 0.12 | 8.6  |
| <i>Chlorurus microrhinos</i>      | 0.08 ± 0.03 | 4.5  | <i>Caesio teres</i>               | 0.11 ± 0.08 | 4.8  | <i>Naso hexacanthus</i>           | 0.06 ± 0.03 | 2.1  |
| <i>Ctenochaetus marginatus</i>    | 0.08 ± 0.04 | 4.4  | <i>Chlorurus microrhinos</i>      | 0.09 ± 0.02 | 3.9  | <i>Chlorurus microrhinos</i>      | 0.06 ± 0.03 | 1.8  |
| <i>Acanthurus nigricans</i>       | 0.06 ± 0.02 | 3.7  | <i>Acanthurus nigricans</i>       | 0.09 ± 0.01 | 3.8  | <i>Ctenochaetus cyanocheilus</i>  | 0.05 ± 0.01 | 1.6  |
| <i>Triaenodon obesus</i>          | 0.04 ± 0.03 | 2.3  | <i>Ctenochaetus cyanocheilus</i>  | 0.08 ± 0.01 | 3.5  | <i>Caesio teres</i>               | 0.04 ± 0.02 | 1.4  |
| <i>Ctenochaetus cyanocheilus</i>  | 0.04 ± 0.04 | 2.1  | <i>Monotaxis grandoculis</i>      | 0.05 ± 0.02 | 2.3  | <i>Acanthurus nigricans</i>       | 0.04 ± 0.01 | 1.3  |
| <i>Thalassoma quinquevittatum</i> | 0.03 ± 0.01 | 2.0  | <i>Melichthys niger</i>           | 0.05 ± 0.02 | 2.0  | <i>Myripristis berndti</i>        | 0.04 ± 0.02 | 1.3  |
| <i>Scarus frenatus</i>            | 0.03 ± 0.01 | 1.5  | <i>Cephalopholis argus</i>        | 0.03 ± 0.01 | 1.4  | <i>Naso vlamingii</i>             | 0.03 ± 0.01 | 1.2  |

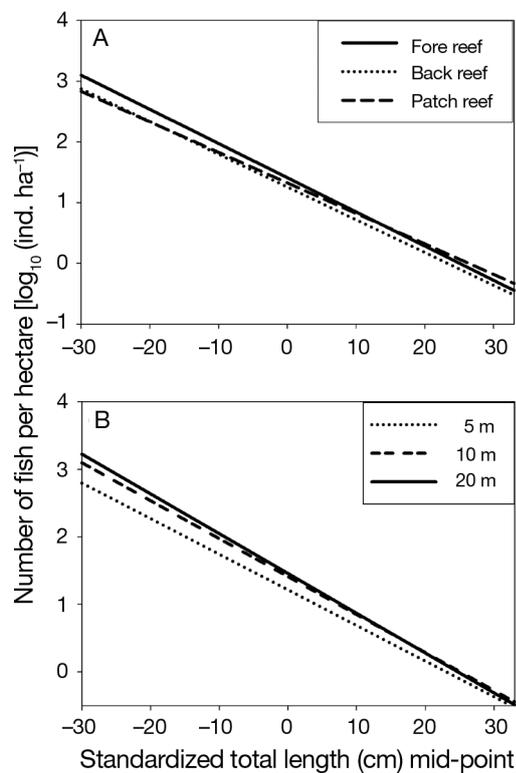


Fig. 6. Size spectra of log<sub>10</sub>-transformed number of fish per hectare by standardized size class for all prey fishes (A) among habitat strata at 10 m and (B) among depth strata on the fore reef. Prey size range: 5 to 60 cm

2008) with dominance by apex predators, primarily sharks and large snappers, across all depth and habitat strata examined. This pattern is most pronounced at greater depths (20 m) on the fore reef, although apex predators dominated biomass in back-reef, patch-reef, and shallow fore-reef habitats as well. Increasing shark density at greater fore-reef depths is consistent with data from shark control programs in Hawaii that have shown an increase in catch rates for adult grey reef sharks with increasing depth (from 5 to 30 m; Wetherbee et al. 1997, Papastamatiou et al. 2006).

Slopes of the prey size-abundance spectrum became more negative with increasing predator biomass across habitats and among fore-reef depths. This change in the distribution of prey across size classes indicates the cropping of larger prey and an increase in the relative number of individuals in the smaller prey size classes with increasing predator biomass. Slopes of size spectra for patch-reef and shallow fore-reef habitats with fewer predators were less negative, reflecting the larger and less abundant prey in these habitats. A perhaps more important fact that these data illustrate is that predation effects on prey body size distributions at Kingman Reef are strong overall across habitats and depths on the fore reef (i.e. not restricted to just a single depth on the fore reef at Kingman), and are large relative to those previously observed at exploited atolls elsewhere in the northern Line Islands (DeMartini et al. 2008, Sandin et al. 2008).

Fishes from lower trophic levels in general showed predictable patterns consistent with more typical fished areas. Abundance and biomass increased with proximity to the pelagic environment (from patch reefs to back reef to fore reef) and with increasing depth on the fore reef. Planktivores numerically dominated all habitats and depths, largely driving the trends in total abundance. Species density and diversity showed similar patterns across habitats, with the exception of a disproportionately lower diversity at 20 m depth on the fore reef. The fish assemblage in this stratum was dominated numerically by 1 species of planktivore, the central Pacific endemic *Pseudanthias olivaceus*. In general, the planktivore guild was the largest contributor to diversity, while benthic carnivores composed the largest proportion of total species across strata. Herbivores showed highest density and biomass on the fore reef, although they were least abundant at the deepest (20 m) stratum. Conversely, benthic carnivore abundance increased at greater depths, reflecting the greater abundance of small wrasses (Labridae) with depth.

Many studies, dating back to the 1960s, have examined the spatial distribution of fishes on coral reefs (Hitt & Strasburg 1960, Goldman & Talbot 1976, Russ 1984, Williams 1991). Prominent factors affecting the size and composition of reef fish assemblages include physical characteristics (e.g. depth, wave exposure), resource availability (e.g. food, shelter), and interspecific interactions (e.g. predation, competition). While many assemblage changes generally apply across fish taxa, others are more specific to particular trophic guilds.

Two gradients have received particular attention in their effects on tropical reef fish assemblage structure: depth and proximity to the pelagic environment. Many characteristics of fish assemblages (richness, numerical abundance, biomass) have been shown to change consistently with depth (from the surface to about 30 m) and can be attributed to the closer proximity to habitats with greatly different physical and biological diversity (Gosline 1965, Friedlander & Parrish 1998, Brokovich et al. 2008). Planktivores and herbivores appear to respond particularly strongly to depth gradients. In particular, planktivore density commonly increases with depth on the fore reef as a result of the proximity to reef edges that provide higher concentrations of plankton (Hobson & Chess 1978, Thresher & Colin 1986). Conversely, herbivores tend to decrease in density with depth, likely responding to lesser availability, productivity, and/or quality of algal resources at greater depths (Russ 1984, Fox & Bellwood 2007).

Similarly, proximity to the pelagic environment has been shown to predictably alter the structure of reef fish assemblages. Patch reefs and back-reef habitats often have smaller areal extents, lower habitat diver-

sity, and lower structural complexity relative to adjacent fore-reef habitats (Parrish 1989). As such, numerical density and species diversity tend to increase from inshore patch or lagoonal habitats toward outer reef slope and fore-reef habitats (Galzin 1987, Lecchini et al. 2003, Alvarez-Filip et al. 2006).

The present study demonstrates that spatial patterns of distribution among habitats and depths can be consistent between fished and unfished reefs yet obscure some fundamental differences resulting from extraction. Several general and readily demonstrable similarities between fished and unfished reefs (depth and habitat predilections of herbivores and planktivores) are static characteristics that reflect fundamental processes of photosynthesis and ocean currents and plankton transport. Gross patterns of similarity between fished and unfished reefs in relative trophic level abundance and biomass distributions among habitats and depths gloss over the fundamental fact that, on fished reefs, size structure and abundance-to-biomass relationships are shifted among trophic levels at depth and within particular habitats. Our observations clearly show that the extraction of apex predators that results in meaningful biomass shifts among trophic levels within habitats on reefs does not necessarily result in changes in the spatial (among habitat and across-depth) distribution of biomass for particular guilds and trophic levels.

Impressions of similarity based on static properties of abundance and biomass distributions, however, overlook the less obvious and more difficult to demonstrate dynamic properties of fish assemblages. These include the species-specific age and size distributions and growth and mortality rates that are undoubtedly important for resource production and sustainable fisheries management. Regardless of whether overextraction results in the 'fishing down' (Pauly et al. 1998) or the 'fishing through' (Essington et al. 2006) of food webs, it is clear that the dynamic properties of resource species populations are key to understanding and managing their sustainable use.

Apex predators clearly exert a strong top-down control on the entire ecosystem (DeMartini et al. 2005, Sandin et al. 2008), yet these species are the most vulnerable to exploitation (Myers & Worm 2003). The removal of these species can lead to reefs that are dominated by small-bodied, lower trophic-level species that do not represent the natural state and may give a false impression of true ecological processes (Friedlander & DeMartini 2002, DeMartini et al. 2008). This shifting baseline syndrome (Pauly 1995, Sheppard 1995) plagues most contemporary studies on coral reefs and the results of our work will help set a baseline for comparisons with reefs under varying degrees of human disturbance.

Remote, uninhabited locations represent some of the last remaining 'pristine' coral reefs left on earth and give us a window into the past as to what reefs looked like prior to human extraction (Knowlton & Jackson 2008). These few remaining large-scale, intact, predator-dominated reef ecosystems offer a chance to examine what could occur if larger, more effective, no-take marine protected areas (MPAs) were implemented elsewhere. The creation of large MPAs that protect entire ecosystems like the northwestern Hawaiian Islands, Great Barrier Reef, Phoenix Islands, and US Pacific Remote Islands offer a tremendous opportunity to conserve the remaining intact coral reefs and avoid the pitfall of further promulgating the shifting baseline.

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