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Ecosystem Ecology – *Original Research*

Foraging consistency of coral reef fishes across environmental gradients in the central Pacific

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Abstract –

We take advantage of a natural gradient of human exploitation and oceanic primary production across five central Pacific coral reefs to examine foraging patterns in common coral reef fishes. Using stomach content and stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses we examined consistency across islands in estimated foraging patterns. Surprisingly, species within the piscivore-invertivore group exhibited the clearest pattern of foraging consistency across all five islands despite there being a considerable difference in mean body mass (14g-1.4kg) and prey size (0.03-3.8g). In contrast, the diets and isotopic values of the grazer-detritivores varied considerably and exhibited no consistent patterns across islands. When examining foraging patterns across environmental contexts, we found that $\delta^{15}\text{N}$ values of species of piscivore-invertivore and planktivore closely tracked gradients in oceanic primary production; again, no comparable patterns existed for the grazer-detritivores. The inter-island consistency in foraging patterns within the species of piscivore-invertivore and planktivore and the lack of consistency among species of grazer-detritivore suggests a linkage to different sources of primary production among reef fish functional groups. Our findings suggest that piscivore-invertivores and planktivores are likely linked to well-mixed and isotopically constrained allochthonous oceanic primary production while grazer-detritivores are likely linked to sources of benthic primary production and autochthonous recycling. Further, our findings suggest that species of piscivore-invertivore, independent of body size, converge toward consuming low trophic level prey, with a hypothesized result of reducing the number of steps between trophic levels and increasing the trophic efficiency at a community level.

Keywords: *Fishes; Foraging; Trophic; Stomach contents; Isotopes; Primary production*

Introduction – The high diversity of fishes living on coral reefs is a distinguishing feature of this community, provoking considerations of how so many species can coexist in a limited area. Foraging specializations appear to be one axis along which reef fishes partition niche space (Adam et al. 2015). The first-order foraging constraints linked to body and gape size are represented broadly among reef fishes, with species ranging 7-8 orders of magnitude in mean adult mass (most species between 0.1g and 100kg) with a putatively wide range of associated specialties of prey size ranges across fish size classes. Notable adaptations that introduce specialized foraging opportunities include extreme morphological characteristics (e.g., elongated mouths within the *Forcipiger*, fused teeth of the scarinae) and behavioral peculiarities (e.g., tight microhabitat specialization within *Paracirrhites*) (DeMartini 1996; Wainwright and Bellwood 2002). Detailed dietary assessments have elucidated additional forms of dietary specialization among taxa that have seemingly very similar autecologies, for example as observed from compound-specific stable isotope diet reconstructions among two species of cohabitating *Lutjanus* with non-overlapping diets (McMahon et al. 2016).

Despite an often-astounding degree of morphological specialization (Motta 1988; Wainwright and Bellwood 2002), evidence suggests that some species of coral reef fish can exhibit a broad flexibility in diet, and generalist or omnivorous feeding can be found ubiquitously across trophic levels (Bellwood et al. 2006; Crossman et al. 2005). Some such foraging generalizations are ontogenetic within species, with juveniles exploiting distinct food resources from adults within the same environment (Lukoschek and McCormick 2001; St John 1999). Even within taxa of similar age classes, some mid-to-low-trophic level consumers (operationally defined as ‘carnivores’ or ‘herbivores’) may feed opportunistically or incidentally across traditional trophic boundaries. For instance, putative herbivore species often consume

micro-invertebrates hidden within algal turfs or coralline algae (Crossman et al. 2005; Kramer et al. 2013). Further, some large-bodied top-predatory fishes subsidize a predominantly piscivorous diet with invertebrate prey and forage across multiple habitats serving as important couplers of discrete energetic pathways (Matich et al. 2011; McCauley et al. 2012). Recent research has suggested that some species of mesopredatory fishes will shift prey in response to dramatic changes in reef environmental context (e.g., bleaching; (Hempson et al. 2017)). It remains an open question whether such generalized foraging patterns themselves are characteristic, with species (or specific age classes of species) consistently consuming a distinct combination of prey relative to heterospecifics.

Despite our growing understanding of the diverse feeding ecologies observed among reef fishes, we have a limited understanding of how the diets of reef fishes within putative trophic groupings respond across anthropogenic and environmental gradients. Most reef fisheries target species across larger size classes and multiple trophic levels, the consequences of which alters food web structure even at moderate levels of extraction (Graham et al. 2017; Zgliczynski and Sandin 2017). The influence of shifted food web structure, with potentially compounding behavioral shifts (Dill et al. 2003), on species-specific foraging patterns is less-well understood. Superimposed over these predator-prey relationships are abiotic forcings including ocean currents, internal waves, and eddy-diffusion that deliver pelagic energy and nutrient subsidies in the form of dissolved nutrients and allochthonous plankton to coastal marine communities (Gove et al. 2016; Williams et al. 2018). While oceanographic context certainly influences the composition of reef fish assemblages, much less is known about these influences on species-specific foraging patterns and food web structure.

The diversity of coral reefs, while providing an invaluable opportunity for studying foraging specialization, also provides significant challenges in quantifying feeding patterns. The potential prey field is highly diverse, including micro- and macro-algae, benthic invertebrates, and other fishes (Plaisance et al. 2009; Stella et al. 2010). Further, the relative trophic structure of the prey field can be similarly diverse with prey species consuming food resources stemming from distinct basal sources including oceanic production, benthic production, and myriad microbial shunts of production and remineralization (Gove et al. 2016; Silveira et al. 2017; Somera et al. 2016). As such, in order to investigate the realized foraging patterns of reef fish across environments, there can be extreme data demands. If one were to employ stomach contents analyses to compare diets of fishes across environments, the guts of very many individuals per environment would need to be sampled. Because there are so many potential prey items and species, and because stomach contents represent only a brief window of foraging time for the sampled individual (determined by species-specific gut transit times), 100s to 1000s of individual guts must be sampled to gain a precise estimate of site-specific foraging patterns for a particular species (Deb 1997; Hyslop 1980).

Stable isotope analysis is a complementary approach used to infer foraging patterns (Bearhop et al. 2004). When the potential diet items are known and carry relatively distinct isotopic signatures, mixing models can be used to estimate the proportional representation of each to a sample individual's diet (McCauley et al. 2012; McMahon et al. 2016). However, among many coral reef fishes the potential diet items are many and some fishes are known to forage across multiple sub-habitats (e.g., fishes moving from reef flats to forereefs). As such, a taxonomically precise estimate of foraging patterns of a coral reef fish would require extensive stable isotopic sampling of myriad potential prey sources (perhaps from multiple sub-habitats).

Most successful applications of stable isotopic analysis among coral reef fishes have focused on the testing of hypotheses of broad habitat use (McCauley et al. 2012; Wyatt et al. 2012), focal investigations of target taxa from individual locations (Hempson et al. 2017; McMahon et al. 2016), and human induced changes to food web-structure (Layman et al. 2007).

While there are limitations linked to the use of stomach contents analysis (SCA) and stable isotope analysis (SIA) to resolve the diets of individual species, these approaches provide value for exploring hypotheses of relative foraging patterns of species across locations. These tools can provide a snapshot of context-specific foraging habits, i.e., proxies of foraging patterns (SCA and SIA) collected factorially across multiple species and multiple environments. A robust null model of foraging consistency across environments would be the expectation that relative differences in SCA or SIA data between species in a single environment are maintained consistently among the multiple environments. This null model would be supported if realized foraging patterns of species are little affected by environmental context, and is consistent with views of species-specific foraging specialization. In contrast, a null model of consistent relative differences in SCA or SIA data can be rejected due to multiple mechanisms. Biologically, if the foraging of individual species varies as a matter of environmental context, we will expect relative differences among species to vary – SCA will reveal different food items by context and SIA will reveal non-consistent inter-species differences. Notably, and especially for SIA, vagaries of isotopic signatures of potential prey across environmental contexts can also lead to rejection of this null model. If basal isotopic signatures vary in a non-consistent manner across geography and change one species' prey differently than another, it is possible to observe variable inter-species relative isotopic positions even without changes in foraging patterns. In sum, rejection of the null of consistent relative differences of species among environments can

occur via multiple mechanisms, both biological and operational; failure to find strong evidence rejecting the null however is most consistent with evidence of among-species foraging consistency across environments.

In this study, we explore how the relative foraging habits of common coral reef fishes are affected by local environmental context, namely the forereef habitats of five islands in the Line Islands Archipelago (central Pacific). The islands span a gradient in oceanic primary production, in the form of allochthonous nutrient and planktonic delivery, and a distinction of fisheries exploitation including three unfished and two moderately exploited reefs. We target eight species of coral reef fishes that are among the most abundant species in the region, representing three trophic groups (piscivore-invertivore, planktivore, and grazer-detritivore). We test hypotheses of foraging consistency across islands, determining which, if any, species groups show relative invariability of diets across this well-described gradient of oceanic primary production and fishing pressure.

Methods –

Study Sites

The northern Line Islands (NLI) are located more than 1500 km south of the Hawaiian Archipelago in the central Pacific (Fig. 1). Islands range from unfished reefs representative of intact ecosystems, through to fished reefs with significantly reduced predator biomass (DeMartini et al. 2008; Sandin et al. 2008). Fish assemblages surrounding the unfished islands are characterized by an abundance of large-bodied species including the prevalence of top-level predators that often contribute over 50% of the total fish biomass (DeMartini et al. 2008; Sandin et al. 2008). In contrast, inhabited islands support modest nearshore fisheries and fish assemblages characterized by lower overall biomass and a disproportionate reduction in the

large-bodied predatory species (Zgliczynski and Sandin 2017). Further, the NLI are exposed to a latitudinal gradient in oceanic primary production, with estimates of production nearly doubling across the island chain (Fig. 1). Regional current patterns and localized upwelling result in greater nutrient availability and enhanced planktonic production at islands with increasing proximity to the equator (Gove et al. 2016).

Fish Sampling

Sampling was conducted across five of the NLI (from north to south: Kingman, Palmyra, Teraina, Tabuaeran, and Jarvis; Fig. 1) during a ship-based expedition between Oct - Nov 2010. At each island, we collected samples of eight coral reef fish species across a range of body sizes and functional trophic groups. We used the results of previous survey efforts as a guide to identify species that represent the largest contributors to abundance and biomass of the fish assemblage (DeMartini et al. 2008; Sandin et al. 2008) (Table 1). Targeted species included (with putative functional trophic group): *Lutjanus bohar* (piscivore-invertivore), *Cephalopholis urodeta* (piscivore-invertivore), *Paracirrhites arcatus* (piscivore-invertivore), *Pseudanthias bartlettorum* (planktivore), *Chromis margaritifer* (planktivore), *Stegastes aureus* (grazer-detritivore), *Acanthurus nigricans* (grazer-detritivore), and *Ctenochaetus marginatus* (grazer-detritivore). Reviews of the general feeding ecology of these species can be found in natural historical reports and field guides (Randall 2005). Together these eight species accounted for 30% and 23% of the total fish abundance and biomass from coral reefs in the region (Table 1).

A target number of 50 individuals across a range of body sizes were collected using hand nets, pole spears, and hook-and-line to obtain representative samples for each species-island combination. To minimize the effects of ontogenetic dietary variation for this study, we constrained the size classes of samples for each species-island combination to the regional mean

standard length (SL) based on collection efforts across islands (Table 1). In a few instances, samples were collected during previous research campaigns, and to minimize impacts to coral reef fish communities, we supplemented collecting efforts with these samples (Ruttenberg et al. 2011; Wood et al. 2014). We recognize that using samples from different years may introduce potential dietary variability across years, however, samples collected during previous expeditions represented only a small proportion (10%) of the total number of samples included in this study (Table 1). Further, efforts were made to minimize the effects of dietary variation across all sampling campaigns by collecting specimens along leeward forereef habitats (the reef slope habitat exposed to the open ocean) at depths between 8-15 m. Therefore, the effects of potential dietary variation across sampling campaigns are likely to be minimal.

Assessment of Dietary Consistency

To evaluate foraging consistency of focal species across islands we used a combination of stomach content and stable isotope analyses. Traditional stomach content analysis was used to quantify dietary composition and the relative contribution of prey items to the diet of each species (Hyslop 1980). Efforts were made to select 20 stomach contents samples from each species-island combination around the regional mean SL for each species whenever possible (Table 1). In some cases, the stomachs of fishes were empty and additional specimens were dissected in an effort to include 20 individuals for each species island combination in the diet assessment. Items within the stomach were removed, weighed, and assigned to the finest taxonomic resolution feasible. With all diet constituents identified, a two-tiered hierarchy of diet categories was constructed (Online Resources 2-4). Diet category subgroups were identified, which were composed of taxonomically (or functionally) consistent diet items that composed a threshold representation within stomachs. Subgroups were used only if the category represented

a mean of at least 1% of total stomach contents for at least one species of fish. Dietary groupings were used to compare inter-island differences of relative diet composition across trophic groupings.

Based on the nature of differing diet items and digestion process, slightly different definitions of relative composition were used across fish trophic groups. For the piscivore-invertivores (*L. bohar*, *C. urodeta*, and *P. arcatus*), diet composition was described by estimating the proportional weight of each diet category to the total weight of diet items removed from the individual fish's stomach. The diet composition of planktivores (*P. bartlettorum* and *C. margaritifera*) was described using a similar protocol, however, due to the small size of diet items observed across diet categories, we used relative abundance of items rather than proportional weight. Relative abundance was also used to characterize the diets of the three grazer-detritivores (*S. aureus*, *A. nigricans*, and *C. marginatus*). Due to difficulties associated with classifying partially digested algae to high taxonomic resolution, we assigned diet items to one of three algal functional group categories, namely early stage algae (e.g., low-lying turf algae), late stage algae (e.g., upright fleshy seaweeds), and calcified algae (e.g., algae that contained CaCO_3); invertebrate, sand (detritus), and 'other' categories also were included in the diet assessment. Stomach content analysis provides a valuable tool for describing the types of prey and general feeding habits of consumers. However, this approach provides only a snapshot of feeding habits and may not reflect the long-term diet of target species, especially for piscivore-invertivores that can switch prey sources frequently or that consume items that are digested at different rates (Hyslop 1980).

Complementing stomach contents analysis, we used stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to obtain an integrated view of diets and evaluate relative position across species-island

combinations. This was accomplished by selecting 10 individuals from each species-island combination included in the stomach contents assessments whenever possible (Table 1). A section of muscle tissue (0.05-1.0 g) was removed from the left dorsal region of each fish and samples were stored frozen (-20° C) and processed following standardized stable isotope protocols (Michener and Lajtha 2007; Post 2002). Presenting mean values of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ of an organism or population in either single-plot or bi-plot space can provide important information regarding relative trophic position, food web structure, and niche width (Layman et al. 2007; Post 2002). To describe context-specific shifts in relative isotope position among species, we focused our interpretation on the $\delta^{15}\text{N}$ values using single-plots across islands but we also provide summaries of $\delta^{13}\text{C}$ values as bi-plots to complement $\delta^{15}\text{N}$ data and reinforce models of relative trophic position observed across islands. Additional methodological details and data interpretation are provided in Electronic Supplemental Material (Online Resource 1).

Statistical Analyses

To formally test the null hypothesis that the diets of individual fish species did not differ among islands, we used a resampling approach that accounts for the multinomial (non-independent) nature of percentage stomach content data. For example, the diet composition of individual fish is the result of numerous multinomial choices made during foraging activities. Each item consumed can be assigned to a diet category based on taxonomy (or functional group) and the number of diet categories is determined by the operational level of dietary resolution. The total percentage of each diet category represents an estimation of the multinomial probabilities for foraging events made by an individual fish. Further, the total percentage of each diet category is bound between 0% - 100% and is dependent on the percentage values of the other diet categories

observed during the assessment. As such, stomach contents data violate a number of assumptions of normality and independence required for many traditional statistical approaches.

To address the multinomial nature of diet data we used a tailored resampling routine following an analytical approach introduced previously (Barott et al. 2012). Consider a visualization in which data are plotted in n dimensions, where n is the number of diet categories. Mean relative diet composition for individuals from one island is calculated as the island-specific centroid of the data in n -dimensional space, and the mean for all individuals from across islands is calculated as the global centroid from all samples. The mean intercentroid distance among island samples was calculated by measuring the Euclidean distances between the centroids for each island from the global centroid. A resampling routine (10,000 iterations) was used to generate a null distribution of mean intercentroid distances, by repeatedly scrambling island affiliations of diet composition data from all individuals and calculating the intercentroid distance. The actual mean intercentroid distance was compared to this null distribution to test whether mean diets differed among islands for each species. If the null hypothesis of no difference among islands was rejected for data from a species, the procedure above was repeated individually for all pairs of islands to generate pairwise comparisons among each species-island combination; the null hypothesis for the post-hoc test was rejected if $p \leq 0.01$. This analytical procedure using Euclidean distances is robust, in most cases, across levels of aggregation of diet categories given that the approach does not *de facto* create higher sensitivity to increased number of functional groups. However, to assure empirically that the level of aggregation of diet categories did not affect conclusions, analyses and figures presented in the main text using high-resolution diet category subgroups are complemented by comparable analyses and figures with diet category subgroups lumped into course groupings (the latter presented in the Online

Resources). Notably, the results did not differ qualitatively between the two hierarchical categorizations of diets.

To test whether the relative $\delta^{15}\text{N}$ signal of individual fish species differed across islands, we used a single factor analysis of variance (ANOVA) treating island (5 levels) as the fixed factor. This was completed for all species-island combinations but recognizing *a priori*, that the planktivore, *P. bartlettorum* lacked one species-island combination due to biogeographic absence at Kingman. Tukey pairwise comparisons (planned contrasts between islands) were used to identify which species-island combinations differed in relative $\delta^{15}\text{N}$ space and examine consistencies among species and functional trophic groups. Our prediction was that foraging patterns within a species would remain consistent across environmental contexts and be reflected in the stable isotope signatures among species. All statistical analyses were completed using R version 3.0.1 and RStudio version 1.1.453 (R Development Core Team; www.r-project.org).

Results – The eight fish species included in this assessment spanned a range of body sizes and three functional trophic groups (Table 1). The two planktivores were the smallest species processed, and the piscivore-invertivore, *Lutjanus bohar*, was the largest species, with the total collection of fishes spanning a range of standard lengths (SL) from 1.55 cm to 61.50 cm. The remaining species ranged in size from 1.79 cm SL to 20.30 cm SL. Representative samples for stomach content analysis were obtained for all eight species-island combinations with the exception of *P. bartlettorum* which was not present at Kingman (Table 1). In some instances, the stomachs of a subset of species-island combinations were observed to be empty and the lack of stomach contents data was reflected in the reduced number of individuals reported as processed

(i.e., *L. bohar*, *C. urodeta*, and *A. nigricans*; Table 1). Stomachs contained food items in the remaining species-island combinations and were processed accordingly.

Stomach contents from 730 specimens from eight coral reef fish species across the NLI were examined to evaluate diet composition (Table 1). Coarse evaluation of stomach contents revealed variability among species but food items observed in the stomachs were generally distinct within functional trophic groups (Fig. 2; Online Resources). For example, the diets of piscivore-invertivores consisted primarily of fishes (diet composition range: 28%-77%) and decapod-crustaceans (diet composition range: 0%-46%) while the diets of planktivores consisted primarily of copepods (diet composition range: 51%-81%) and to a lesser extent egg sacks (diet composition range: 5%-26%) and foraminifera (diet composition range: 0%-17%; Fig. 2; Online Resources). The diets of grazer-detritivores were the most variable within functional trophic groupings with stomach contents primarily comprised of varying proportions of early stage algae, (complex cylinders diet composition range: 6%-55% and filamentous algae diet composition range: 11%-36%), sandy detritus (diet composition range: 3%-57%), and to a lesser extent invertebrates (diet composition range: 0%-21%) and late stage algae (foliose algae diet composition range: 0%-18% and calcified algae diet composition range: 0%-14%)(Fig. 2, Online Resources). Some material in the guts was unidentifiable due to digestion process, resulting a proportion of the mass being labeled as ‘Other’. This unidentified group within the stomach contents was most prominent in *L. bohar*, perhaps due to the longer gut passage time for larger gut volumes. Removal of this group within the stomach contents results did not alter the qualitative conclusions of stomach contents data presented.

Pairwise comparisons revealed that the diets of each piscivore-invertivore species was indistinguishable among islands (Table 2). The mean weight of prey was positively related to the

mean size of the piscivore-invertivore species, and mean prey weight scaled approximately an order of magnitude between each of the three piscivore-invertivore species (Online Resource 5). These findings suggest that the prey field and foraging patterns among the piscivore-invertivores remained consistent across islands regardless of the individual's body size. For the planktivores, there was a lack of consistency in the diets among species across islands, but we found the species-specific diet of *P. bartlettorum* to be consistent across 3 of the 4 islands where samples were collected (Fig. 2; Table 2; Online Resources). In contrast, pairwise comparisons revealed a substantial variation and a lack of consistency in the diets within the grazer-detritivore group across islands (Table 2). However, there were some instances at the island level where the diets of grazer-detritivores were similar (e.g., Kingman and Tabuaeran; Table 2). The variability and lack of consistency in stomach contents across islands suggests that grazer-detritivores forage generally across a diverse and trophically complex prey field particular to each island-species combination.

A total of 383 samples were processed for bulk stable isotope analysis across each species-island combination with a couple of exceptions. Several of the processed isotope samples from Jarvis for the piscivore-invertivore, *L. bohar*, were outside of acceptable range and deemed unusable, and the planktivore, *P. bartlettorum*, did not occur at Kingman. Graphical analysis of stable isotopes ($\delta^{15}\text{N}$) revealed consistency in the relative positions of some species pairs in isotopic space across islands (Fig. 3; Online Resources). The relative isotopic signatures of the three piscivore-invertivore species appeared to be similar across islands decreasing in isotopic space moving from north to south (Kingman to Jarvis) along the gradient of oceanic primary production. Notably, beyond relative isotopic signature, the actual mean isotopic signature among the three species of piscivore-invertivore never differed by more than 1.5‰. The

planktivores also appeared to follow the same decreasing trend but exhibited more variability among species-island combinations. In contrast the grazer-detritivores revealed no clear pattern or consistency in stable isotopes ($\delta^{15}\text{N}$) among species across islands with the greatest variability observed at the islands furthest from the equator.

Examining the isotopic patterns for species-island combinations in more detail revealed significant differences (<0.001) in the $\delta^{15}\text{N}$ values for all species across the NLI (Table 3). Pairwise comparisons provided insights into species-specific patterns within each functional trophic group (Table 4). For the piscivore-invertivores, pairwise comparisons of $\delta^{15}\text{N}$ signatures revealed similarity in the integrated diets between *C. urodeta* and *P. arcatus* across all five islands ($p \leq 0.01$; Table 4). *L. bohar* $\delta^{15}\text{N}$ signatures were also similar to the other piscivore-invertivores at Kingman and Palmyra but not for the islands further south. The integrated $\delta^{15}\text{N}$ signatures of the planktivores were consistent across all islands where both species were present. In contrast, there were limited-to-no consistent patterns in $\delta^{15}\text{N}$ values for the grazer-detritivores across the NLI. Jarvis was the only island where $\delta^{15}\text{N}$ signatures were similar across all three species. For the remaining species-island combinations, the results were variable across species suggesting inconsistencies in the integrated diets among grazer-detritivores (Table 4).

Discussion – Coral reef fishes are exceptionally diverse and represent a model system to explore relative foraging habits of species across gradients of environmental context. Using stomach contents and stable isotope analyses, we found evidence of foraging consistency among common coral reef fishes from the central Pacific. However, these patterns were distinct between putative functional trophic groupings. An examination of stomach contents revealed the diets of focal species to be distinct among functional trophic groups, as expected based on assignments from

web-based (i.e., fishbase.org) and published references (Myers 1999; Randall 2005). For instance, fishes within the piscivore-invertivore group preyed upon fishes and mobile invertebrates, the planktivores preyed upon microscopic plankton from the water column, and the grazer-detritivores primarily foraged upon algae, sandy detritus, and micro-invertebrates. Our findings are consistent with an established natural historical perspective suggesting that variation in the foraging ecologies observed among coral reef fishes is driven by the distinction of functional roles and the manner in which groups of fishes exploit distinct energetic resources.

By design, we focused analyses on patterns of inter-island variation in foraging, contrasting variability of multiple species of fish within these three functional trophic groups. Using data on both short-term (stomach contents) and longer-term (somatic stable isotopic composition) foraging patterns, we find that species have differential patterns of variation across the northern Line Islands. The species of grazer-detritivore (*Stegastes aureus*, *Acanthurus nigricans*, and *Ctenochaetus marginatus*) exhibited the greatest variation in stomach contents and stable isotope ($\delta^{15}\text{N}$) values across islands. Post-hoc estimates of stomach contents reveal variable groupings of diet similarity across the three species of grazer-detritivore (Table 2), suggesting that the determinants of diets at an island differ among the species (e.g., due to differences in species-specific foraging preferences and island-specific availability of food items). The more integrated measure of foraging, somatic tissue $\delta^{15}\text{N}$, shows more qualitative consistency in values across islands (each species showing highest $\delta^{15}\text{N}$ values at Teraina, the island at the middle latitude in this study; Fig. 3b, Table 4), but a consistent cause for this similarity across species is not obvious. Notably, the benthic habitats are quite variable in algal and other composition across this region, due to both oceanographic forcing and alterations of

the fish assemblage structure due to fishing (DeMartini et al. 2008; Sandin et al. 2008; Smith et al. 2016).

There was notably less estimated variation in foraging across islands for the species of planktivore, and the least for the species of piscivore-invertivore. Review of the stomach contents analyses showed some inter-island differences in prey composition for the two species of planktivore (Table 2); *Chromis margaritifer* showed different relative abundances of prey for each island (except for Kingman, which was indistinguishable from all islands aside from Jarvis), while *Pseudanthias bartlettorum* showed similar relative abundances for all islands, except for Jarvis. The stomach contents of each species piscivore-invertivore (*Lutjanus bohar*, *Cephalopholis urodeta*, and *Paracirrhites arcatus*) were indistinguishable across islands (Table 2). Notably, stomach contents data have limited taxonomic resolution of prey, highlighted clearly by the ‘fish’ prey category within piscivore-invertivore that may contain any of hundreds of potential prey fish species. It is possible that results at the functional-group resolution presented here belie taxonomic differences of prey among islands. Finer analyses of stomach contents at taxonomic- or species-level would require advances in stomach contents methodology (e.g., metabarcoding) and dramatic increases in numbers of individuals sampled.

For each species of planktivore and piscivore-invertivore, stable isotope analysis showed a consistent pattern across islands, with more equatorial islands systematically associated with similar or lower somatic tissue $\delta^{15}\text{N}$ estimates relative to more northern islands (Table 4, Fig. 3). When examining the results of stable isotope estimates for species of piscivore-invertivore across islands, we observed evidence of latitudinal consistency that appeared to be linked to the north-south gradient of oceanic primary production (Fig. 1; Online Resources). In the NLI, regional and nearshore biogeophysical processes deliver essential energetic subsidies to shallow coral reef

communities (Gove et al. 2016). The frequency and magnitude of these events increase with proximity to the equator and directly influences the marine biogeochemical cycle (Altabet 2001; Gove et al. 2016). Specifically, internal waves and localized upwelling deliver sub-thermocline ^{15}N -depleted inorganic nitrogen that directly affects the basal source signature of $\delta^{15}\text{N}$ whereby, isotope values are generally lower near the equator due to increased availability and, preferential biological uptake and fractionation of lighter NO_3^- (see Fig. 4, bottom panel in Altabet 2001). In our study, the $\delta^{15}\text{N}$ values of the piscivore-invertivores decreased with proximity to the equator and suggests that the diets are linked allochthonous sources of oceanic primary production (Fig. 4).

Another surprising finding was that the $\delta^{15}\text{N}$ values of the three species of piscivore-invertivores were similar across all 5 islands despite exhibiting distinct size-structured diets and differing in body size by an order of magnitude (Fig. 3; Online Resource 8). The observed size structuring in the diets of the piscivore-invertivores was not surprising considering the ubiquity of gape limitation associated with morphological constraints in aquatic food webs (Hairston and Hairston 1993; Romanuk et al. 2011). However, the consistency in the $\delta^{15}\text{N}$ values across species was contrary to the common expectation of a positive scaling relationship between relative trophic position and body size in coral reef food webs (Jennings et al. 2001; Romanuk et al. 2011). While we recognize that the results of pairwise comparisons indicated a lack of quantitative consistency in the $\delta^{15}\text{N}$ values of the piscivore-invertivores across islands (Table 4), when examining the mean $\delta^{15}\text{N}$ values of the three piscivore-invertivores within each island we observed the values to be within 1.5‰ $\delta^{15}\text{N}$ of each other and are unlikely to be ecologically relevant (Fig. 3). Recall that most assessments of relative trophic position suggest that one trophic level is matched with a 2.5-4.0‰ enrichment in $\delta^{15}\text{N}$ (Post 2002).

The latitudinal consistency of the stable isotope estimates combined with the size structuring in the diets suggests that on central Pacific coral reefs, the diets of piscivore-invertivores, regardless of body size and feeding ecology, reveal close trophic similarities and appear linked closely to basal planktonic energetic resources. Further, these data provide empirical dietary evidence of tight trophic linkages from lower to higher functional trophic levels (planktivore to piscivore-invertivore, without intermediate trophic steps) consistent with hypotheses generated from fish biomass distributional patterns explored across the Indian Ocean (Graham et al. 2017). Our findings suggest that both larger and smaller bodied piscivore-invertivores derive much of their energy by preying on species closely linked to basal resources (e.g., planktivores feeding near to source of oceanic primary production). Such tight linkages with basal sources of oceanic primary production can reduce the number of steps between trophic levels and may be a mechanism contributing to increased energetic efficiency within the trophic ecology of some reef fish assemblages.

In contrast to the piscivore-invertivores, the $\delta^{15}\text{N}$ values of the grazer-detritivores did not track estimates of oceanic primary production along the north-south latitudinal gradient (Fig. 3). Instead, we found the feeding ecologies of the grazer-detritivores to be distinct among species and this distinction was reflected in their diets and stable isotopic values (Fig. 2; Fig. 3; Online Resources). For example, the stable isotope values of *S. aureus* and *C. marginatus* exhibit greater enrichment in ^{15}N , likely a result of consuming a greater proportion of diet items (i.e., invertebrates and detritus) that are themselves enriched in $\delta^{15}\text{N}$ compared to common groups of algae consumed by grazer-detritivores. In the case of *C. marginatus*, $\delta^{15}\text{N}$ values were equal to or often greater than the $\delta^{15}\text{N}$ values of the piscivore-invertivores, which is consistent with a feeding mode that includes coprophagy and the consumption of detritus (McMahon et al. 2016).

Further, the presence of physiological food processing mechanisms, including gut fermentation and microbial activity can contribute to higher rates of trophic fractionation and result in higher $\delta^{15}\text{N}$ values than expected in some grazer-detritivores (Mill et al. 2007). The variability in the diets and isotopic values observed among grazer-detritivores highlights the complex nature of this benthic-foraging group (Choat et al. 2004; Clements et al. 2009) as well as the prevalence of omnivory and coprophagy in coral reef ecosystems (Crossman et al. 2005; McMahon et al. 2016).

Across islands, we found a significant effect of oceanic primary production (estimated as concentration of water-column chlorophyll-*a*) on the $\delta^{15}\text{N}$ stable isotopic values of tissue from piscivore-invertivores with $\delta^{15}\text{N}$ values decreasing with increasing oceanic primary production (Online Resource 8). Interestingly, the isotope values of the piscivore-invertivores and planktivores were consistent across islands with the piscivore-invertivores tracking between 2.5 and 4.0‰ greater in $\delta^{15}\text{N}$ than the isotopic values of the mean of the two species of planktivore surveyed as would be expected for stepwise enrichment between trophic groups (Post 2002) (Fig. 3; Online Resource 9). While it was somewhat obvious that the diet and isotopic signature of planktivores was linked to oceanic energetic subsidies (i.e., copepods comprised >65% of their diet based on stomach contents), the consistency in diet and isotope position observed for the piscivore-invertivores was rather surprising. Our results suggest that piscivore-invertivores across body sizes primarily exploit prey species positioned low in the food web and derived from allochthonous sources of oceanic primary production.

It should not be surprising that coral reef communities should support a wide range of species with diverse trophic ecologies that often exploit varying energetic resources. Our observations indicate that coral reefs exhibit relatively consistent patterns in food web structure,

but they are not necessarily the same as those expected on the basis of simple concepts of niche differentiation (e.g., larger taxa systematically eating at higher trophic level). Our results suggest that planktivores and piscivore-invertivores both seemingly exploit prey derived primarily from sources of oceanic primary production. In contrast, grazer-detritivores on coral reefs support diets that are more complicated, with species exploiting a diverse prey field linked not only to benthic primary production but also linked indirectly to sources of oceanic primary production as a result of autochthonous recycling. The topological pathways by which energetic resources are transferred through complex communities has important implications for the function and stability of coral reef food webs, and we may need to change the way that we think about these systems if we aim to incorporate multi-species approaches into coral reef fisheries management. In the northern Line Islands, exploiting energetic resources derived from sources of oceanic primary production likely increases trophic productivity among piscivore-invertivores (Rooney and McCann 2012) and may serve as one of the mechanisms for why intact coral reef ecosystems can support such a high biomass of piscivore-invertivores towards the top of the food web (McCauley et al. 2018; Sandin and Zgliczynski 2015). Together these findings provide important insight into the foraging patterns of coral reef fish assemblages and should inspire myriad research questions and field experiments that aim to increase our understanding of the influence environmental gradients in driving the trophic dynamics of hyperdiverse aquatic ecosystems.

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506

507

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611 **Table 1.** Characteristics of the eight coral reef species identifying sample sizes for stomach
612 content and stable isotope (in parentheses) analyses by island: KIN = Kingman; PAL = Palmyra;
613 TER = Teraina; TAB = Tabuaeran; and JAR = Jarvis. The regional contribution of each species
614 to total mean fish abundance and biomass is given as a percentage (%). Satellite derived
615 estimates of oceanic primary production (Chlorophyll-*a*) are provided for each island. Values for
616 Chlorophyll-*a*, abundance, and biomass are means with standard error given in parentheses.
617 Sizes of fishes are given in standard length and NP denotes that the species was not present at the
618 island. Samples supplementing the 2010 field expedition are identified with an Asterix (* =
619 2006; and ** = 2011).
620

Functional Group, Species	Size Range Collected (cm)	Mean Size Collected (cm)	Mean Size Processed (cm)						Contribution to:	
				KIN	PAL	TER	TAB	JAR	Fish Abundance (%)	Fish Biomass (%)
Piscivore-invertivores										
<i>Lutjanus bohar</i>	10.15-61.50	40.33	44.27	20 (10)	20 (10)	9 (10)	7 (10)	4 (3)	0.31	16.71
<i>Cephalopholis urodeta</i>	7.30-18.82	13.63	14.92	15 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.38	0.91
<i>Paracirrhites arcatus</i>	3.33-10.60	7.58	8.64	20 (10)	20 (10)*	20 (10)	20 (10)	20 (10)	0.61	0.29
Planktivores										
<i>Pseudanthias bartlettorum</i>	1.99-5.92	3.66	4.54	NP	20 (10)**	20 (10)	20 (10)	20 (10)	7.92	0.35
<i>Chromis margaritifer</i>	1.55-6.57	4.14	4.84	20 (10)	20 (10)*	20 (10)	20 (10)	20 (10)	19.57	0.77
Grazers-detritivores										
<i>Stegastes aureus</i>	1.79-8.70	6.14	7.36	20 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.56	0.29
<i>Acanthurus nigricans</i>	5.80-18.50	12.38	15.45	20 (10)	15 (10)*	20 (10)	20 (10)	20 (10)	0.73	2.63
<i>Ctenochaetus marginatus</i>	2.45-20.30	12.19	14.31	20 (10)	20 (10)	20 (10)	20 (10)	20 (10)	0.43	1.45
TOTAL				135 (70)	155 (80)	149 (80)	147 (80)	144 (73)	30.50	23.41
Mean Chlorophyll- <i>a</i> (mg m ⁻³)				0.21 (0.001)	0.18 (0.001)	0.17 (0.002)	0.16 (0.002)	0.12 (0.002)		
Total Reef Fish Abundance (# m ⁻²)				27.79 (3.74)	11.82 (0.70)	6.61 (0.61)	7.56 (0.80)	3.52 (0.18)		
Total Mean Reef Fish Biomass (g m ⁻²)				412.02 (98.08)	112.29 (6.26)	159.51 (18.28)	90.45 (13.98)	225.86 (27.22)		
Total Mean Top-predator Biomass (g m ⁻²)				256.62	29.53	37.31	12.26	155.55		

Table 2. Output results of pairwise comparisons using a multinomial approach to examine stomach contents of eight species across the Northern Line Islands. Significant difference based on $p \leq 0.01$. NP denotes that the species was not present at the island. Dashes indicate stomachs of sampled individuals were observed to be empty.

Functional Group Species	Kingman	Palmyra	Teraina	Tabuaeran	Jarvis
Piscivore-invertivores					
<i>Lutjanus bohar</i>	A	A	A	A	--
<i>Cephalopholis urodeta</i>	A	A	A	A	A
<i>Paracirrhites arcatus</i>	A	A	A	A	A
Planktivores					
<i>Pseudanthias bartlettorum</i>	NP	A	A	A	B
<i>Chromis margaritifer</i>	A, B, C	A	B	C	D
Grazer-detritivores					
<i>Stegastes aureus</i>	A	A, C	A	B	C
<i>Acanthurus nigricans</i>	A	B	B, C	B	C
<i>Ctenochaetus marginatus</i>	A,B,C	A, C	A	B	C

Table 3. Output results of one-way analysis of variance (ANOVAs) testing the effect of Island on the $\delta^{15}\text{N}$ values of key coral reef fish across multiple functional trophic groups.

Functional Group				
Species	MS	df	F-value	p-value
Piscivore-invertivores				
<i>Lutjanus bohar</i>	5.50	4	14.35	<0.001
<i>Cephalopholis urodeta</i>	15.48	4	137.90	<0.001
<i>Paracirrhites arcatus</i>	14.24	4	121.00	<0.001
Planktivores				
<i>Pseudanthias bartlettorum</i>	8.20	3	19.44	<0.001
<i>Chromis margaritifer</i>	28.31	4	46.77	<0.001
Grazer-detritivores				
<i>Stegastes aureus</i>	12.79	4	81.98	<0.001
<i>Acanthurus nigricans</i>	3.10	4	13.29	<0.001
<i>Ctenochaetus marginatus</i>	7.09	4	16.29	<0.001

Table 4. Output results of pairwise comparisons using Tukey honest significant difference (HSD) to examine consistency in $\delta^{15}\text{N}$ of eight species of coral reef fishes across islands. Significance based on $p \leq 0.01$. NP denotes that the species was not present at the island.

Functional Group	Kingman	Palmyra	Teraina	Tabuaeran	Jarvis
Species					
Piscivore-invertivores					
<i>Lutjanus bohar</i>	A	A	A, B	B	C
<i>Cephalopholis urodeta</i>	A	A	B	C	D
<i>Paracirrhites arcatus</i>	A	A	B	C	D
Planktivores					
<i>Pseudanthias bartlettorum</i>	NP	A	B	B	B
<i>Chromis margaritifer</i>	A	A	B	B	B
Grazer-detritivores					
<i>Stegastes aureus</i>	B, C	A	A	B	C
<i>Acanthurus nigricans</i>	B, C	B	A	B	B
<i>Ctenochaetus marginatus</i>	C	A	A	A	B

Figures

Fig. 1. Map of the northern Line Islands identifying the three remote islands (Kingman, Palmyra and Jarvis) and two inhabited islands (Teraina and Tabuaeran) that served as study sites. Long-term (10 years) estimate of mean chlorophyll-*a* used as a proxy of phytoplankton biomass for the region highlighting the south to north gradient of oceanic primary production observed across study sites. (color figure online)

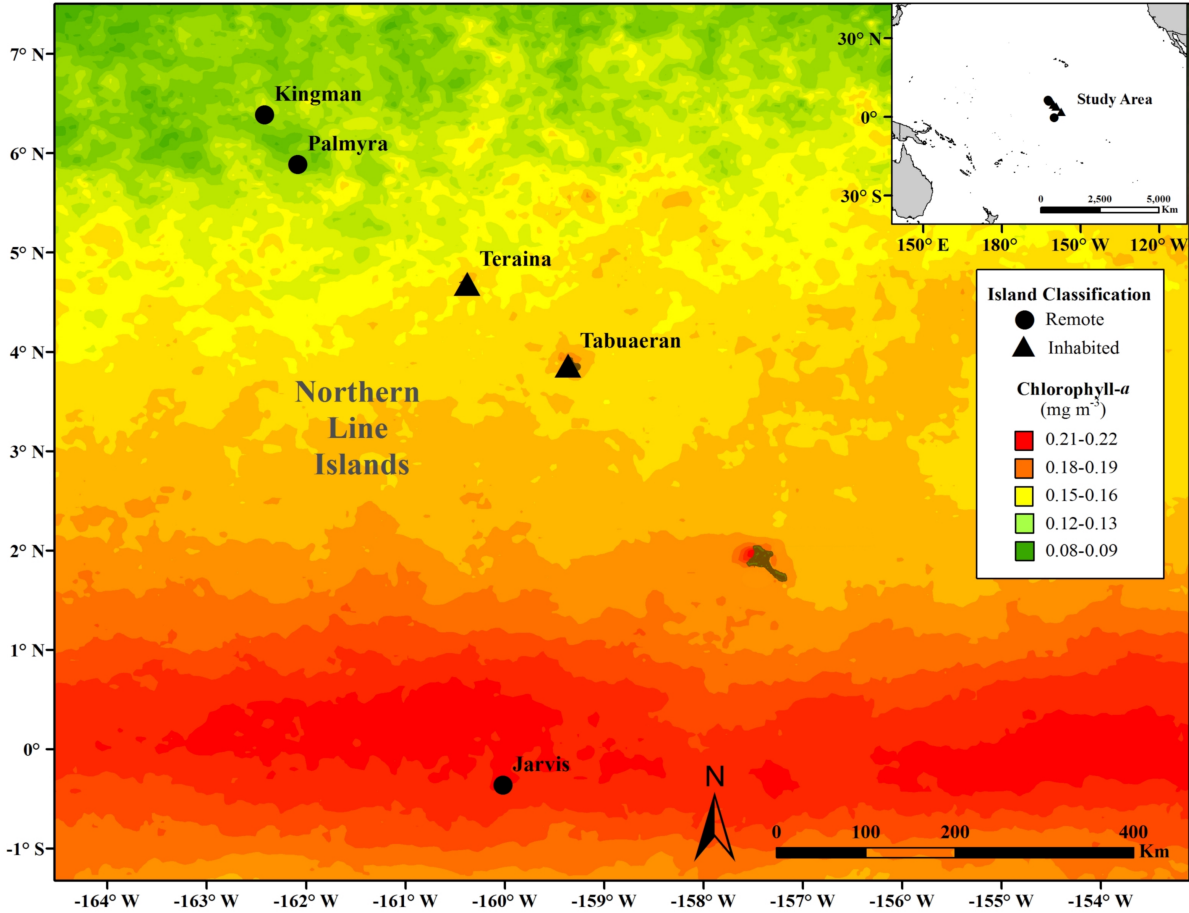
Fig. 2. Percent composition of dietary category subgroupings observed in the stomachs of the: (a) piscivore-invertivores (*Lutjanus bohar*, *Cephalopholis urodeta*, *Paracirrhites arcatus*); (b) planktivores (*Pseudanthias bartlettorum* and *Chromis margaritifer*); and (c) grazers-detritivores (*Stegastes aureus*, *Acanthurus nigricans*, *Ctenochaetus marginatus*) across islands. Island codes are as follows: KIN = Kingman; PAL = Palmyra; TER = Teraina; TAB = Tabuaeran; JAR = Jarvis. Blanks indicate missing diet data for species-island combination and “NP” indicates species-island combination where a species was not present at the island. At Jarvis, the guts of *L. bohar* were empty. Letters above plots indicate results of multinomial pairwise comparisons. (N=20 for all species-island combinations with exception of the following: *L. bohar*, Teraina N=9, Tabuaeran N=7, Jarvis N=4; *C. urodeta*, Kingman N=15; *A. nigricans*, Palmyra N=15) (color figure online).

Fig. 3. Values of $\delta^{15}\text{N}$ for coral reef fish species plotted across the northern Line Islands in north to south orientation (left to right). Plot (a) includes focal species representing piscivore-invertivore and planktivore functional trophic groups while plot (b) includes focal species representing the grazer-detritivore functional trophic group. All values are mean and ± 1 standard

662 deviation. (N=10 for all species-island combinations with exception of the following: *L. bohar*,
663 Jarvis N=3) (color figure online).

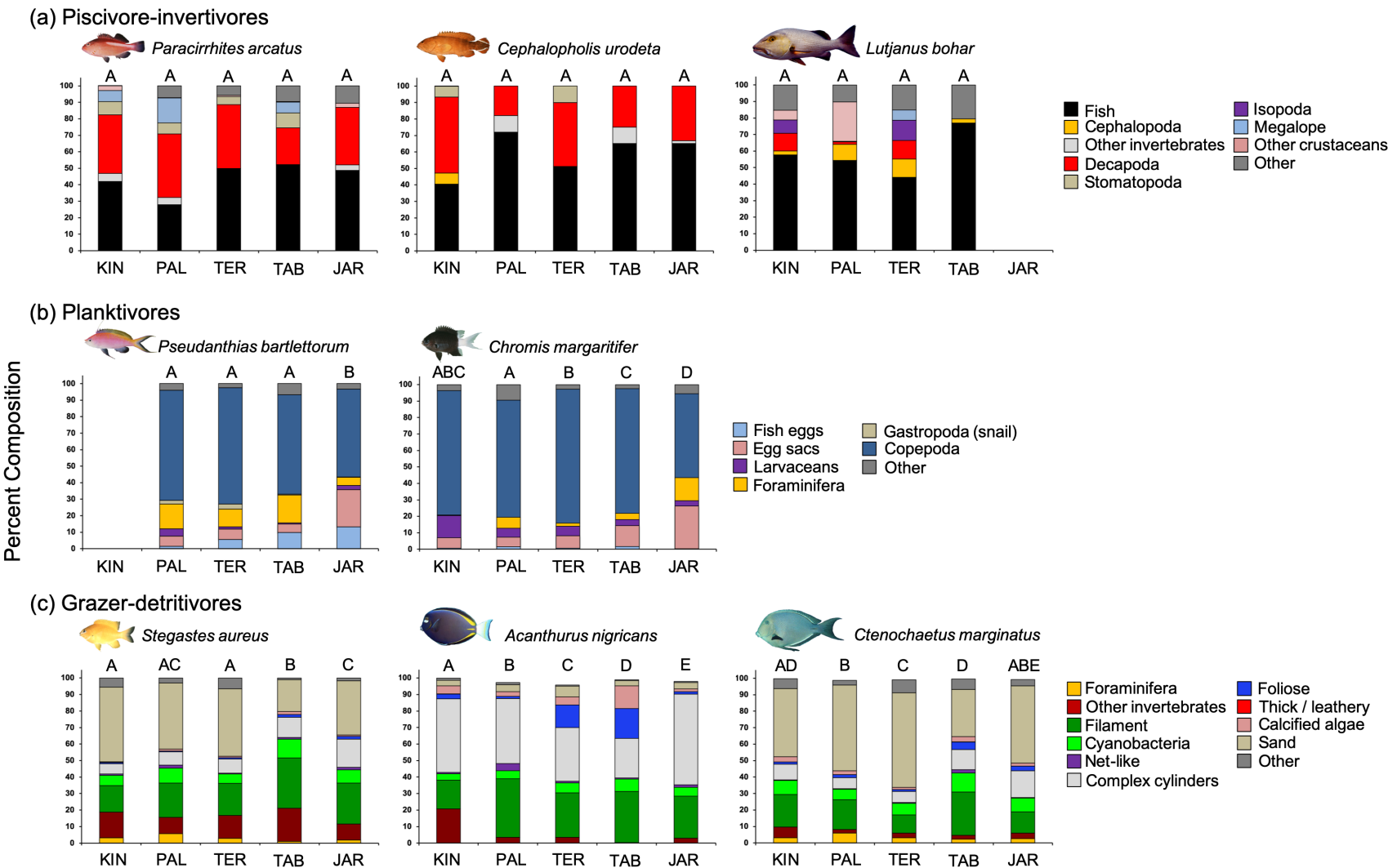
664

665 **Fig. 1.**

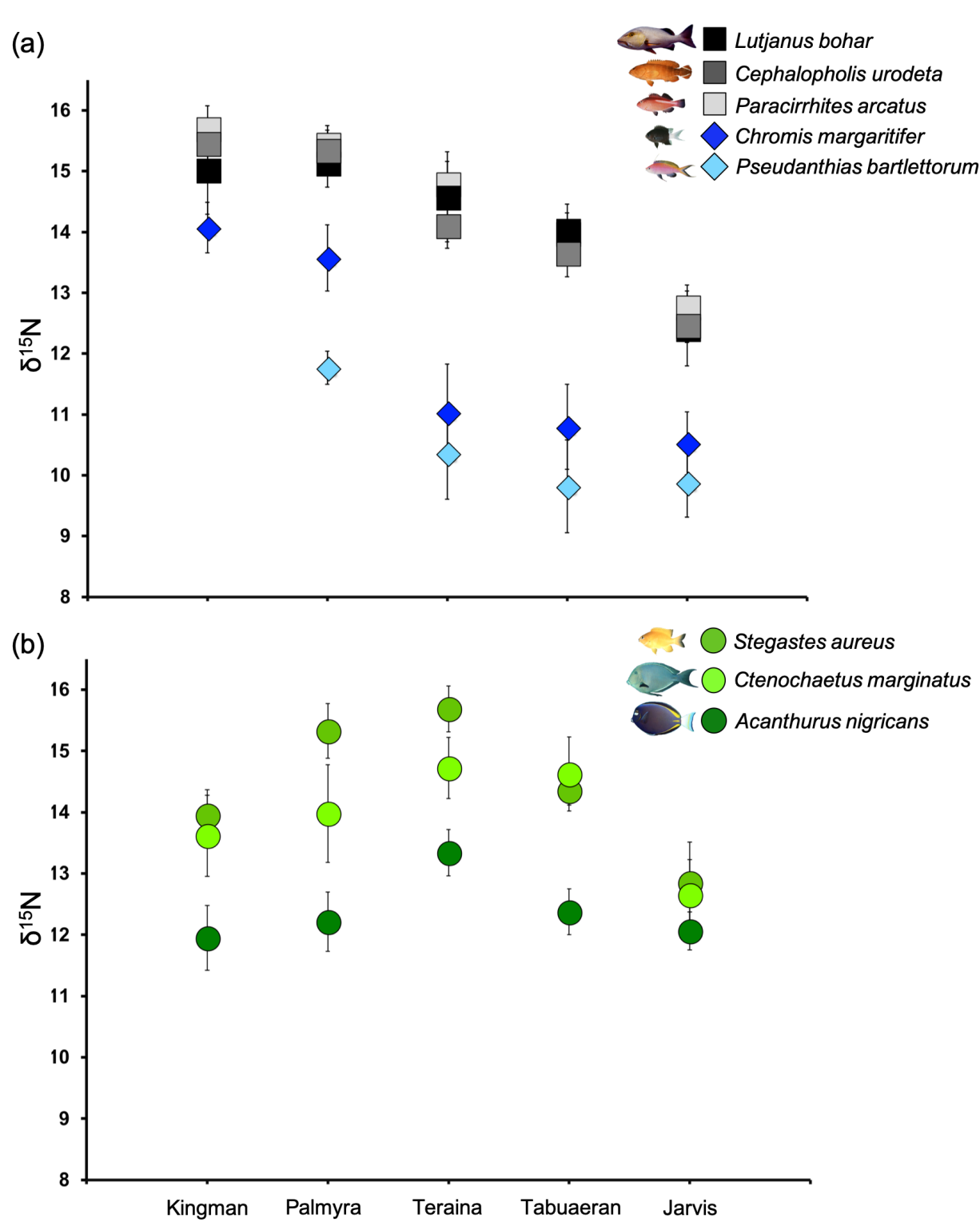


666

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670 Fig. 3



671

Electronic Supplemental Materials (ESM) – Online Resources

Foraging consistency of coral reef fishes across environmental gradients in the central Pacific

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Online Resource 1. Additional details regarding the study system and the methods used to examine dietary consistency across the Line Islands.

Study sites

Teraina and Tabuaeran are part of the Republic of Kiribati and contain human population densities ranging from several hundred to several thousand people (DeMartini et al. 2008, Sandin et al. 2008). Fishing serves as the primary source of income for island residents with hook and line, spearfishing, and hand-nets being the most common methods. In contrast, Kingman, Palmyra and Jarvis are uninhabited U.S. possessions protected from fishing as part of the U.S. Pacific Remote Islands Marine National Monument and previously protected as U.S. National Wildlife Refuges (Maragos et al. 2008, Bush 2009). As such these protected islands contain some of the most intact coral reef ecosystems in the Pacific (DeMartini et al. 2008, Sandin et al. 2008). Efforts to compare coral reef fish assemblages across the northern Line Islands have revealed stark differences between inhabited and uninhabited islands (DeMartini et al. 2008, Sandin et al. 2008). At uninhabited islands, total fish biomass is 2-4 times higher than at inhabited islands, with top-predators comprising the highest proportions of fish biomass. Conversely, fish assemblages at inhabited islands are comprised of smaller-bodied species from lower-trophic levels. Importantly, there is only limited evidence of prey release associated with changes in top-predator density (DeMartini et al. 2008, Sandin et al. 2010).

The northern Line Islands are also exposed to a latitudinal gradient of oceanographic primary production, whereby sea surface temperature increases and nutrient concentrations decrease with increasing latitude and distance from the equator (Altabet 2001, Sandin et al. 2008, Gove et al. 2013, Gove et al. 2016). At the regional scale, Jarvis and to a lesser extent Tabuaeran,

are influenced by upwelled nutrient-rich waters of the westward-flowing South Equatorial Current and the eastward-flowing Equatorial Undercurrent, while Kingman, Palmyra, and Teraina are geographically located in the path of the warmer oligotrophic flow of the North Equatorial Countercurrent. Additionally, islands within proximity of the equator are influenced by localized upwelling events as a result of the eastward flowing Equatorial Undercurrent coming into contact with steep island topography (Gove et al. 2006). We use satellite-derived (MODIS) estimates of chlorophyll-*a* (mg m^{-3}) as a proxy for nearshore oceanographic primary production using a masking routine to omit any compromised data associated with island or lagoon reflectance. Means were calculated by averaging eight-day chlorophyll-*a* values for each island over a ten-year time period (2005-2015). A masking routine was used to estimate the nearshore chlorophyll-*a* values along the 30 m isobath or a distance of 250m from the reef crest around each island and to omit any contaminated data associated with island or lagoon reflectance inshore of the 30-m isobath or directly adjacent to each pixel.

Stomach Content Analysis

Approaches used to identify trophic position or niche width in marine systems have traditionally relied on stomach content analysis (Hyslop 1980, Bearhop et al. 2004), which offers an invaluable tool for identifying the types of prey and the general feeding habits of a consumer (Randall 1967). We followed these traditional approaches to evaluate the relative contribution of prey items to the diet of each targeted species we used stomach content analyses. For the piscivore-invertivores (*L. bohar*, *C. urodeta*, and *P. arcatus*), we removed all stomach contents and weighed each food item individually to create a mean weight of item consumed (all food items combined). To characterize diet composition, we estimated what proportion of this total

weight was made up of different prey items. Prey items were defined as broad taxonomic groups. For the planktivores (*C. margaritifer* and *P. bartlettorum*), diet composition was based on the relative abundance of food items in the stomach, again assigned to broad taxonomic groups. For the grazer-detritivores (*S. aureus*, *A. nigricans*, and *C. marginatus*), diet composition was, like the planktivores, based on relative abundance of food items in the stomach. However, due to the difficulty of identifying algae that have undergone partial digestion to a high taxonomic resolution, all algae were assigned to one of three functional group categories, namely early stage algae (e.g., low-lying turf algae), late stage algae (e.g., upright fleshy seaweeds), and calcified algae (e.g., algae that contained CaCO_3). Additionally for herbivores, food items were also classified into the invertebrate and sand categories.

Stable Isotope Analysis

Frozen tissue samples from each species-island combination served as the source for stable isotope data. Sample analysis followed previously established protocols (Post 2002, Michener and Lajtha 2007, Post et al. 2007) and was completed at the Boston University Stable Isotope Laboratory and the Scripps Institution of Oceanography Mass-Spectrometry Lab. In summary, frozen tissue samples were first freeze-dried for 24 hours to remove moisture and then ground to a fine powder using a mortar and pestle or mechanical grinder mill (Wig-L-Bug®). A 1.0-1.25 mg sample of powdered tissue was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then flash combusted at 1800°C in a Eurovector Carbon and Nitrogen elemental analyzer and the combustion products (CO_2 , N_2 and H_2O) were separated chromatographically and introduced into GVI IsoPrime isotope ratio mass spectrometer, with

water removed using a magnesium perchlorate water trap. Stable isotope ratios of nitrogen (^{15}N to ^{14}N) and carbon (^{13}C to ^{12}C) were expressed as the relative per mil (‰) difference between the samples and international standards (Vienna PDB carbonate and N_2 in air, respectively). Values were reported in δ notation where $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ ratios were expressed by the equation:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000,$$

where R is $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$, respectively. To increase sample accuracy, one replicate per 10 samples as well as any initial anomalous results were rerun. To ensure consistent combustion among sample replicates, a known standard (e.g. peptone, a hydrolyzed animal protein from Sigma Chemical Company, glycine, or citrus leaves, SRM 1572) was run every 15 consecutive samples. If the known standard yielded results 0.15 ‰ above or below the documented standard value, the samples preceding the standard were rerun.

The dominant marine macroalgae in the central Pacific, *Halimeda* spp., was collected and processed for isotopic analysis to complement the examination of dietary consistency across islands. *Halimeda* spp. samples were collected from each island or atoll in the vicinity of the fish collection sites and brought back to the research vessel to be dried and stored individually in labeled sample bags. To prepare samples for stable isotope analysis, a small segment (~1.0 g) of each sample was cut near the tip of new growth. A total of 20 individual segments were collected from each island. For analysis, *Halimeda* spp. samples were placed in pre-labeled cleaned (acid washed using 5% HCl) 15 ml falcon tubes. Samples were then de-calcified by adding ~5 ml of 5% HCl to each falcon tube. After 24 hours the HCl solution was decanted and an additional 5 ml of 5% HCl was added to each falcon tube to ensure de-calcification of samples had taken place. The HCl solution was again decanted and samples were rinsed by adding ~10 ml of DI

water to each falcon tube, which was then capped, and gently shaken. The DI water was decanted and the process was repeated 3 times to ensure most of the HCl solution had been removed. Samples were then placed on labeled clean (combusted at 450°C for 12 hours) aluminum weigh boats and placed in drying oven at 60°C for 72 hours. Samples were then removed from the drying oven and ground to a fine powder using a mechanical grinder mill (Wig-L-Bug®). A 1.4-1.6 mg sample of powdered *Halimeda* spp. was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then processed through a mass spectrometer as outlined above to obtain stable isotope values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$).

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Online Resource 2. Results of the systematic stomach analyses outlining the two-tiered hierarchical approach used to classify diet constituents for the Piscivore-invertivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows:
 LU.BOHA = *Lutjanus bohar*; CE.UROD = *Cephalopholis urodeta*; and PA.ARCA = *Paracirrhites arcatus*.

Diet category (coarse groups)	Diet category (subgroupings)	Example constituents	LU.BOHA	CE.UROD	PA.ARCA
Fishes	Fishes	Labridae (<i>Pseudocheilinus</i> sp)	X	X	X
		Pomacentridae (<i>Chromis</i> sp)		X	
		Gobiidae			X
Invertebrates	Cephalopoda Other invertebrates	octopi and squid	X	X	X
		Echinodermata (brittle stars, sea urchins)			X
		Gastropoda (snails)		X	X
		Unidentified invertebrate		X	X
Crustaceans	Decapoda Stomatopoda Isopoda Megalope	crabs, megalopes, shrimp	X	X	X
		mantis shrimp		X	X
		isopods	X		
		larval crustacean	X	X	

	Other crustaceans		X		X
		Amphopoda (amphipods)			X
		Copepoda (Calanoida, Poecilostomatoida, Cyclopoida, Harpacticoida)	X		X
		Unknown crustacean	X		
Other	Other	Calcified algae (<i>Halimeda</i> sp)		X	X
		Early and Late algae	X	X	
		Other	X		

Online Resource 3. Results of the systematic stomach analyses outlining the two-tiered hierarchical approach used to classify diet constituents for the Planktivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows: PS.BART = *Pseudanthias bartlettorum*; and CH.MARG = *Chromis margaritifer*.

Diet category (coarse groups)	Diet category (subgroupings)	Example constituents	PS.BART	CH.MARG
Eggs			X	X
	Fish eggs		X	X
	Egg sacs		X	X
Larvacea	Larvaceans	tunicate, appendicularia	X	X
Foraminifera	Foraminifera	amoeboid protist	X	X
Other			X	X
	Gastropoda	Snail	X	
	Other		X	X
		Isopoda (isopod)		X
		Cladocera (water fleas)	X	
		Ostracoda (seed shrimp)	X	X
		Worm		X
		Trichodesium (cyanobacteria)	X	X

Clear case	X	X
Textured ball	X	X
Unidentifiable	X	X
Other	X	X

Online Resource 4. Results of the systematic stomach analyses outlining the two-tiered hierarchical approach used to classify diet constituents for the Grazer-detritivores. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Abbreviated fish species codes are as follows: AC.NIGR = *Acanthurus nigricans*; CT.MARG = *Ctenochaetus marginatus*; and ST.AURE = *Stegastes aureus*.

Diet category (coarse groups)	Diet category (subgroupings)	Example constituents	AC.NIGR	CT.MARG	ST.AURE
Invertebrates			X	X	X
	Foraminifera			X	X
	Other invertebrates	snails, bivalves	X	X	X
Early algae			X	X	X
	Filament	<i>Cladophora</i> sp., <i>Polysiphonia</i> sp., <i>Sphacelaria</i> sp.	X	X	X
	Cyanobacteria	<i>Moorea</i> sp., <i>Lyngbya</i> sp., <i>Schizothrix</i> sp.	X	X	X
	Net-like	<i>Microdictyon</i> sp., <i>Martensia</i> sp.	X	X	X
Late algae			X	X	X
	Complex cylinders	<i>Gelidium</i> sp., <i>Gracilariaria</i> sp., <i>Laurencia</i> sp.	X	X	X
	Foliose	<i>Ulva</i> sp., <i>Dictyota</i> sp.	X	X	X
	Thick / leathery	<i>Sargassum</i> sp., <i>Turbinaria</i> sp.	X	X	X

Calcified algae			X	X	X
	Calcified algae	jointed calcareous (<i>Jania</i> sp., <i>Amphiroa</i> sp., <i>Halimeda</i> sp.) calcareous crust (<i>Peyssonellia</i> sp., Crustose Coralline Algae)	X	X	X
Sand	Sand		X	X	X
Other	Other		X	X	X

Online Resource 5. Results of the systematic stomach analyses for the piscivore-invertivores species across 5 survey islands identifying the mean size of prey (g) for each species and sample size given as number analyzed.

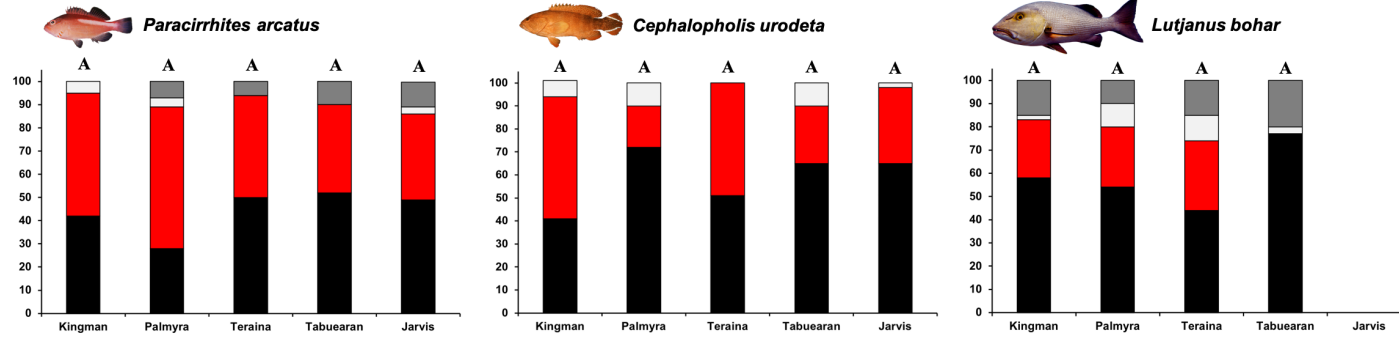
Species		Kingman	Palmyra	Terraina	Tabuaeran	Jarvis
<i>Lutjanus bohar</i>	Sample size	20	20	9	7	4
	Mean Prey Size (g)	4.16	13.29	13.11	1.78	
<i>Cephalopholis urodeta</i>	Sample Size	15	20	20	20	20
	Mean Prey Size (g)	0.55	0.59	0.37	2.29	0.54
<i>Paracirrhites arcatus</i>	Sample Size	20	20	20	20	20
	Mean Prey Size (g)	0.05	0.03	0.06	0.05	0.05

Online Resource 6. Output results of pairwise comparisons using a multinomial approach to examine stomach contents of eight species across the Northern Line Islands. Analysis was performed using the high-resolution dietary subgrouping data. Higher resolution dietary category subgroupings were used only if the category represented a mean of at least 1% of total stomach contents for at least one species of fish. Significant difference based on $p \leq 0.01$. NP denotes that the species was not present at the island. Dashes indicate stomachs of sampled individuals were observed to be empty.

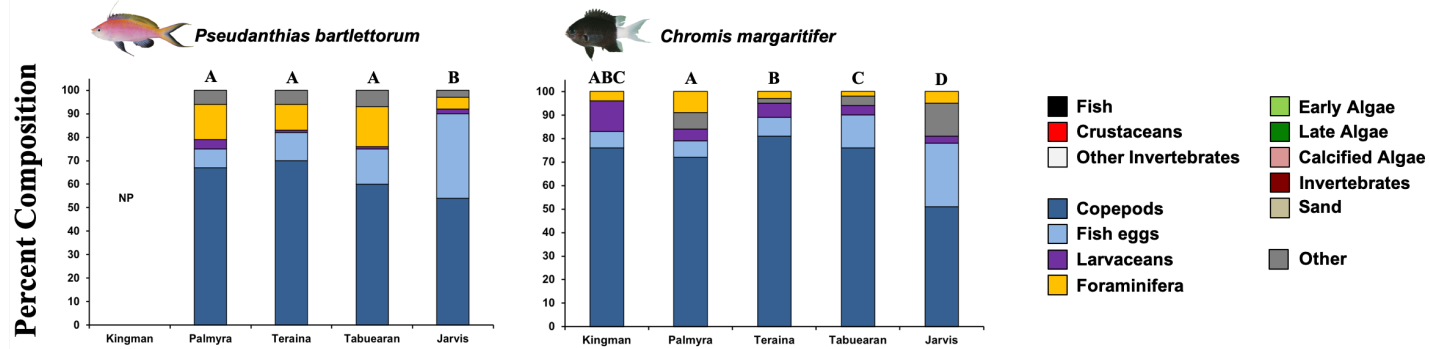
Functional Group Species	Kingman	Palmyra	Teraina	Tabuaeran	Jarvis
Piscivore-invertivores					
<i>Lutjanus bohar</i>	A	A	A	A	--
<i>Cephalopholis urodeta</i>	A	A	A	A	A
<i>Paracirrhites arcatus</i>	A	A	A	A	A
Planktivores					
<i>Pseudanthias bartlettorum</i>	NP	A	A	A, B	B
<i>Chromis margaritifer</i>	A, B	A	B	B	C
Grazer-detritivores					
<i>Stegastes aureus</i>	A	A, C	A	B	C
<i>Acanthurus nigricans</i>	A	B	C	D	E
<i>Ctenochaetus marginatus</i>	A, D	B	C	D	A,B,E

Online Resource 7. Percent composition of diet items observed in the stomachs of (a) the three piscivore-invertivores (*Lutjanus bohar*, *Cephalopholis urodeta*, *Paracirrhites arcatus*); (b) the two planktivores (*Pseudanthias bartlettorum* and *Chromis margaritifer*); and (c) the three grazers-detritivores (*Stegastes aureus*, *Acanthurus nigricans*, *Ctenochaetus marginatus*). Blanks indicate missing diet data for species-island combination and “NP” indicates species-island combination where species was not present at the island. At Jarvis, the sampled guts of *Lutjanus bohar* were observed to be empty. Letters above plots indicate results of multinomial pairwise comparisons.

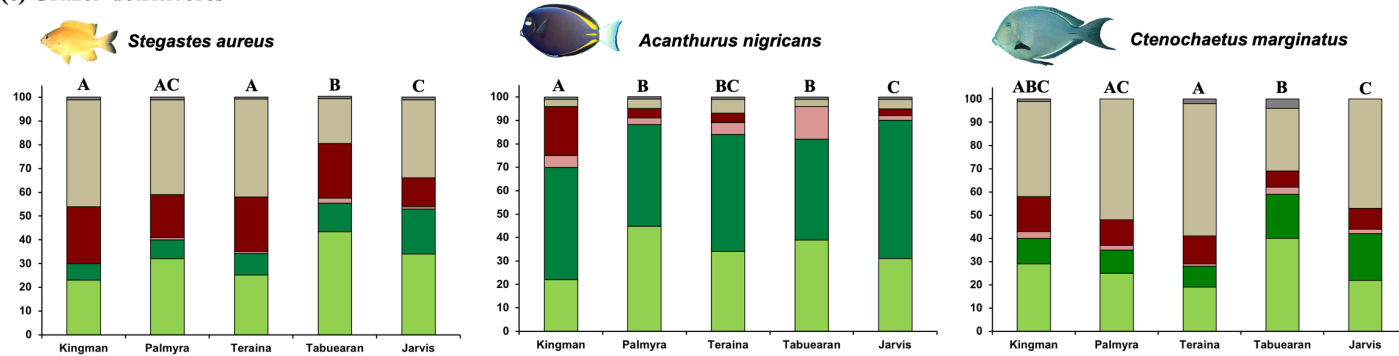
(a) Piscivore-invertivores



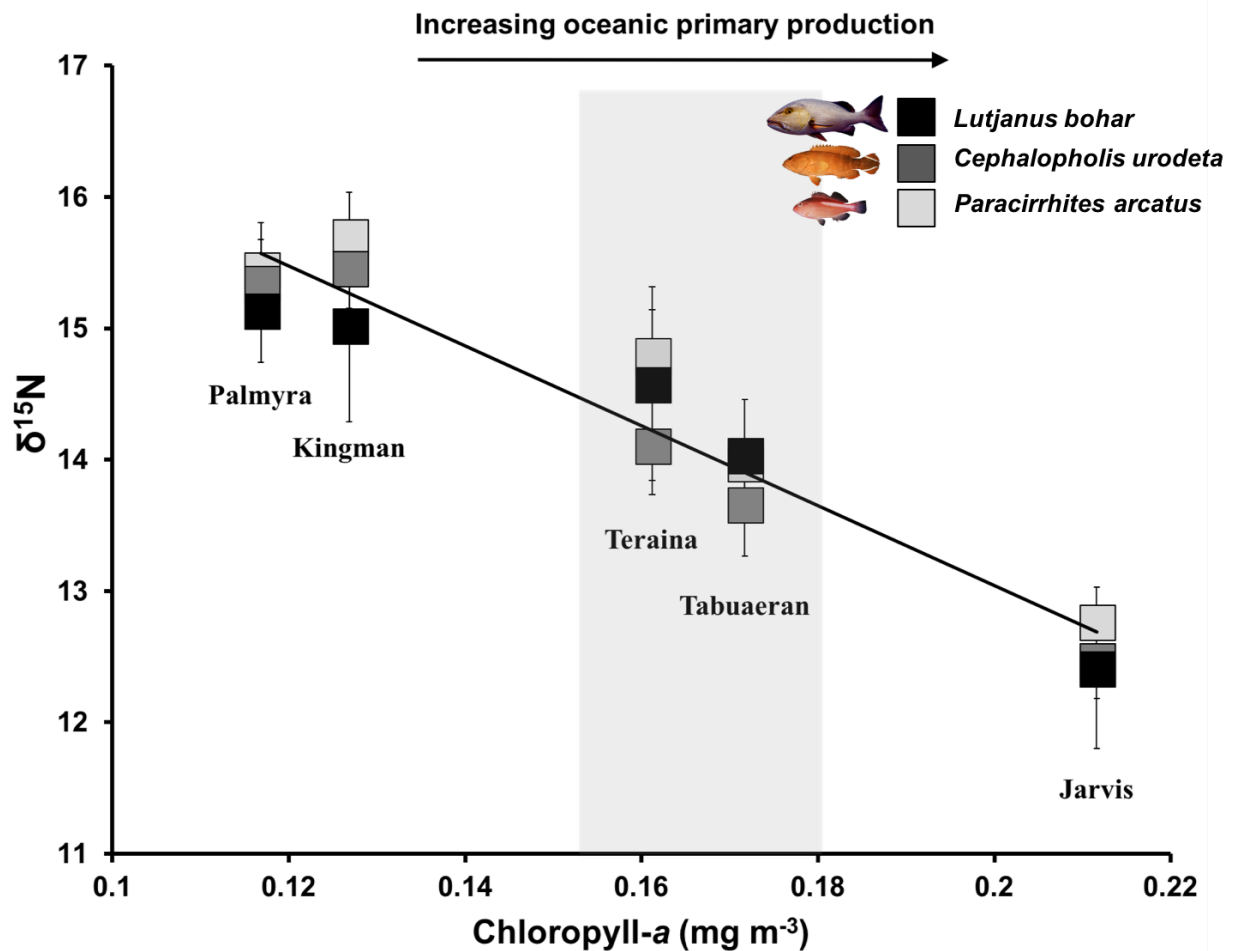
(b) Planktivores



(c) Grazer-detritivores

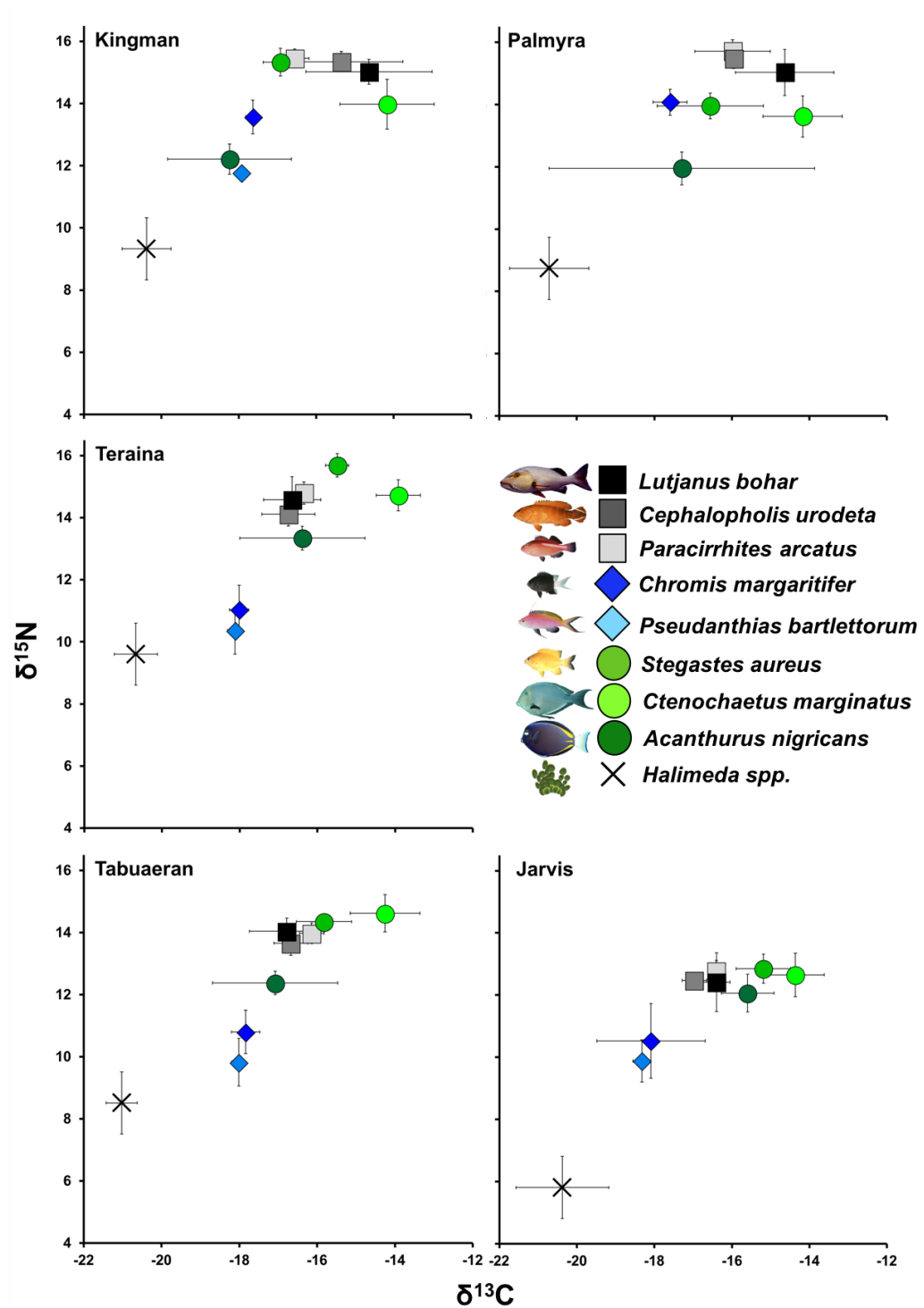


Online Resource 8. Relationship between the mean $\delta^{15}\text{N}$ values (mean and ± 1 standard deviation) of three piscivore-invertivore fish species and estimates of nearshore primary production (mean chlorophyll-*a*) across the northern Line Islands. Solid line represents the fit from a least-squares linear regression ($R^2 = 0.97$, $P < 0.01$). Shaded area represents inhabited islands.



Online Resource 9. Description of stable isotope values ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$) for 8 species of coral reef fishes and the macroalgae (*Halimeda* spp.) plotted as bi-plots across the 6 northern Line Islands.

All values are mean and ± 1 standard deviation.



Online Resource 10. Description of species-specific stable isotope values ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$) for eight species of coral reef fishes from the northern Line Islands. Symbols indicate island classifications (circles = remote islands; triangles = inhabited islands) and shading represents scale of oceanic primary production (lighter shading = less primary production). All values are means and ± 1 standard deviation.

