

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Diets Shifts in Coral Reef Fishes in Response to Changes in Food Availability and  
Predator Density

A Thesis submitted in partial satisfaction of the requirements for the degree Master of  
Science

in

Biology

by

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2013



The Thesis of Elisabeth Gibson Cordner is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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2013

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## ACKNOWLEDGEMENTS

I would like to acknowledge Professor Stuart Sandin for his support as the chair of my committee and for being the inspiration behind this study.

I would also like to thank Professor Jonathan Shurin and Professor Carolyn Kurle for being members of my committee.

I would like to thank all of the members of the Sandin and Smith labs for their guidance, support, and great company. I would especially like to thank Brian Zgliczynski and Gareth Williams for their contributions to this thesis. Thank you to Jennifer Smith, Emily Kelly, and Molly Gleason for their guidance in categorizing algae. I would also like to thank Kate Hanson for teaching me how to identify zooplankton.

I would like to thank the Birch Aquarium for providing the filtered seawater used in this study.

I would like to thank my lab assistants Atalani Jackson, Jesse Ellison, and Gabrielle Rossbach for their many hours of data collection.

The entirety of this thesis is currently being prepared for submission for publication of the material. Corder, Elisabeth G.; Zgliczynski, Brian; Williams, Gareth. J; Sandin, Stuart A. The dissertation author was the primary investigator and author of this material.

## ABSTRACT OF THE THESIS

Diets Shifts in Coral Reef Fishes in Response to Changes in Food Availability and  
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Master of Science in Biology

University of California, San Diego, 2013

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Food availability and predation risk are the primary factors that influence an individual's diet composition. Reduced food availability will result in populations with broader diet breadths due to individual diet specialization. This effect can be enhanced when predators limit foraging movement of prey. Predators can also force prey to forage in lower-risk habitats. An opportunity for us to study these influences on fish diets in a natural system exists in coral reefs. The reefs of the Northern Line Islands vary in their predator biomass and the amount of food available to each trophic guild.

To determine the effects of changing food availability and predator densities on the diets of fishes we quantified the diets of species from three trophic guilds from the Northern Line Islands. Populations experiencing higher predation pressure and/or lower food availability are expected to have wider diet breadths. Trends in diet breadth varied across species. The results do not offer a clear indication that fish are shifting their foraging habitats to be closer to reef refuges in response to increased predation pressure. So, changes in predator density and the amount of food available seem to influence shifts in diet breadth, but the influences vary across species. There are two factors that may also influence diets: habitat complexity and resource patchiness.

## **Introduction**

Food availability and predation risk are two factors that influence an individual's diet. In classic optimal foraging theory, food availability strongly affects the encounter rate an individual has with a prey type, affecting their decision to continue consuming that prey type or continue searching for a higher value item (Stephens and Krebs 1986). Predation risk, on the other hand, influences an individual's decision to forage or to hide (Randall 1965, Gerking 1994).

The quantity of food available to an individual can influence the diversity of that individual's diet. Food availability here refers to the mean amount of food accessible to an individual, therefore linking both the level of competition and the total amount of food present in a habitat. Decreased food availability reduces an individual's encounter rate with its most preferred resources so that lower value, less preferred resources become relatively profitable to consume (Stephens and Krebs 1986), resulting in higher dietary diversity as more novel resources are ingested. This has been found in herbivorous fishes from a rocky intertidal zone, whose dietary diversity was inversely proportional to food supply (Horn 1983). However, no other empirical studies were found addressing diet diversity in response to food supply levels.

Along with increases in diet diversity, the maximum dietary overlap between individuals decreases as food supply decreases. This phenomenon is described in Pianka's (1974) niche overlap hypothesis, which states that the maximum tolerable dietary overlap between individuals should be lower in intensely competitive situations. Evidence for this has been found in cases of increased competition and decreased food availability. For example in sticklebacks and perch, when the density of conspecifics is

high, individuals' diets become more diversified and less similar to conspecifics (Svanbäck and Persson 2004, Svanbäck and Bolnick 2007). Decreased between-individual diet overlap, often referred to as individual specialization, has also been found in cases of decreased food availability in owls and sea otters (Korpimäki 1987, Tinker et al. 2008). Dietary overlap decreases because individuals within a population frequently share their most-preferred prey item, but vary in their preference for lower-quality prey items in order to avoid intraspecific competition (Robinson and Wilson 1998, Svanbäck and Bolnick 2005). The combination of increased individual diet diversity and decreased between-individual diet overlap will result in an increase in the diet breadth (or niche width) of a population of organisms (Bolnick et al. 2010).

In addition to food availability, predation risk can significantly influence the diets of prey species. The trade-off between exposure to predation risk and obtaining more valuable food resources is recognized as an important contribution to an individual's foraging decisions (Stephens and Krebs 1986, Brown et al. 1999). Randall (1965) was one of the first to report the result of this trade-off in herbivorous reef fishes that only grazed sea grasses adjacent to the reef in order to remain close to the shelter from predators provided by the reef. Similar results have been found in more recent studies looking at coral reef fishes (Sackely and Kaufman 1996, Madin et al. 2010). The presence of predators can also force prey to forage in less-preferred food patches (Mittelbach 1986). Numerous studies have described foraging habitat shifts resulting from predator presence in aquatic, marine, and terrestrial systems through both observational and experimental studies (Edwards 1983, Werner et al. 1983, Lima and Dill 1990, Heithaus and Dill 2006). These indirect behavior-mediated effects have the

potential to influence the diets of individuals more than the more commonly considered direct mortality-mediated effects (Křivan and Schmitz 2004).

The majority of the studies that address the influence of food availability on diet composition were done experimentally, using simple set-ups with one consumer species at different competition levels, so it is unclear if these results will carry over into natural systems. And while the effects of predation risk on habitat use and foraging excursion size have been well studied through observation done in natural systems, few investigate how the effects of predation risk and food availability may interact to affect the diets of consumers. An opportunity for us to study the interaction between these two influences *in situ* exists in coral reefs. Coral reefs are highly diverse ecosystems with a large number of trophic links and high regional and local variability in food availability and predator biomass (Grigg et al. 1984, Jackson et al. 2001, Gove et al. 2013). Specifically, the reefs of the Northern Line Islands provide us with a system that varies from reef to reef in the predator biomass and the amount of food available to each trophic guild. This archipelago contains some of the few reefs that still have high densities of apex predators (DeMartini et al. 2008, Sandin et al. 2008). Most reefs have been over-fished, effectively removing large-bodied, apex predators from the system (Hodgson 1999, Jackson et al. 2001, Myers et al. 2003). Diet shifts in coral reef fishes could potentially have cascading effects and therefore need to be understood in order to comprehensively predict how coral reef ecosystems will respond to the removal of top predators.

To determine the effects of changing predator densities and food availability on the diets of coral reef fishes we quantified the diets of fishes from the Northern Line

Islands belonging to three trophic guilds: mid-level carnivores, planktivores, and herbivores. Based on the studies described previously, we predicted that fish populations would have a broader diet breadth when food availability is low due to increased intraspecific competition (Svanbäck and Persson 2004). We also predicted that fish would have a broader diet breadth when predator densities are high, since these fish would have smaller foraging excursion areas, effectively reducing the amount of food available to a fish (Madin et al. 2010). We expected planktivores and carnivores to consume a higher proportion of prey of benthic origin when predator densities are high because they will shift their foraging from the water column to the lower-risk habitat of the reef benthos.

The introduction, in full, is currently being prepared for submission for publication of the material. Corder, Elisabeth G.; Zgliczynski, Brian; Williams, Gareth. J; Sandin, Stuart A. The dissertation author was the primary investigator and author of this material.

## Materials and Methods

### *Study area*

The Northern Line Islands are located in the central Pacific Ocean, approximately 1,500 km SSW of the Hawaiian Archipelago (Figure 1), and consist of two atolls, Kingman and Palmyra, and four islands, Teraina, Tabuaeran, Kiritimati, and Jarvis. Kingman, Palmyra, and Jarvis are U.S. unincorporated territories while Teraina, Tabuaeran, and Kiritimati are part of the Republic of Kiribati. The three U.S. territories have never supported long-term human populations, though Palmyra was briefly used as a military base during WWII. As of 2010, Teraina, Tabuaeran, and Kiritimati support populations of 1,690, 1,960, and 5,586 respectively (Kiribati 2010 Census). These populations rely heavily on both commercial and subsistence fishing (Sandin et al. 2008). Because of this, the coral reef ecosystems of Kiritimati, Teraina, and Tabuaeran have a significantly lower biomass of apex predators than the reefs of Palmyra, Kingman, and Jarvis (Figure 2) (Sandin et al. 2008, B. Zgliczynski *unpub.*). Large predators such as sharks and snappers make up 85% of the total fish biomass at Kingman and only 19% of the total fish biomass at Kiritimati (Sandin et al. 2008). The presence of a permanent population on Teraina, Tabuaeran, and Kiritimati also results in human and solid waste being dumped into the lagoon and washed onto the reef (Sandin et al. 2008). In addition to the differences in human population, these reefs also experience varying oceanographic conditions. The more southern reefs are located in an upwelling zone and therefore receive more nutrient and planktonic inputs than the other islands (Baars 1990, Maragos et al. 2008, Gove et al. 2013). There is a clear increase in

the monthly average chlorophyll-*a* concentration on reefs closer to the equator (Figure 3, S.A. Sandin *unpub.*). Chlorophyll-*a* has been shown to be positively correlated with zooplankton abundance (Holmes et al. 1957, Liston 1990), indicating an increasing gradient of zooplankton abundance across the Northern Line Islands from north to south. These reefs also have varying benthic compositions (Figure 4, J.E. Smith *unpub.*). The variation across these islands creates habitats with different levels of predation risk and food availability.

### *Fish Collections*

Seven different species of fish from three trophic guilds were collected for this study. The herbivorous species collected were the goldrim surgeonfish (*Acanthurus nigricans*), an aggressive roving herbivore, the bluespotted bristletooth (*Ctenochaetus marginatus*), a detritivore/herbivore, and the golden gregory (*Stegastes aureus*), a territorial herbivore. The planktivorous fish species collected were the bicolor chromis (*Chromis margaritifer*) and Bartletts' anthias (*Pseudanthias bartlettorum*). The carnivorous species were the darkfin hind (*Cephalopholis urodeta*) and the arc-eye hawkfish (*Paracirrhites arcatus*), both benthic species that feed on small fishes and invertebrates. Fishes were collected at all reefs from forereef and terrace habitats between 5 and 20 m depth using a variety of methods including hand nets, three-prong Hawaiian slings, anesthetic (clove oil), and hook-and-line fishing. The collections were targeted to obtain samples from all observed size classes. Fish were measured, weighed, and dissected either in the field or in the lab after being frozen. The stomachs were then preserved in formalin or through freezing.

## *Stomach Contents Analysis*

### *Herbivores*

The frozen stomachs were opened and the stomach contents washed out onto a gridded Petri dish using ultra filtered seawater. The seawater was ozonated for 2 hours, run through a 25  $\mu\text{m}$  filter sock, and exposed to a UV sterilizer overnight. Twenty 7 mm diameter circles were drawn onto the bottom of the gridded Petri dish at grid intersections prior to use. Stomach contents were evenly distributed around the Petri dish. Within each circle, the stomach contents were identified to functional group and their percent composition of the total stomach content in that circle was estimated by eye in increments of 5%. The functional groups used were based on Littler and Littler (1984) and are as follows: filamentous, foliose, complex cylinder, cyanobacteria, jointed calcareous, calcified crust, net-like, thick & leathery, invertebrate, and non-biological. The algal groups were then lumped in three broad categories for analysis based on succession: “early algae” (filamentous, cyanobacteria, net-like), “late algae” (complex cylinder, foliose, thick & leathery), and “calcified algae” (jointed calcareous, calcified crust) (Figure 5) (Wanders 1977). For *C. marginatus* and *S. aureus* sand was removed from the data for statistical analysis. Identifications were conducted using a Leica EZ4 dissecting microscope. Empty stomachs and stomachs smaller than 0.5 cm in length empty were excluded. In four cases, the first cm of intestines was used in place of the stomach due to a lack of stomachs larger than 0.5 cm.

### *Planktivores*

Stomach contents were removed and washed into a small round Petri dish using filtered seawater. The contents were washed using 53  $\mu\text{m}$  plankton mesh and returned to the Petri dish. Using a plastic pipette, the sample was transferred to a Bogorov counting chamber, and prey items were counted and identified to functional group, order, or, if the prey item was a copepod, to family. Empty stomachs (with  $< 10$  prey items) were excluded.

### *Carnivores*

The stomachs were opened and then the contents were scraped out using a scalpel or picked out using forceps, minimizing the amount of stomach lining stuck to the prey items. Prey items were identified to order or family level, if possible, and then weighed to the nearest 0.0001 g. Empty stomachs were included in data collection but excluded from the analysis. If multiple small prey items were present in a stomach (e.g. isopods, copepods), they were counted and then weighed together to calculate an average prey weight.

### *Statistical Analyses*

The data collected was multinomial and multivariate in nature. The diet composition of each individual fish is the result of numerous multinomial choices made about what to consume. So the prey item percentages of each fish's diet represent an estimation of the multinomial probabilities for the choices made by that fish. This type of data creates a problem when analyzing it because the percentage value of each prey

item depends on the percentage of all of the other prey items. Additionally, the values of each prey item percentage are bounded between 0% and 100%, intrinsically violating the assumption that data fit a normal distribution that most statistical tests require. So to deal with this multinomial nature of the data, we used a custom statistical approach (Barott et al. 2012).

To formally test the null hypothesis that diets did not differ among islands, we used a resampling approach to estimate the probability that group membership explains the variability among group clouds (analogous to the logic of analysis of variance). First the data was plotted in  $m-1$  dimensions, where  $m$ =the number of prey item categories. We used  $m-1$  dimensions because the value of the last prey item category depends on the first  $m-1$  categories. The Euclidean distances between each group centroid were then calculated and used to find the mean intercentroid distance among groups. A null distribution of the mean intercentroid distances was created using re-sampling with replacement (10,000 iterations) and then compared to the actual mean intercentroid distance. This procedure was then used to complete pairwise comparisons between islands. To do this, resampling was limited to the two groups being compared for each comparison. The null hypothesis was rejected if  $p \leq 0.01$ .

To assess the diet breadth of individual fish species within each island, we quantified the dispersion of the individual group (island) clouds in multivariate space again using a customized routine (G.J. Williams, *unpub*). Plotting the data in the same multivariate space as above, for each island, we calculated the Euclidean distances between each data point and the island cloud's centroid. The premise for this is that if there is more variability in diet composition between individuals within an island then

the island cloud would be more dispersed, so the median distance from each data point to the centroid would be larger. After calculating the deviations of each data point from the centroid for each island, we ran a Kruskal-Wallis test to formally test the null hypothesis that deviations are the same across islands. We then ran pairwise comparisons using the post-hoc Dunn's test. All analyses were completed using R 2.14.0 (R-Core-Team 2012).

The materials and methods section, in full, is currently being prepared for submission for publication of the material. Cordner, Elisabeth G.; Zgliczynski, Brian; Williams, Gareth. J; Sandin, Stuart A. The dissertation author was the primary investigator and author of this material.

## Results

The number of stomachs analyzed from each species by island is shown in Table 1

### *Herbivores*

The diets of *Acanthurus nigricans* were significantly different among all islands in terms of algal functional group ( $p < 0.01$ ), with the population of *A. nigricans* from Kingman having a significantly wider diet breadth than Palmyra and Jarvis (Figure 6a). Diet breadth also decreases slightly with decreasing latitude (Figure 6a). See Table 2 for detailed diet composition.

On a broad taxonomic scale (referring to the lumped categories of “early algae,” “late algae,” and “calcified algae”), diets from Kingman were significantly different from all other islands ( $p < 0.01$ ). Pairwise comparisons are shown in Table 3. Stomachs from Jarvis contained more late algae, while stomachs from Palmyra and Tabuaeran tended to contain more early algae. Fish diets on Kingman were characterized by a lower proportion of early algae and higher proportion of invertebrates (Figure 7).

The diets of *Ctenochaetus marginatus* from all islands were significantly different from one another in terms of algal functional group ( $p < 0.01$ ), with *C. marginatus* populations from Tabuaeran having significantly wider diet breadths than Kingman, Teraina, and Kiritimati (Figure 6b). Diet breadth was the same across the uninhabited islands Kingman, Palmyra, and Jarvis. Large proportions of sand characterized diets of fish from Teraina and Kiritimati, while stomachs from Kingman tended to contain more fleshy invertebrates (Table 4).

Diets of *C. marginatus* were significantly different among islands on a broad taxonomic scale ( $p < 0.001$ ). Pairwise comparisons are shown in Table 3. A higher proportion of late algae characterized *C. marginatus* diets from Jarvis, followed by Tabuaeran and Kiritimati (Figure 7).

Diets of *Stegastes aureus* were significantly different among islands. All pairs of islands were found to be significantly different except for Kingman, Palmyra, and Teraina ( $p < 0.01$ ). A higher proportion of sand characterizes diets from Kiritimati, while a lower proportion of sand and higher proportion of fleshy invertebrates characterizes diets from Tabuaeran (Table 5). No differences in diet breadth were found (Figure 6c).

Diets of *S. aureus* were significantly different among islands on a broad taxonomic scale. Pairwise comparisons are shown in Table 3. Fish diets from Jarvis and Kiritimati were characterized by containing more late algae (Figure 8).

### *Planktivores*

The proportions of major prey groups from *Chromis margaritifer* diets were significantly different among islands ( $p < 0.01$ ). Pairwise comparisons are shown in Table 3. Stomachs from Jarvis were characterized by a lower proportion of copepods and higher proportion of foraminifera, while stomachs from Kingman had a higher proportion of larvaceans (Figure 9).

On a finer taxonomic scale, diets of *C. margaritifer* were also significantly different across islands ( $p < 0.01$ ) and the population sampled from Kingman appears to

have the widest diet breadth (Figure 10a). Diet breadth decreases slightly with decreasing latitude (Figure 10a). Detailed diet contents shown in Table 6.

For the major prey groups, *Pseudanthias bartlettorum* diets were significantly different between Teraina and Tabuaeran and Teraina and Kiritimati ( $p < 0.01$ , Table 3). A higher proportion of foraminifera characterize diets from Tabuaeran and Palmyra (Figure 11). Several individuals from Teraina, Kiritimati and Jarvis had stomachs that were essentially 100% round fish eggs.

On a finer taxonomic scale, diets of *P. bartlettorum* were significantly different across islands ( $p < 0.01$ ). Tabuaeran and Jarvis had significantly wider diet breadths than Teraina (Figure 10b). Detailed diet contents shown in Table 8.

### *Carnivores*

For *Paracirrhites arcatus* no significant difference among islands was found on a fine or broad taxonomic scale (Figure 13, Table 9). *Cephalopholis urodeta* appear to consume higher proportions of fish on Palmyra and Tabuaeran, but these differences were non-significant ( $p = 0.0182$ ) (Figure 14, Table 10). Diet breadth of *P. arcatus* was significantly wider on Tabuaeran than Jarvis (Figure 15a), while no significant difference was found for the diet breadth of *C. urodeta* (Figure 15b). 18 *P. arcatus* and 94 *C. urodeta* had completely empty stomachs.

The results section, in full, is currently being prepared for submission for publication of the material. Corder, Elisabeth G.; Zgliczynski, Brian; Williams,

Gareth. J; Sandin, Stuart A. The dissertation author was the primary investigator and author of this material.

## Discussion

Populations experiencing higher predation pressure and/or lower food availability are expected to have wide diet breadths. One herbivorous species and one planktivorous species had wider diet breadths on Kingman reef. This reef has the highest predator biomass of the Northern Line Islands and relatively low food availability for both herbivores and planktivores (Maragos et al. 2008, Sandin et al. 2008). This prediction, however, did not hold for the other islands that have high predator biomass or low food availability, and was not true for the other species studied. The implications of this are that changes in the diet breadth of a population may not occur until the amount food available to an individual is sufficiently low, through the combined effect of low food availability and reduced foraging excursion size in response to higher predation risk. In addition, not all species will respond the same to shifts in food availability and predator density, even if they are members of the same trophic guild.

Overall, the results do not offer a clear indication that planktivores or carnivores are shifting their foraging habitats to the benthos in response to increased predation pressure on Kingman, Palmyra, and Jarvis.

### *Herbivores*

*Acanthurus nigricans* had a wider diet breadth on Kingman, which supports my prediction that decreased food availability and increased predation pressure would correspond to decreased diet breadth of a population. This species' diet breadth also appears to decrease slightly with decreasing latitude. This suggests that the

productivity of an island may play some role in influencing the diet breadth of this species. However, as productivity does not relate to the abundance of algae on these islands it is unclear what the driver of this trend would be. The fact that *A. nigricans* is a surgeonfish (Acanthuridae) could contribute to the weak or absent predator effects observed as they are equipped with a sharp scalpel or spine on their caudal peduncle that is a relatively effective predator deterrent. The reduced effect of predator density on the foraging behavior of surgeonfishes is supported by Madin et al.'s (2010) finding that *A. nigricans* did not have significantly smaller foraging excursion sizes on Palmyra compared to Kiritimati and Tabuaeran despite the increased predation pressure.

Diet breadth of *Ctenochaetus marginatus* was constant on the three uninhabited islands that have high predator biomass, Kingman, Palmyra, and Jarvis. This suggests that the threat of predation on these islands may be influencing the diet breadth of this species. However, diet breadth varied more among the islands that have low predator biomass, Teraina, Tabuaeran, and Kiritimati. This may be because when predators are absent from a reef, the diet breadth of this species depends more on other island factors. Specifically, the diet breadth of *C. marginatus* is significantly higher on Tabuaeran than Teraina and Kiritimati. The reef on Tabuaeran is different from Teraina and Kiritimati for two reasons. First, it is much patchier, there are areas that have high coral cover and areas that have low coral cover and a high cover of fleshy algae. Teraina and Kiritimati are more homogenous, having a high cover of fleshy algae everywhere. Additionally, Tabuaeran has the highest biomass of herbivores of the Northern Line Islands (B. Zgliczynski *unpub.*). This means that there is a higher level of competition within this trophic guild, which could contribute to the wider diet breadth observed at Tabuaeran.

There were no differences in diet breadth among *S. aureus* across the island gradient. There is virtually no published information about the behavior or diet of this damselfish, making it difficult to interpret this result. Based on colleagues' observations, *S. aureus* is loosely site-attached to coral heads, and so they may be limited to foraging in the area directly adjacent to their shelter, regardless of food availability or predation risk. It is also interesting to note the high overall proportion of sand consumed by *S. aureus*, as congeners such as *S. focus*, *S. variabilis*, and *S. lividus* typically consume a much larger proportion of algae (Lassuy 1984, Feitosa et al. 2012).

Qualitatively, the majority of the algal material consumed by the study species appeared to be made up of turf. The algae were generally small fragments and didn't appear to have been bitten off of macroalgae. Turf, or the epilithic algal community, is characterized by a small standing crop, a fast rate of primary productivity, and high species richness. It is usually characterized by aggregates of small filamentous and fleshy algae with some developmental stages of larger algal species and crustose coralline algae (Scott and Russ 1987). Grazing on turf can significantly alter its abundance and species composition (Gerking 1994, Hixon and Brostoff 1996). Since turf is one of coral's major competitors for space (McCook 2001), understanding what dictates how much and what turf herbivores consume is key in predicting and preventing possible shifts from coral-dominated to algal-dominated systems.

The shifts in the proportions of algal functional groups consumed did not reveal any clear trends that correlated with predator densities or food availability. Generally, selective grazers such as *Acanthurus nigricans* tend to select the bigger, more complex

functional forms of turf algae first (Gerking 1994). Based on this, we expected this species to consume significantly more “late algae” on Tabuaeran as there is more turf available (Sandin et al. 2008, J.E. Smith *unpub.*). It is possible that the level of competition on Tabuaeran is confounding the expected result that *A. nigricans* would have consumed more “late algae” on Tabuaeran. Tabuaeran has the highest biomass of herbivores of the Northern Line Islands, suggesting that this guild experiences higher levels of competition for food on this island (Sandin et al. 2008, B. Zgliczynski *unpub.*). Instead, *A. nigricans*, as well as the other two herbivorous species, consumed higher proportions of “late algae” on Jarvis. This is very unexpected as Jarvis has the lowest percent turf cover (J.E. Smith *unpub.*). One possible explanation for this is that increased nutrient input from the upwelling increases the growth and turnover rates of fleshy “late algae,” on which fish quickly graze (Smith et al. 2001, Smith et al. 2010). *Stegastes aureus*, however, did consume the most “late algae” on Kiritimati, the islands with the highest cover of turf (Sandin et al. 2008), suggesting that individuals will consume more of their assumed preferred prey when more food is available to them (Svanbäck and Bolnick 2005).

Both *Stegastes aureus* and *Ctenochaetus marginatus* consumed a higher proportion of sand on Kiritimati. This sand may have been ingested incidentally, as turf with more fleshy algae, as is present on Kiritimati, traps larger amounts of sediment (Smith et al. 2001). These sediments or sand may contain other organic materials that have high nutrient content, but were too digested to identify in the stomach contents through the methodology of this study. In the case of *C. marginatus*, based on studies of other *Ctenochaetus* species such as *C. striatus*, it is possible that individuals are actually

purposefully consuming sand in order to consume diatoms or other microorganisms living within the sand (Fouda and El-Sayed 1996). A more detailed analysis of the stomach contents needs to be done in order to fully explore what this species is targeting in the sand/sediment.

Another interesting result is that both *A. nigricans* and *C. marginatus* ate more fleshy invertebrates on Kingman. Kingman has a relatively low percent turf cover that is generally highly grazed, so one possible explanation for this trend is that the low food availability forces individuals to consume alternate food sources, such as invertebrates. There is evidence that some herbivores intentionally consume animal material in order to supplement their algal diet (Choat et al. 2002). That herbivores require or benefit from consuming animal material for growth is debated and seems to depend on the species (Gerking 1994). The other possibility is that there is a higher abundance of small invertebrates living in the turf on Kingman and so fish are consuming them incidentally along with their targeted food source. This discrepancy, along with others mentioned previously, could be resolved by sampling the turf communities at each of the Northern Line Islands and qualifying and quantifying their community composition.

### *Planktivores*

The diet breadth of *C. margaritifer* was the highest at Kingman, and then decreased slightly with latitude. This supports the prediction that diet breadth will be larger for populations that have less food available to them, as there is lower zooplankton inputs to the reef on Kingman which then increases on the more southern islands (Sandin et al. 2008, B. Zgliczynski *unpub*). This trend weakly supports the

prediction that populations would have wider diet breadths through decreased diet overlap when food availability is lower. However, no trends were found relating diet breadth to high predator density. This is surprising as there is direct evidence that *C. margaritifer* on Palmyra has reduced foraging excursion sizes when confronted with predators (Madin et al. 2010). It is unclear why *Pseudanthias bartlettorum* did not show the same shifts in diet breadth as *C. margaritifer*.

For both *Chromis margaritifer* and *Pseudanthias bartlettorum*, prey of obvious benthic origin, primarily benthic harpacticoids, made up a consistently small proportion of their diet, the maximum island average being only 9%. This suggests that predation pressure is not strong enough to force planktivores to forage directly adjacent to the benthos. This could be due to a potential mesopredator release effect (Myers et al. 2007, Stallings 2008), which would reduce changes in predation risk to planktivores. Both species of planktivores were found in the stomachs of *Cephalopholis urodeta* and *Paracirrhites arcatus*, and the density of this trophic guild (carnivores) does not change as dramatically across islands as does the biomass of apex predators. In order to investigate more subtle results of predators forcing planktivores to foraging closer to the reef, the vertical distribution of zooplankton needs to be quantified. This would allow us to test if there are smaller shifts in foraging heights for planktivores under higher risk of predation.

One aspect that was not considered that may contribute to the foraging behavior and diet choices of planktivores on these reefs is habitat complexity. When planktivores are offered refuge higher up in the water column where more zooplankton is available (Motro 2005) they are able to gain access to more resources without increasing their

risk of predation (Clarke 1992). So an increase in habitat complexity could negate the potential effects of predation pressure on the amount of food that an individual fish has access to.

### *Carnivores*

The carnivore stomachs analyzed were highly variable, and most contained only 1 or 2 prey items of similar type. This probably contributed to the non-significant differences among islands for *Cephalopholis urodeta*. The proportion of fish and crustaceans in the diets of *Paracirrhites arcatus* remained more or less constant across islands. They did, however, consume slightly more crustaceans on Kingman and Jarvis, which weakly supports the prediction that individuals consume more items of benthic origin on islands with higher predator densities. It is possible that differences in diet composition and breadth of these species exist at a finer taxonomic resolution, such as family, however consistent identification to this level was difficult due to the highly digested state of many prey items. It is interesting to note the number of empty stomachs, however this result cannot be interpreted, as the fish were not collected at a consistent time of day.

No significant effect of food availability or predator density was found on the diet of *P. arcatus*. This hawkfish is a sit-and-wait predator that shelters in the heads of branching corals, such as *Pocillopora* spp. (Hobson 1974, DeMartini 1996). Hobson (1974) found that this species primarily consumes benthic crustaceans, which held true in this study. It is possible that, since this species does not actively search for prey, fish simply consume whatever happens to wander into the area surrounding their coral head.

In the direct presence of predators, Schmitt et al. (2009) observed *P. arcatus* sheltering deeply into the branches of coral heads. This behavior would not necessarily change the types of prey that these fish are consuming, but may change their foraging frequency or the fullness of their stomachs. In addition, the distribution and abundances of *P. arcatus* may be determined by the distribution of their preferred shelter, *Pocillopora* coral heads (Kane et al. 2009), suggesting that shelter, and not food, may be the limiting resource for these populations. *P. arcatus* is involved in systems of intraguild predation, which was found to obscure expected trophic cascades on coral reefs (Schmitt et al. 2009). The influence of a strong site-attachment and intraguild predation may have contributed to the lack of diet shift across the Northern Line Islands in *P. arcatus*.

No significant effect of food availability or predator densities was found on the diet of *C. urodeta*. The diet of this species varies on a relatively large spatial scale, with individuals consuming mostly fish (68%) on the Society Islands (Randall and Brock 1960) and equal proportions of fish and crustaceans on Iriomote Island off of southern Japan (Nakai et al. 2001). This implies that the species is flexible in what they consume, so they have the potential to respond to changing conditions by changing their diets. However, other *Cephalopholis* spp. have been found not to change their diet seasonally, despite increases in the abundance of small prey fishes in the environment (Beukers-Stewart and Jones 2004). It was posited in that study that the lack of diet shift might be due to the abundances of prey not crossing some threshold required for a change in prey selection behavior. This may have contributed to the similar findings of this study.

For both species of carnivore, the proportion of fish in their diet was likely underestimated as fish is digested more quickly than crustaceans are (Beukers-Stewart

and Jones 2004). However since the focus of this study was comparing diets based on gut content analysis, all stomach contents should be similarly biased.

Based on this study, changes in predator density and the amount of food available influence shifts in diet breadth, but only when they are both at extreme values. There are two factors at play here that may influence diets when predation pressure and food availability are at intermediate levels: habitat complexity and resource patchiness.

As discussed for planktivores and carnivores, habitat complexity may alter a species expected response to predation threats, especially if a species relies heavily on physical refuges. An increase in habitat complexity could dampen the indirect or behavioral effects of predation on prey foraging behavior and diet. An increase in the number of refuges would, in theory, increase the potential low-risk foraging area available to a guild (Motro 2005). This would increase both gross food availability and reduce competition within the guild (Gilliam and Fraser 1987, Kotler and Holt 1989), resulting in smaller diet breadths than predicted using predator densities alone.

The distribution of resources in an environment will also modify shifts in diet resulting from indirect predation effects. There are, in general, three types of distributions of resources, clumped, uniform, and random. Changes in resource distribution can alter foraging strategies, as shown in juvenile walleye pollock, who forage in groups when their prey is clumped, but forage as individuals when prey is uniformly distributed (Ryer and Olla 1995). If one can imagine a consumer whose foraging range becomes restricted due to the threat of predation, its resulting diet would depend on the type of distribution of its food. If this consumer feeds on uniformly

distributed resources, then a range restriction would result in an increase in diet diversity, as it is forced to consume less preferred resources. However, if the consumer's resources are patchily distributed, it will be forced to consume only one type of resource, whichever happens to be in its foraging area. So the distribution of resources potentially has a dramatic effect on diet shifts resulting from indirect predator effects.

In addition, diet shifts appear to be more dramatic or likely in fishes from lower trophic guilds. The lower trophic guilds had a higher proportion of significant pairwise comparisons than the higher trophic guilds. The lower trophic guilds also showed a stronger relationship between island and diet breadth than the higher trophic guilds. This may be because the types of resources available to lower trophic guilds are more variable across the Northern Line Islands. However, it is also possible that lower trophic guilds are more dramatically affected by changes in food availability and predator density due to some quality of their foraging behavior. This is the only study that has addressed changes in diets of multiple trophic guilds in a system with varying food availability levels and predator densities making this a unique and novel finding that should be explored further.

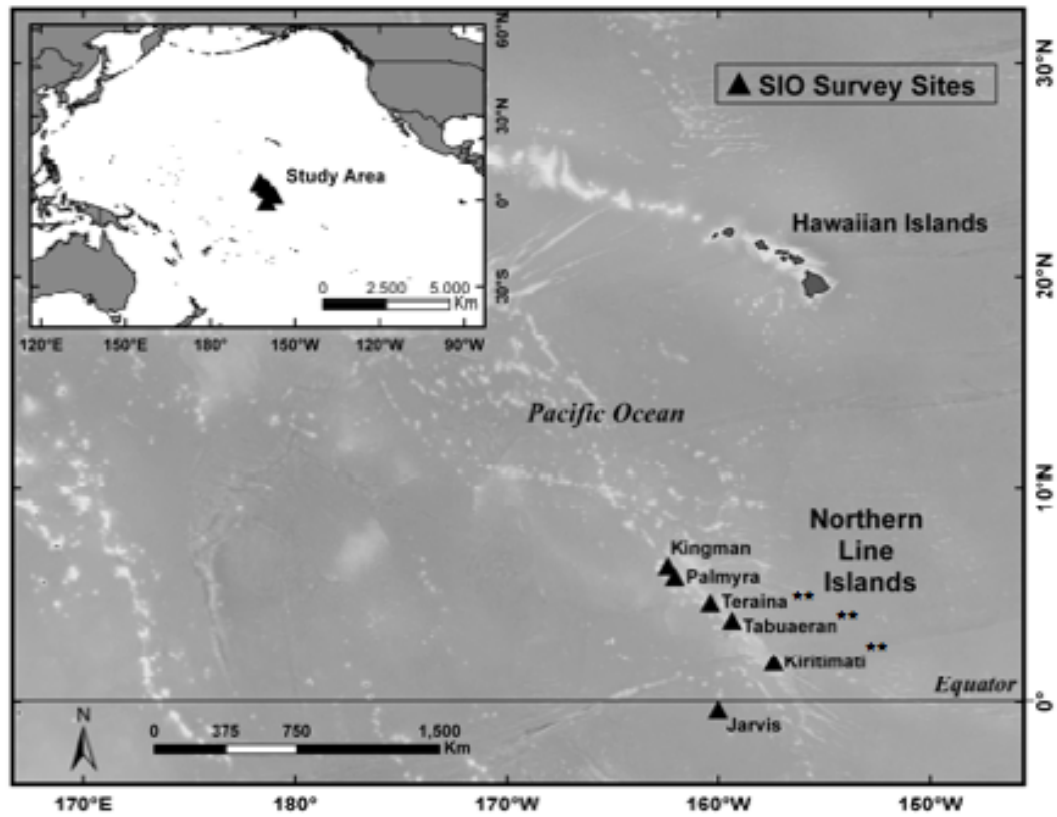
Overall this study provides a good starting point for complementary studies investigating the diet and foraging decisions of these seven species from the Northern Line Islands. This is the only study that has quantified the diets of these species from the Northern Line Islands, and the only study that has quantified the diets of *Ctenochaetus marginatus*, *Stegastes aureus*, *Chromis margaritifer*, and *Pseudanthias bartlettorum*. More data should be collected on the abundances, types, and distribution

of prey available to all trophic groups in order to determine their selectivity and to explore other causes for the observed shifts in diet. Behavioral observations of these species would also shed light on how they respond to the immediate threat of predation, as well as general differences in behavior between fish that regularly encounter predators and those that do not.

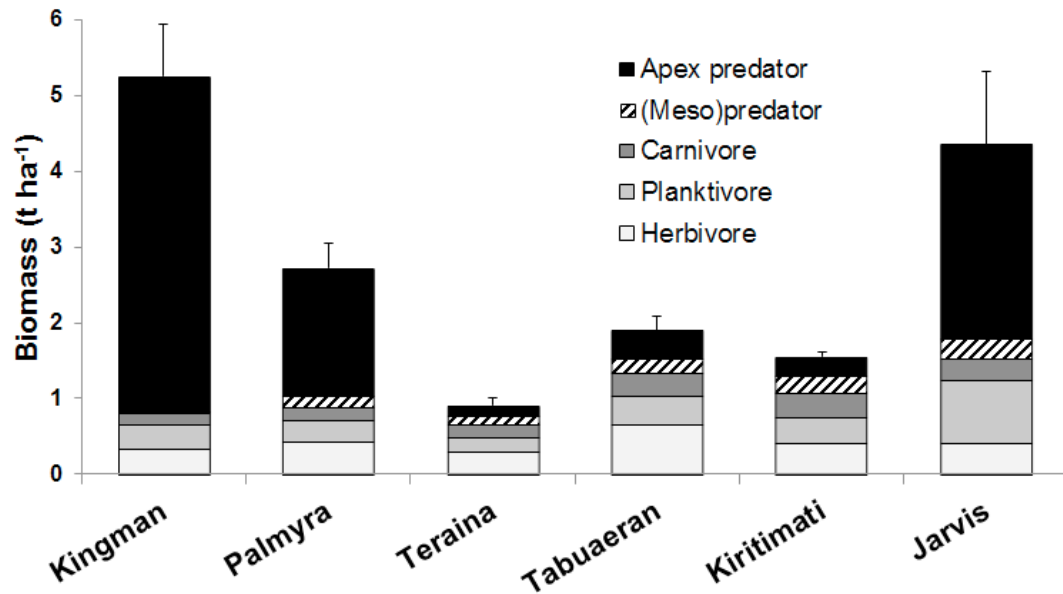
Finally, there are some caveats to using gut content analysis to examine diet. Gut contents only give us a snapshot of what a fish is eating. While they are very useful in determining the types of resources a consumer eats, they do not give us the whole picture. In order to look at what these fish are eating and their diet overlap over a longer timescale, these data should be complemented with stable isotope data, which gives a broader picture of how the diets of these fishes compare to each other.

The discussion, in full, is currently being prepared for submission for publication of the material. Corder, Elisabeth G.; Zgliczynski, Brian; Williams, Gareth. J; Sandin, Stuart A. The dissertation author was the primary investigator and author of this material.

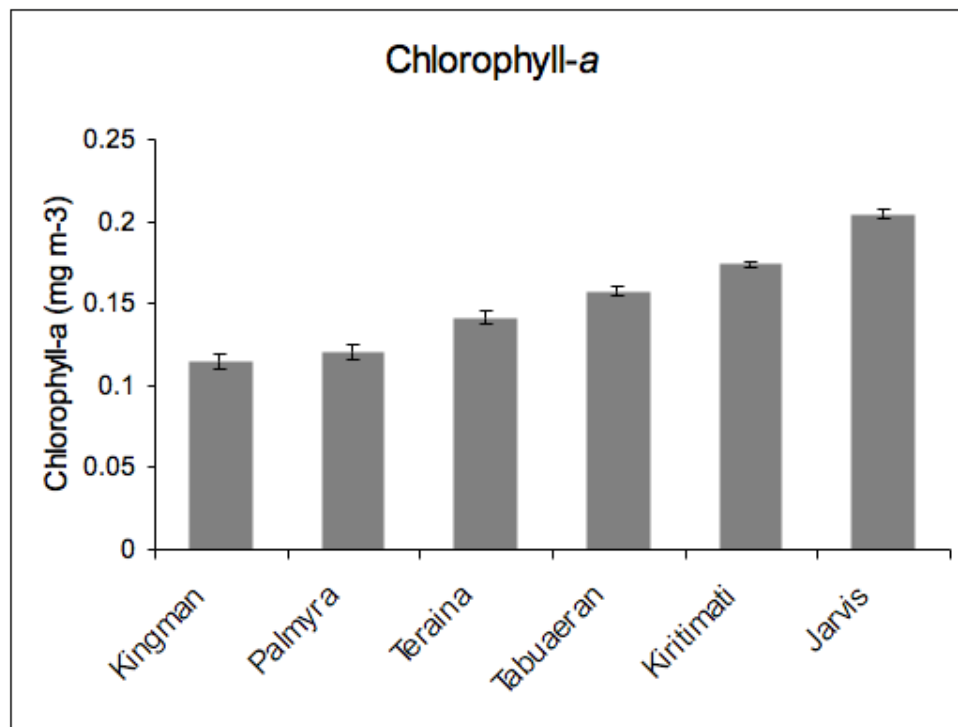
## Figures



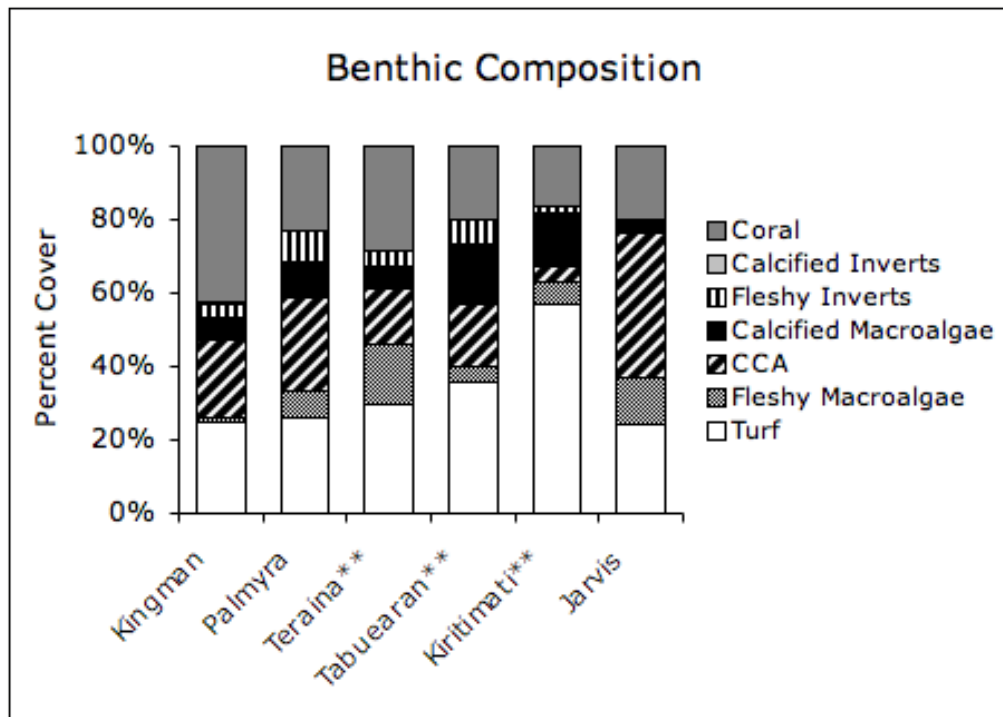
**Figure 1.** Location of the Northern Line Islands. Triangles indicate study areas. \*\* indicates an inhabited island.



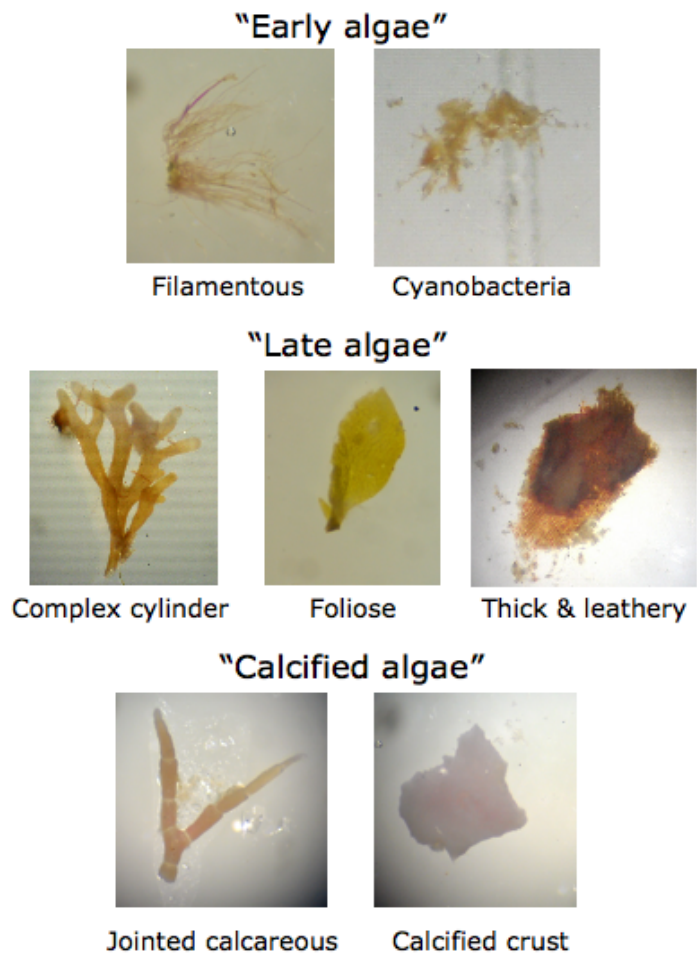
**Figure 2.** Fish biomass by trophic guild on the Northern Line Islands (B. Zgliczynski *unpub*). Islands listed from north to south; Teraina, Tabuaeran, and Kiritimati are inhabited.



**Figure 3.** Monthly island averages of chlorophyll-*a* ± SE (S.A. Sandin *unpub.*)

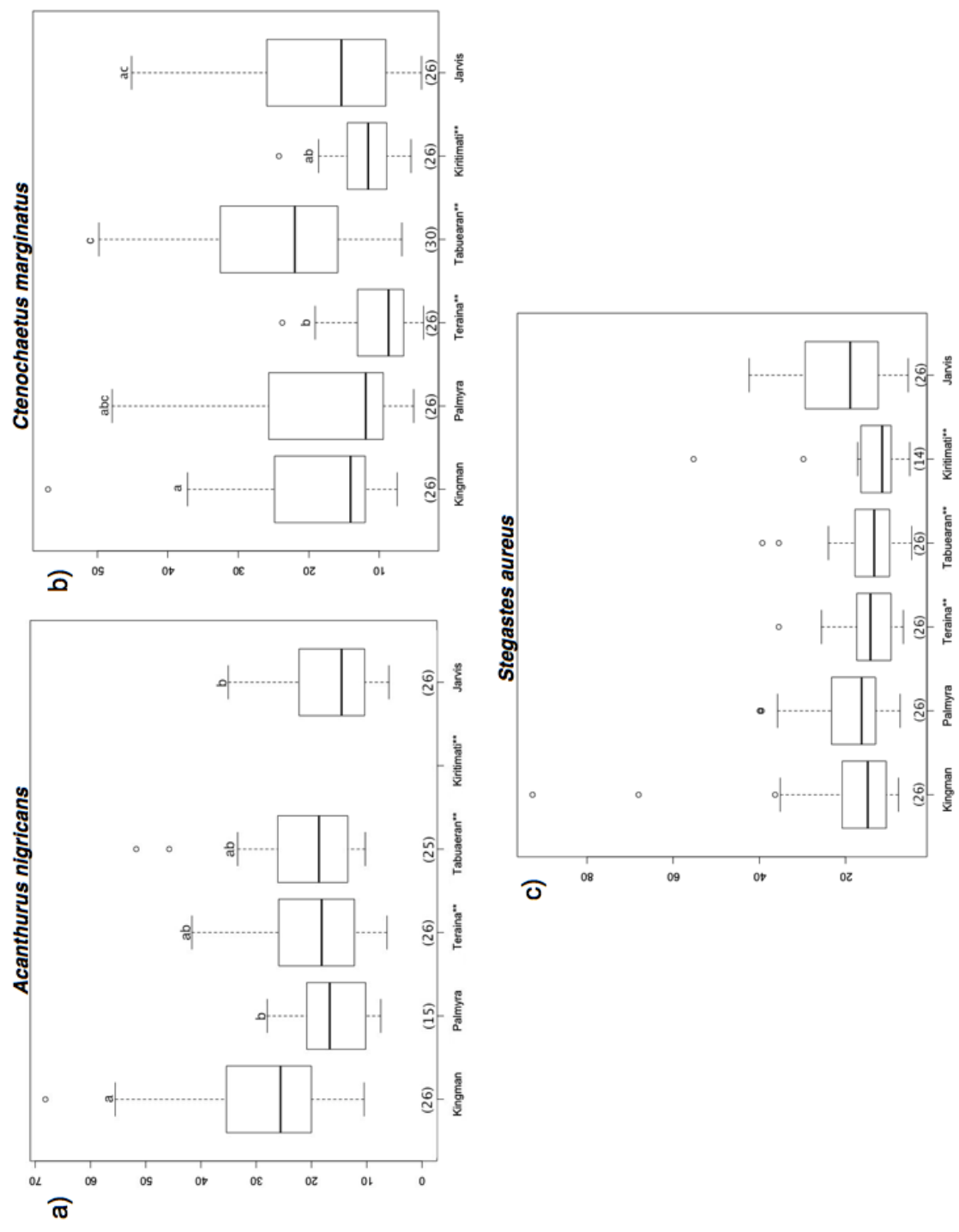


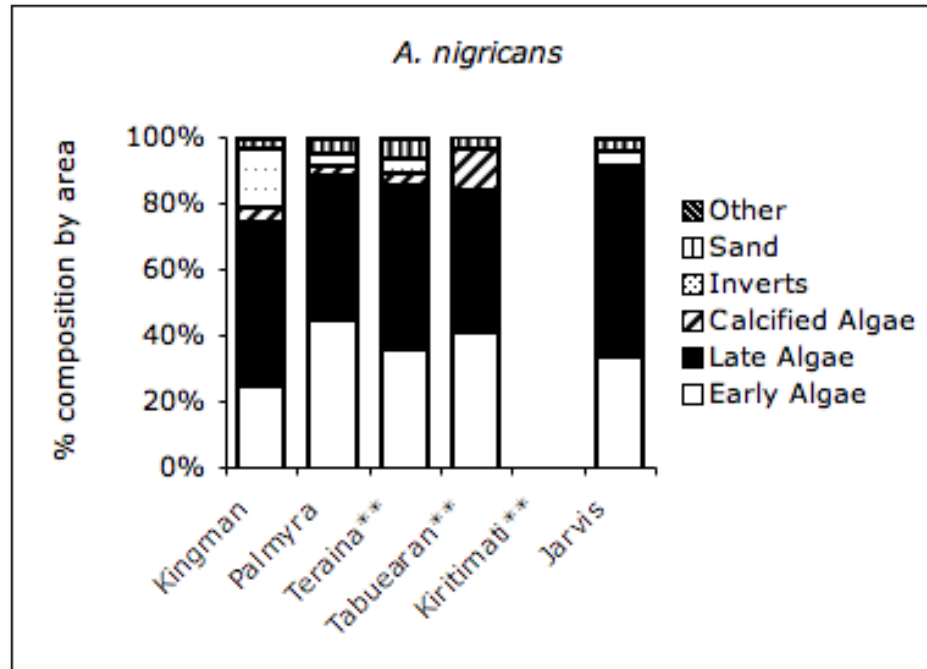
**Figure 4.** Benthic composition by percent cover of major functional groups of the Northern Line Islands, CCA = crustose coralline algae (J. E. Smith *unpub*). Islands listed from north to south, \*\* indicates an inhabited island.



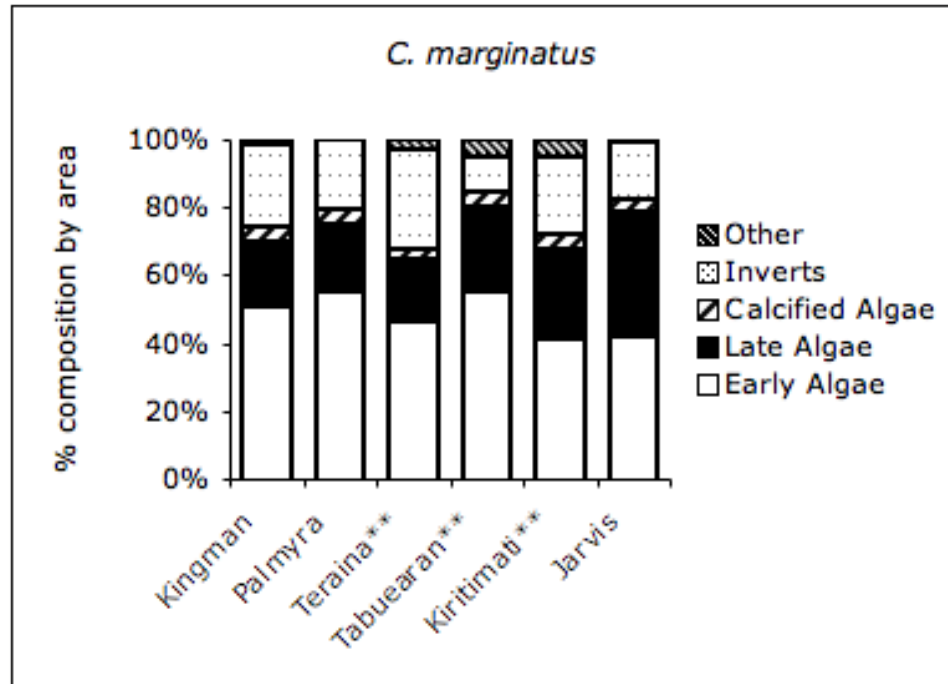
**Figure 5.** Major algal functional groups divided into successional categories.

**Figure 6.** Boxplot of Euclidean distances from individual data points (each data point represents an individual fish's diet) from the island cloud's centroid for a) *Acanthurus nigricans* b) *Ctenochaetus marginatus* and c) *Stegastes aureus*. Y axis is deviation from centroid, X axis is island listed from north to south, \*\* indicates an inhabited island. Numbers are sample sizes used.

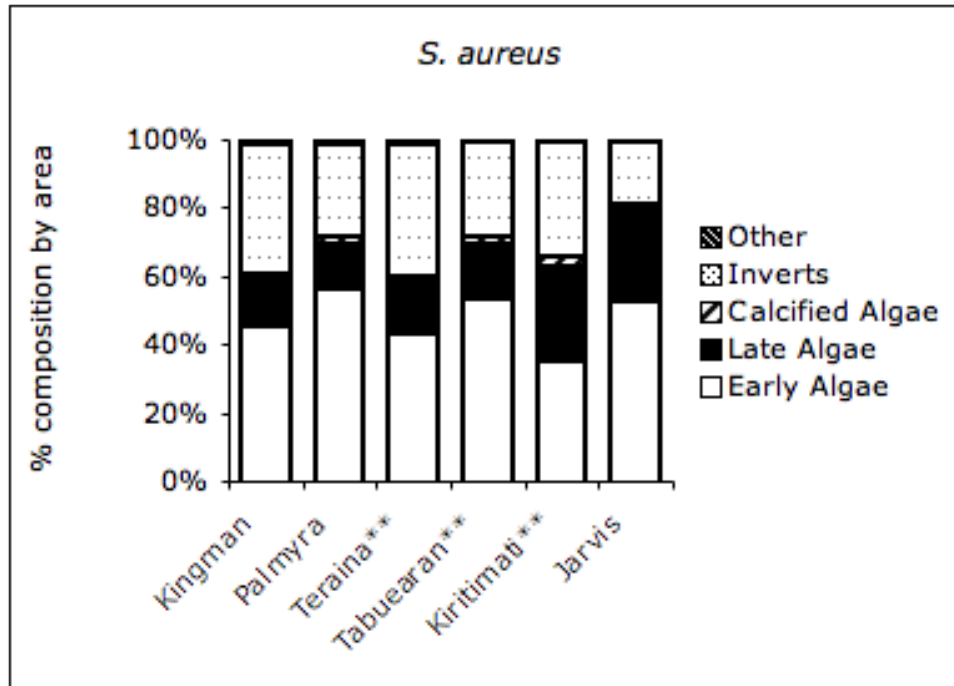




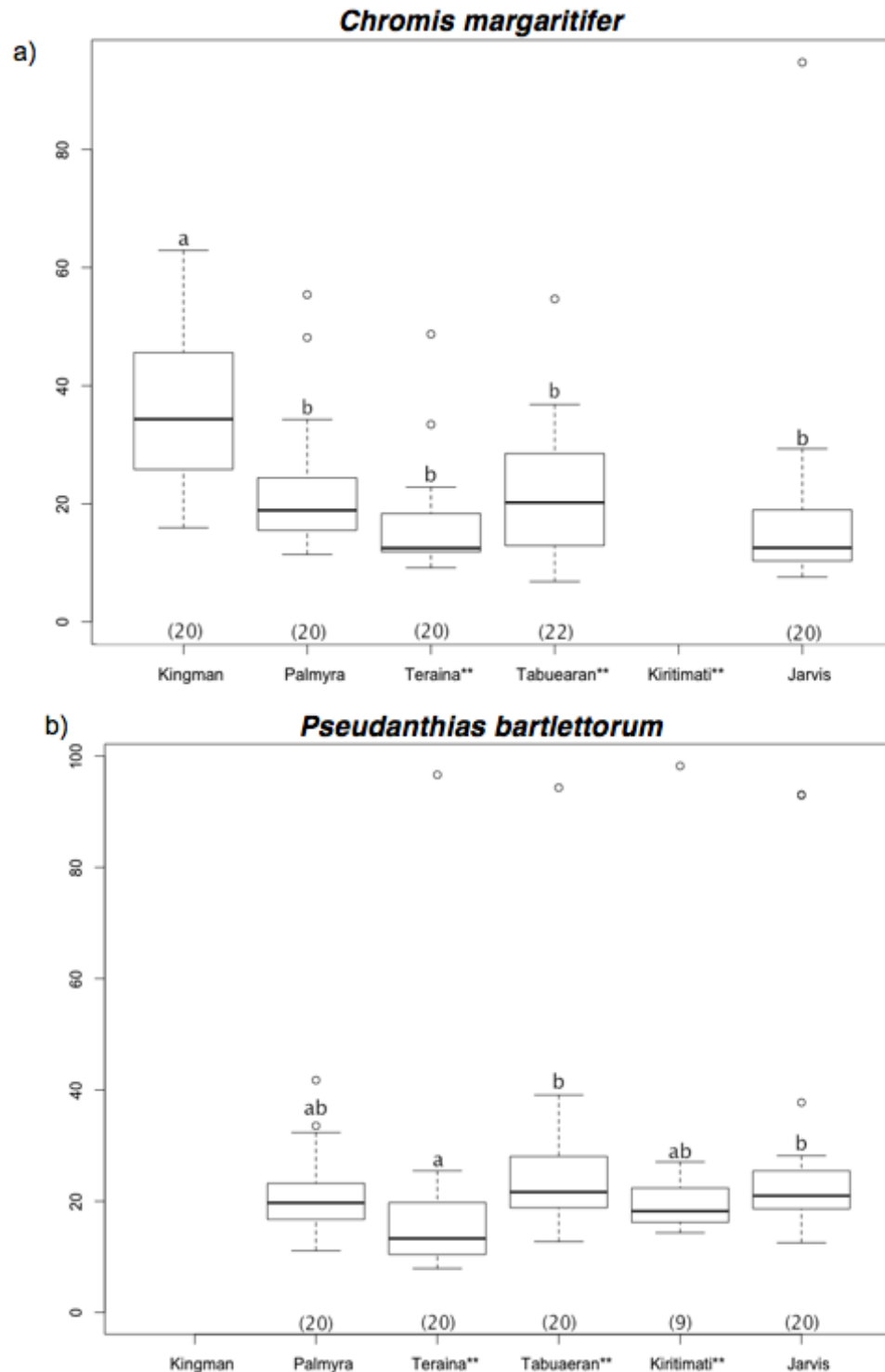
**Figure 7.** *Acanthurus nigricans*' diet composition across the Northern Line Islands. Prey groups lumped into Early Algae (Filamentous, Cyanobacteria, Net-like), Late Algae (Complex Cylinder, Foliose, Thick & Leathery), Calcified Algae (Jointed Calcareous, Calcified Crust), Invertebrates, Sand, and Other. Islands listed from north to south, \*\* indicates an inhabited island.



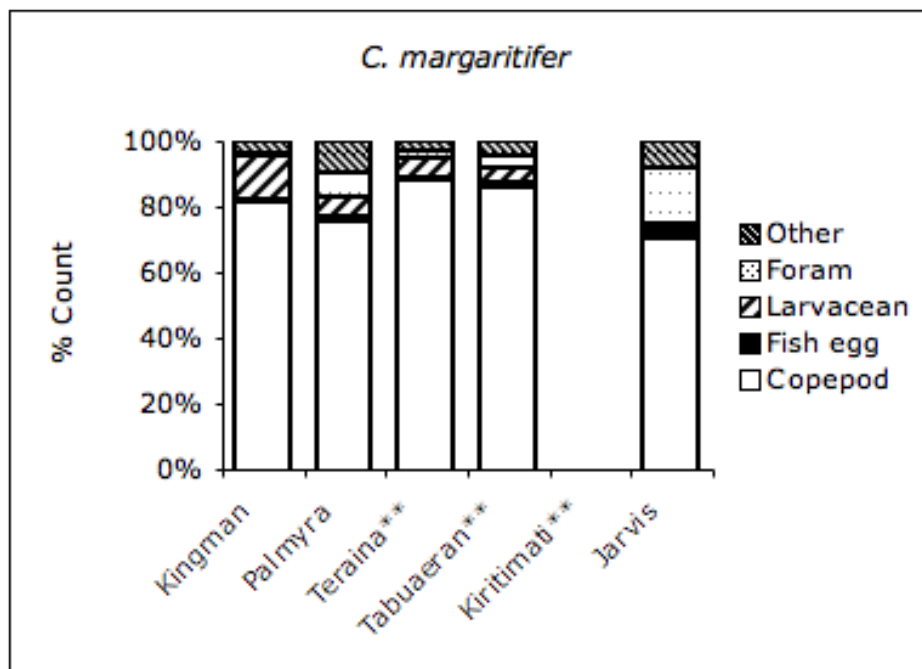
**Figure 8.** *Ctenochaetus marginatus* diet composition across the Northern Line Islands. Prey groups lumped into Early Algae (Filamentous, Cyanobacteria, Net-like), Late Algae (Complex Cylinder, Foliose, Thick & Leathery), Calcified Algae (Jointed Calcareous, Calcified Crust), Invertebrates, and Other. Sand was removed from the diet. Islands listed from north to south, \*\* indicates an inhabited island.



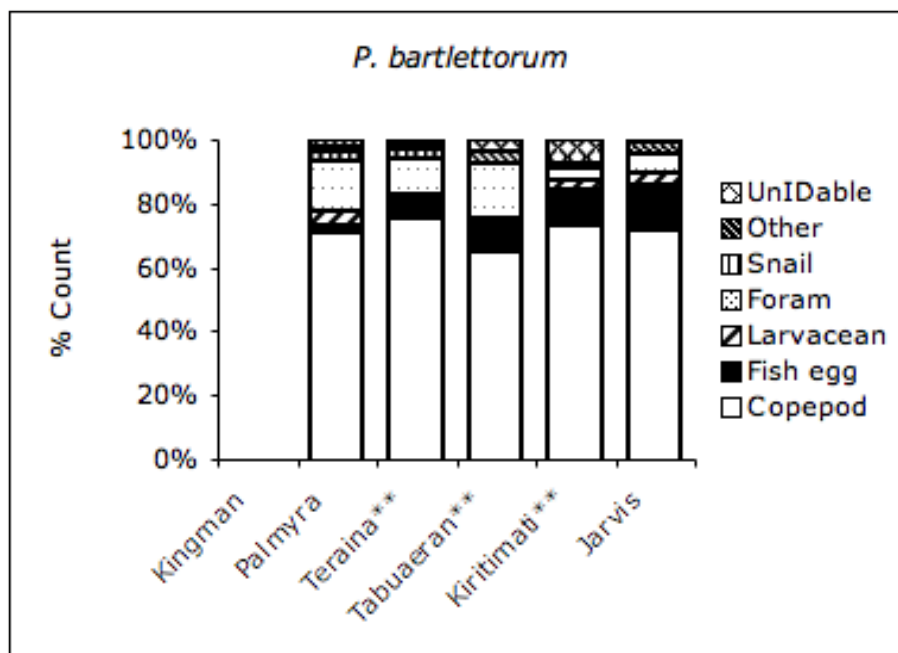
**Figure 9.** *Stegastes aureus* diet composition across the Northern Line Islands. Prey groups lumped into Early Algae (Filamentous, Cyanobacteria, Net-like), Late Algae (Complex Cylinder, Foliose, Thick & Leathery), Calcified Algae (Jointed Calcareous, Calcified Crust), Invertebrates, and Other. Sand was removed from the diet. Islands listed from north to south, \*\* indicates an inhabited island.



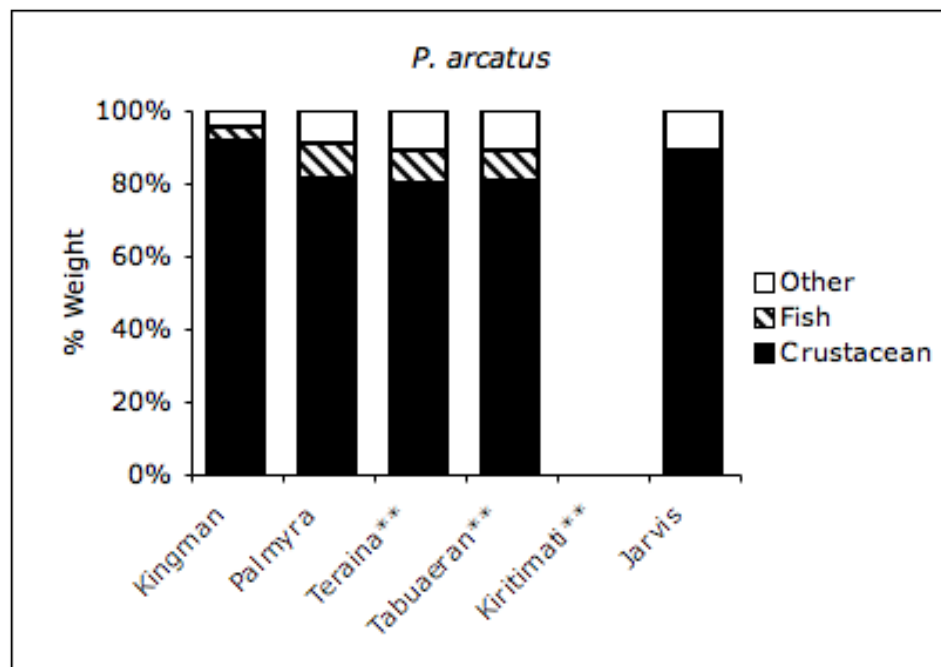
**Figure 10.** Boxplot of Euclidean distances of individual data points (each data point represents an individual fish's diet) from the island cloud's centroid in multivariate space for a) *Chromis margaritifer* and b) *Pseudanthias bartlettorum*. Y axis is deviation from centroid, X axis is island listed from north to south, \*\* indicates an inhabited island. Numbers are sample sizes used.



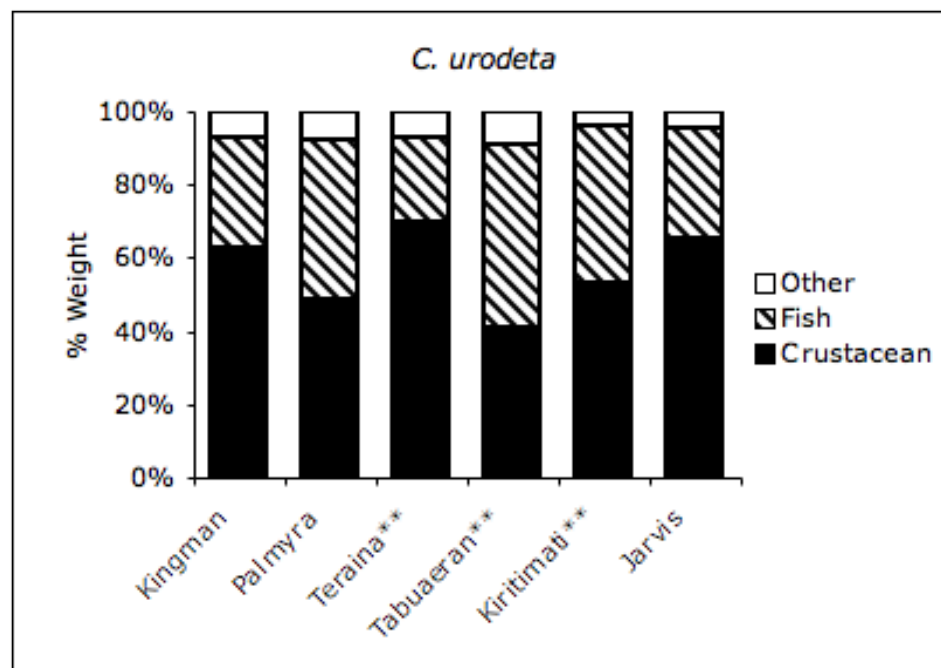
**Figure 11.** *Chromis margaritifer* diet composition by major prey group from the Northern Line Islands. Percentages are by count. Islands listed from north to south, \*\* indicates an inhabited island.



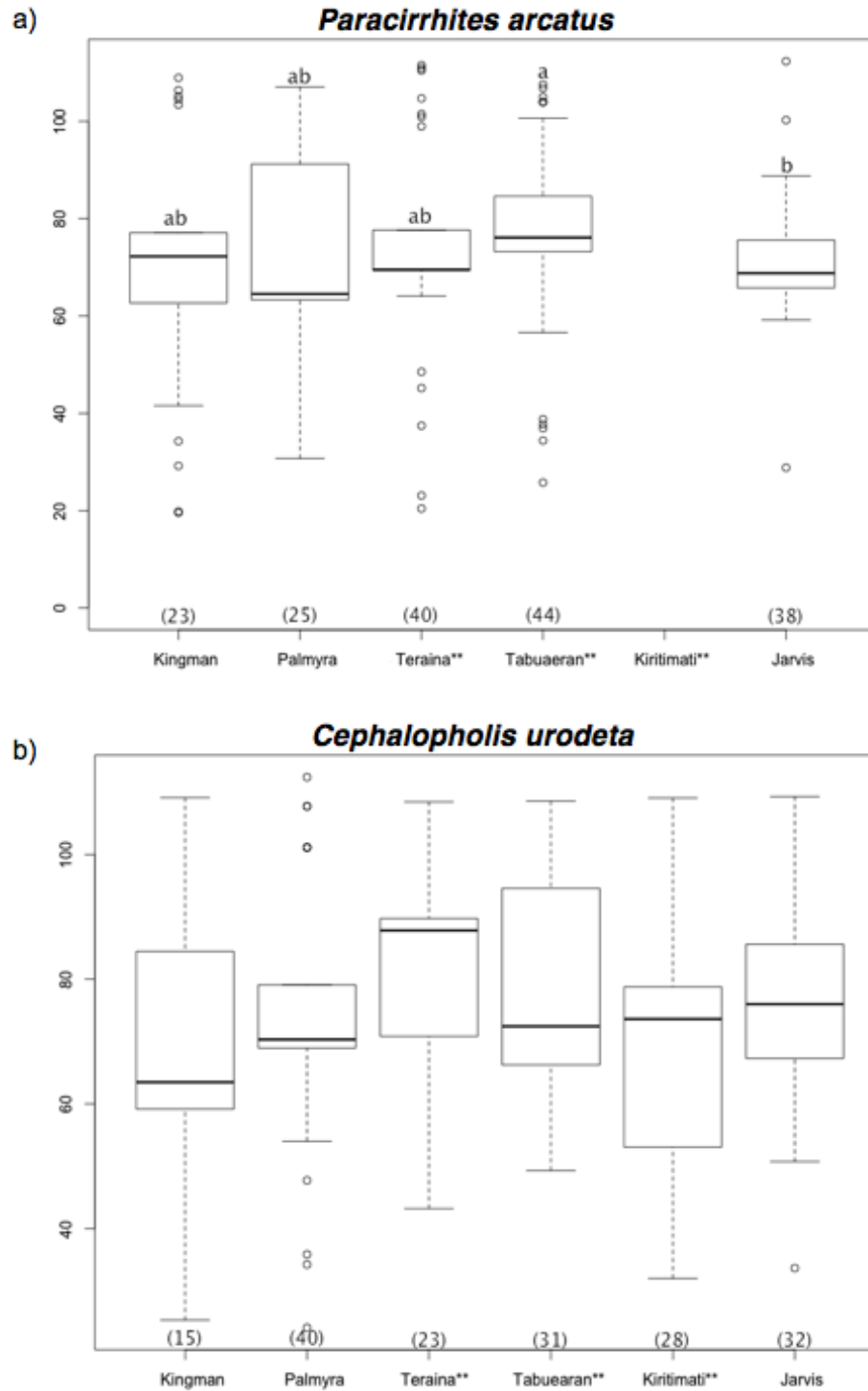
**Figure 12.** *Pseudanthias bartlettorum* diet composition by major prey group from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.



**Figure 13.** Percent composition of fish, crustaceans, and other by weight in the diets of *Paracirrhites arcatus* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.



**Figure 14.** Percent composition of fish, crustaceans, and other by weight in the diets of *Cephalopholis urodeta* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.



**Figure 15.** Boxplot of Euclidean distances of individual data points (each data point represents an individual fish's diet) from the island cloud's centroid in multivariate space for a) *Paracirrhites arcatus* and b) *Cephalopholis urodeta*. Y axis is deviation from centroid, X axis is island listed from north to south, \*\* indicates an inhabited island. Numbers are sample sizes used.

**Table 1.** Total number of stomachs analyzed from each species by island

Species	Kingman	Palmyra	Teraina	Tabuaeran	Kiritimati	Jarvis	Total
<i>Acanthurus nigricans</i>	26	15	26	25	0	26	118
<i>Ctenochaetus marginatus</i>	26	26	26	30	26	26	160
<i>Stegastes aureus</i>	26	26	26	26	14	26	144
<i>Chromis margaritifer</i>	20	20	20	22	0	20	102
<i>Pseudanthias bartlettorum</i>	0	20	20	20	9	20	89
<i>Parracirrhites arcatus</i>	26	29	47	49	0	48	199
<i>Cephalopholis urodeta</i>	15	62	46	55	37	54	269

**Table 2.** Mean percentages (1 SE) of prey groups by area in the diets of *Acanthurus nigricans* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Kiritmati**	Jarvis
Algae						
Early Algae						
Filamentous	19.69 (2.8)	35.57 (2.46)	27.82 (2.29)	32.9 (2.58)		25.18 (2.3)
Cyanobacteria	3.97 (0.73)	4.88 (0.35)	6.58 (0.71)	7.3 (0.76)		5.51 (0.41)
Net-like	0.93 (0.57)	4.33 (1.04)	0.94 (0.43)	0.48 (0.25)		2.35 (1.09)
Late Algae						
Complex cylinder	46 (3.46)	39.37 (3.23)	33.82 (2.69)	23.43 (3.09)		52.3 (2.09)
Foliose	3.76 (0.62)	1.37 (0.33)	11.77 (1.6)	18.44 (1.99)		2.11 (0.61)
Thick & leathery	0.09 (0.05)	2.77 (0.74)	4.25 (0.85)	0.93 (0.6)		2.01 (0.45)
Calcified Algae						
Jointed calcareous	0.23 (0.12)	0.07 (0.07)	1.13 (0.28)	0.98 (0.34)		0.44 (0.18)
Calcified crust	4.08 (0.8)	2.73 (0.64)	3.16 (0.46)	11.82 (1.55)		1.34 (0.33)
Invertebrate	17.14 (4.07)	3.43 (1.01)	4.32 (1.49)	0.33 (0.09)		4.43 (1.5)
Sand	2.86 (0.33)	4.15 (0.67)	5.97 (0.78)	3.01 (0.47)		3.71 (0.54)
Other	1.25 (0.27)	1.33 (0.27)	0.63 (0.21)	0.44 (0.15)		0.62 (0.2)

**Table 3.** Pairwise island comparisons for broad taxonomic categories for all species. \*\* indicates an inhabited island. Darkness reflects significance level: **p < 0.001**; **p < 0.01**; **p < 0.05**; **p > 0.05**.

Species	Island	Kingman	Palmyra	Teraina**	Tabuaeran**	Kiritimati**
<i>Acanthurus nigricans</i>	Kingman					
	Palmyra	<b>&lt;0.001</b>				
	Teraina**	0.0029	0.0936			
	Tabuaeran**	<b>&lt;0.001</b>	0.0127	<b>&lt;0.001</b>		
	Kiritimati**					
	Jarvis	0.005	0.015	0.074	<b>&lt; 0.001</b>	
<i>Ctenochaetus marginatus</i>	Kingman					
	Palmyra	0.9933				
	Teraina**	0.1947	0.1378			
	Tabuaeran**	0.0012	0.01	<b>&lt;0.001</b>		
	Kiritimati**	0.0034	0.0084	0.0299	<b>&lt;0.001</b>	
	Jarvis	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.0071
<i>Stegastes aureus</i>	Kingman					
	Palmyra	0.0809				
	Teraina**	0.1778	<b>&lt;0.001</b>			
	Tabuaeran**	0.9935	0.1138	0.0296		
	Kiritimati**	0.0081	<b>&lt;0.001</b>	0.0716	<b>&lt;0.001</b>	
	Jarvis	<b>&lt;0.001</b>	0.0038	<b>&lt;0.001</b>	0.0091	<b>&lt;0.001</b>
<i>Chromis margaritifer</i>	Kingman					
	Palmyra	0.0371				
	Teraina**	0.2581	<b>&lt;0.001</b>			
	Tabuaeran**	0.1951	0.0078	0.0659		
	Kiritimati**					
	Jarvis	<b>&lt;0.001</b>	0.1172	<b>&lt;0.001</b>	<b>&lt;0.001</b>	
<i>Pseudanthias bartlettorum</i>	Kingman					
	Palmyra					
	Teraina**		0.0362			
	Tabuaeran**		0.3	0.0081		
	Kiritimati**		0.0365	0.0081	0.0566	
	Jarvis		0.0524	0.0195	0.0657	0.2414
<i>Paracirrhites arcatus</i>	Kingman					
	Palmyra	0.0891				
	Teraina	<b>0.0041</b>	0.1649			
	Tabuaeran	0.0352	0.8979	.1698		
	Kiritimati					
	Jarvis	0.092	0.7379	<b>0.0441</b>	0.5397	
<i>Cephalopholis urodeta</i>	Kingman					
	Palmyra	0.3211				
	Teraina	0.5918	0.0681			
	Tabuaeran	0.1846	0.6403	<b>0.0329</b>		
	Kiritimati	0.3717	0.7485	0.0778	0.3912	
	Jarvis	0.9368	0.1616	0.5835	0.0755	0.2306

**Table 4.** Mean percentages (1 SE) of prey groups by area in the diets of *Ctenochaetus marginatus* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Kiritimati**	Jarvis
Algae						
Early Algae						
Filamentous	21.05 (1.63)	19.34 (2.39)	10.96 (0.59)	24.69 (2.15)	9.62 (1.44)	13.17 (0.99)
Cyanobacteria	8.61 (0.98)	7.12 (1.03)	7.51 (0.61)	11.70 (1.55)	6.99 (0.62)	7.75 (0.83)
Net-like	0.59 (0.2)	0.14 (0.07)	0.65 (0.2)	1.66 (0.53)	0.15 (0.07)	0.28 (0.09)
Late Algae						
Complex cylinder	9.49 (1.26)	6.43 (0.74)	6.02 (0.74)	12.45 (1.45)	9.78 (0.95)	15.91 (1.97)
Foliose	1.40 (0.55)	1.79 (0.49)	1.06 (0.2)	4.02 (0.85)	0.63 (0.17)	2.55 (0.36)
Thick & leathery	0.21 (0.1)	1.10 (0.35)	0.85 (0.19)	1.02 (0.34)	0.44 (0.18)	0.61 (0.21)
Calcified Algae						
Jointed calcareous	0.18 (0.11)	0.30 (0.1)	0.40 (0.11)	0.28 (0.15)	0.11 (0.04)	0.67 (0.14)
Calcified crust	2.50 (0.41)	1.87 (0.34)	0.85 (0.1)	2.86 (0.48)	1.88 (0.3)	0.94 (0.21)
Purple hard unknown	2.15 (0.53)	0.03 (0.02)	3.96 (0.38)	0.38 (0.35)	0.68 (0.14)	0.02 (0.01)
Invertebrate						
Fleshy	6.05 (2.24)	1.32 (0.26)	1.73 (0.38)	1.66 (0.35)	0.84 (0.12)	2.21 (0.34)
Foraminifera	2.88 (0.32)	5.34 (0.68)	3.01 (0.25)	2.41 (0.34)	4.45 (0.55)	2.51 (0.18)
Snail	0.50 (0.11)	0.65 (0.09)	0.96 (0.11)	0.50 (0.09)	0.62 (0.09)	0.67 (0.1)
Bivalve	0.28 (0.05)	0.12 (0.03)	0.10 (0.03)	0.18 (0.05)	0.26 (0.06)	0.30 (0.1)
Unknown calcified invert.	2.82 (0.36)	1.12 (0.16)	1.77 (0.16)	2.13 (0.57)	2.53 (0.25)	3.00 (0.42)
Sand	40.52 (2.65)	51.97 (2.88)	58.40 (1.69)	30.70 (3.47)	58.98 (1.55)	48.98 (3.57)
Other	0.78 (0.33)	0.41 (0.15)	5.23 (0.73)	3.73 (2.11)	2.85 (0.59)	0.48 (0.19)

**Table 5.** Mean percentages (1 SE) of prey groups by area in the diets of *Stegastes aureus* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Kiritimati**	Jarvis
Algae						
Early Algae						
Filamentous	18.04 (1.7)	23.21 (1.95)	18.55 (1.34)	29.94 (1.4)	5.46 (1.28)	26.38 (1.71)
Cyanobacteria	6.15 (0.58)	8.16 (0.68)	5.89 (0.42)	11.63 (0.9)	6.88 (0.45)	8 (0.41)
Net-like	0.63 (0.24)	1.38 (0.53)	0.72 (0.32)	1.90 (0.68)	0	1.26 (0.43)
Late Algae						
Complex cylinder	6.78 (1.27)	7.52 (1.32)	8.34 (1.53)	11.70 (1.53)	9.91 (2.16)	16.79 (2.5)
Foliose	0.98 (0.45)	0.4 (0.18)	0.64 (0.22)	1.5 (0.39)	0.04 (0.04)	1.30 (0.45)
Thick & leathery	0.02 (0.02)	0	0.04 (0.03)	0.13 (0.06)	0	0.02 (0.02)
Calcified Algae						
Jointed calcareous	0.05 (0.02)	0.23 (0.23)	0.45 (0.13)	0.38 (0.23)	0.5 (0.27)	0.28 (0.07)
Calcified crust	0.27 (0.13)	1.03 (0.29)	0.41 (0.16)	1.16 (0.26)	0.46 (0.25)	0.69 (0.21)
Purple hard unknown	3.34 (0.69)	0.62 (0.21)	3.29 (0.42)	0	0.45 (0.24)	0.03 (0.02)
Invertebrate						
Fleshy Invert	11.64 (4.02)	6.84 (1.74)	12.61 (1.65)	20.29 (1.83)	6.3 (1.91)	8.63 (1.18)
Foram	3.09 (0.47)	5.06 (0.69)	2.82 (0.26)	1.17 (0.18)	3.14 (0.28)	1.89 (0.19)
Snail	0.82 (0.2)	1.13 (0.18)	1.92 (0.21)	0.34 (0.07)	0.93 (0.19)	0.45 (0.09)
Bivalve	0.06 (0.02)	0.15 (0.05)	0.08 (0.04)	0.2 (0.06)	0.16 (0.08)	0.28 (0.08)
Unknown calcified invert	1.96 (0.47)	1.93 (0.36)	2.31 (0.59)	0.72 (0.18)	0.84 (0.3)	1.11 (0.27)
Sand	45.55 (3.23)	41.53 (2.98)	41.24 (1.63)	18.44 (1.57)	64.55 (4.48)	32.42 (3.24)
Other	0.63 (0.22)	0.80 (0.61)	0.71 (0.21)	0.49 (0.17)	0.38 (0.11)	0.47 (0.16)

**Table 6.** Mean percentages (1 SE) of prey groups by count in the diets of *Chromis margaritifer* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Jarvis
Copepods	75.67 (4.65)	71.25 (2.64)	81.46 (1.82)	76 (1.81)	50.83 (3.14)
Calanoida					
Candaciidae	0.58 (0.17)	0.2 (0.06)	0.06 (0.02)	0.2 (0.1)	0.04 (0.02)
Other	15.78 (4.53)	4.78 (1.19)	6.94 (1.51)	5.97 (1.37)	3.5 (0.57)
Poecilostomatoida					
Oncaeiidae	38.95 (4.95)	27.80 (2.09)	52.74 (2.55)	41.07 (2.79)	27.03 (1.69)
Corycaciidae	9.17 (1.53)	17.53 (2.12)	13.66 (1.95)	11.97 (1.89)	4.03 (0.57)
Cyclopoida					
Sapphirinidae	0.13 (0.07)	0.01 (0.01)	0.20 (0.05)	0.21 (0.13)	0.03 (0.02)
Oithonidae	0.30 (0.17)	0.61 (0.21)	0.26 (0.07)	0.46 (0.15)	1.91 (0.29)
Other	0	0.05 (0.04)	0	0	0
Harpacticoida					
Benthic	0.25 (0.17)	8.98 (3.52)	0.38 (0.22)	5.77 (2.55)	1.37 (0.54)
Pelagic	2.05 (0.66)	9.26 (1.47)	5.20 (1.4)	8 (1.51)	9.9 (1.62)
Long	0.11 (0.07)	0.04 (0.04)	0.02 (0.01)	0.29 (0.16)	0.83 (0.25)
Other	0.02 (0.02)	0.30 (0.18)	0.02 (0.02)	0.04 (0.04)	0.09 (0.07)
UnIDable	8.34 (2.12)	1.69 (0.53)	1.99 (0.98)	2.02 (0.52)	2.1 (0.72)
Egg sacs	6.35 (1.12)	5.83 (0.95)	7.46 (0.84)	11.62 (1.9)	25.97 (2.26)
Fish eggs	0.63 (0.48)	1.54 (0.58)	0.69 (0.19)	1.72 (0.57)	0.26 (0.08)
Round	0.61 (0.48)	1.23 (0.48)	0.68 (0.19)	1.53 (0.57)	0.26 (0.08)
Round fusiform	0.02 (0.02)	0.12 (0.11)	0.01 (0.01)	0.19 (0.16)	0
Pointed fusiform	0	0.19 (0.11)	0	0	0
Trichodesmium					
Puffs	0.01 (0.01)	0.11 (0.08)	0.08 (0.05)	0.2 (0.16)	0.05 (0.03)
Tufts	0	0.14 (0.08)	0.06 (0.05)	0.36 (0.24)	0.11 (0.05)
Cladocera					
Macrothricidae	0	0	0	0.36 (0.21)	0.33 (0.21)
Larvaceans	13.41 (4.31)	5.47 (1.19)	5.77 (1.05)	4.20 (0.91)	3.14 (0.54)
Appendicularia	11.04 (3.76)	3.19 (0.8)	5.32 (1.11)	3.59 (0.82)	2.93 (0.48)
Tunicates	2.37 (1.68)	1.35 (0.6)	0.07 (0.03)	0.04 (0.04)	0
Other	0	0.98 (0.23)	0.38 (0.11)	0.7 (0.24)	0.21 (0.1)
Ostracoda	0	0.85 (0.36)	0.02 (0.02)	0.31 (0.22)	0.07 (0.05)
Foraminifera	0.36 (0.19)	6.61 (1.86)	1.88 (0.69)	3.78 (0.85)	13.96 (4.74)
Clear case	0	0.99 (0.28)	0	0.14 (0.08)	0.36 (0.18)
Snail	0	0.55 (0.35)	0	0	0
Textured ball	0	3.62 (1.05)	0	0.46 (0.46)	0
Other	0.76 (0.23)	0.45 (0.16)	1.65 (0.64)	0.31 (0.13)	3.86 (0.61)
UnIDable	2.81 (1.66)	2.52 (0.59)	0.94 (0.55)	0.42 (0.19)	1.05 (0.33)

**Table 7.** Pairwise comparisons for the proportions of copepod groups in *C. margaritifer* diets. Listed numbers are p-values; bold numbers indicate a significant difference ( $p \leq 0.01$ ). Islands listed from north to south, \*\* indicates an inhabited island.

	Kingman	Palmyra	Teraina**	Tabuaeran**
Kingman				
Palmyra	<b>&lt;0.001</b>			
Teraina**	<b>0.002</b>	<b>&lt;0.001</b>		
Tabuaeran**	0.0288	<b>&lt;0.001</b>	0.0195	
Jarvis	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.0076</b>

**Table 8.** Mean percentages (1 SE) of prey groups by count in the diets of *Psuedanthias bartlettorum* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Palmyra	Teraina**	Tabuaeran**	Kiritimati**	Jarvis
Copepods	66.63 (2.02)	70.41 (3.86)	60.16 (4.27)	67.42 (8.56)	53.18 (4.23)
Calanoida					
Candacia	0.13 (0.06)	0.12 (0.05)	0.30 (0.14)	0.11 (0.05)	0.31 (0.1)
Other	6.02 (1.46)	5.80 (0.93)	8.42 (1.75)	4.26 (1.02)	13.47 (2.02)
Poecilostomatoida					
Oncaeidae	27.07 (1.61)	29.93 (2.38)	22.77 (1.97)	37.07 (5.31)	17.86 (2.1)
Corycaeidae	22.04 (3.2)	20.77 (1.9)	4.48 (0.85)	1.82 (0.62)	5.34 (0.64)
Cyclopoida					
Sapphirinid	0.07 (0.03)	0.26 (0.09)	0.05 (0.03)	0	0.3 (0.09)
Oithona	1.79 (0.61)	1.17 (0.39)	1.83 (0.4)	1.92 (0.75)	7.12 (1.28)
Other	0.04 (0.04)	0	0	0	0
Harpacticoida					
Benthic	0.11 (0.07)	0.5 (0.12)	1.06 (0.32)	2.3 (0.64)	0.18 (0.12)
Pelagic	8.01 (1.78)	9.86 (1.33)	16.41 (2.67)	17.48 (4.16)	4.9 (1.54)
Long	0	0.02 (0.02)	0	0	2.57 (0.8)
Other	0	0.04 (0.04)	0	0	0
UnIDable	1.34 (0.28)	1.94 (0.5)	4.84 (0.9)	2.47 (0.38)	1.13 (0.47)
Egg Sacs	5.99 (0.78)	6.36 (0.54)	5.07 (0.8)	6.66 (1.13)	22.52 (2.49)
Fish Egg	1.59 (1.05)	5.57 (4.63)	9.83 (5.17)	11.53 (11.06)	13.33 (6.78)
Round	1.51 (1.03)	5.57 (4.63)	9.83 (5.17)	11.53 (11.06)	13.32 (6.78)
Round fusiform	0.02 (0.02)	0	0	0	0.01 (0.01)
Pointed fusiform	0.06 (0.03)	0	0	0	0
Trichodesmium					
Puffs	0.04 (0.03)	0	0	0	0
Tufts	0.04 (0.04)	0	0	0.14 (0.06)	0
Ostracoda	0.76 (0.3)	0.15 (0.07)	1.15 (0.47)	0.18 (0.1)	0.26 (0.14)
Cladocera					
Macrothricidae	0	0.2 (0.1)	0.71 (0.23)	0	0.46 (0.3)
Other	0	0.11 (0.05)	0.26 (0.13)	0	0.13 (0.08)
Larvaceans	4.45 (0.83)	1.29 (0.29)	0.83 (0.23)	2.35 (0.65)	2.42 (0.43)
Appendicularia	3.93 (0.81)	1.24 (0.27)	0.67 (0.2)	1.81 (0.62)	2.34 (0.39)
Tunicates	0.02 (0.02)	0	0	0.07 (0.05)	0.07 (0.06)
Other	0.49 (0.26)	0.05 (0.04)	0.16 (0.08)	0.47 (0.18)	0.01 (0.01)
Foraminifera	15.09 (2.26)	10.79 (1.37)	16.02 (2.6)	3.53 (0.68)	5.08 (1.4)
Clear case	0.07 (0.04)	0.21 (0.08)	0.42 (0.14)	0	0.67 (0.25)
Snail	2.2 (0.74)	3.08 (0.76)	0.49 (0.21)	0.03 (0.03)	0.07 (0.05)
Textured_ball	0.45 (0.2)	0	0	0.33 (0.16)	0
Other	0.27 (0.13)	0.69 (0.31)	1.66 (1.11)	1.14 (0.51)	1 (0.25)
UnIDable	2.43 (0.71)	1.14 (0.33)	3.40 (0.89)	6.69 (1.4)	0.85 (0.28)

**Table 9.** Mean percentages (1 SE) of prey groups by weight in the diets of *Paracirrhites arcatus* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Jarvis
Crustaceans	91.44 (5.9)	81.34 (6.37)	80.15 (5.72)	80.34 (5.68)	88.7 (4.17)
Decapoda	37.59 (9.15)	42.56 (9.39)	34.91 (7)	28.12 (6.15)	43.82 (7.8)
Amphipoda	0	0.24 (0.24)	0.03 (0.02)	3 (2.32)	1.47 (0.96)
Copepoda	7.1 (4.39)	0.01 (0.01)	0.37 (0.32)	0.45 (0.45)	0.1 (0.1)
Stomatopoda	6.97 (4.95)	5.33 (4.16)	2.47 (2.47)	4.53 (2.58)	4.4 (3.13)
Megalopes	5.82 (4.29)	12.21 (5.97)	1.48 (1.48)	10.2 (4.03)	0
Unidentifiable	33.97 (8.23)	21 (7.18)	40.89 (7.25)	34.03 (6.53)	38.91 (7.27)
Fish	4.35 (4.35)	9.4 (5.48)	8.7 (4.09)	8.64 (4.19)	0.62 (0.62)
Gobiidae	0	1.75 (1.75)	0	1.83 (1.83)	0
<i>Pseudanthias</i> spp.	0	0	2.47 (2.47)	0	0
Unidentifiable	4.35 (4.35)	7.65 (5.3)	6.23 (3.38)	6.82 (3.84)	0.62 (0.62)
Other	4.21 (4.19)	9.25 (3.67)	11.15 (4.57)	11.01 (4.37)	10.68 (4.16)
Ophiuroidea	0	1.24 (1.23)	2.49 (2.49)	0	2.52 (1.88)
Gastropod	0	0	0.56 (0.56)	0.07 (0.07)	0.17 (0.15)
Halimeda	0	1.27 (0.97)	0.07 (0.06)	0.13 (0.13)	0.19 (0.19)
Algae	0.02 (0.02)	4.42 (3.13)	0.28 (0.2)	3.8 (2.45)	2.92 (1.57)
Sand	0	0	7.68 (3.69)	3.75 (2.62)	4.81 (2.91)
Worm	0.07 (0.07)	0	0	1.79 (1.71)	0
Unknown	4.12 (4.12)	2.33 (1.92)	0.08 (0.08)	1.11 (1.11)	0.07 (0.07)

**Table 10.** Mean percentages (1 SE) of prey groups by weight in the diets of *Cephalopholis urodeta* from the Northern Line Islands. Islands listed from north to south, \*\* indicates an inhabited island.

Prey Group	Kingman	Palmyra	Teraina**	Tabuaeran**	Kiritimati**	Jarvis
Crustacean	62.69 (12.22)	48.92 (7.49)	69.61 (9.8)	38.51 (8.71)	49.6 (8.57)	63.2 (8.01)
Decapod	46.07 (12.09)	34.39 (7.04)	38.06 (10.13)	16.28 (6.67)	0.06 (0.06)	33.99 (8.18)
Stomatopod	6.67 (6.67)	0	8.65 (5.98)	0.23 (0.23)	16.28 (5.97)	0
Megalope	0	0	0	0	1.26 (0.71)	0
Unidentifiable	9.96 (6.93)	14.52 (5.31)	22.89 (8.7)	22 (7.43)	32 (8.5)	29.21 (7.23)
Fish	30.55 (11.6)	43.44 (7.44)	23.66 (8.78)	46.38 (8.8)	39.46 (8.37)	29.38 (7.62)
<i>Paracirrhites</i> spp.	0	0	0	0	0	3.13 (3.13)
<i>Pseudocheilinus</i> spp.	0	0	0	3.23 (3.23)	0	0
<i>Pseudanthias</i> spp.	0	2.5 (2.5)	0	0	3.51 (3.51)	0
<i>Chromis</i> spp.	0	0	0	2.94 (2.94)	0	3.13 (3.13)
Unidentifiable	30.55 (11.6)	40.94 (7.37)	23.66 (8.78)	40.22 (8.67)	35.94 (8.19)	23.13 (6.96)
Other	6.76 (6.66)	7.65 (4.21)	6.74 (4.86)	8.65 (4.9)	3.8 (3.8)	4.29 (3.24)
Cephalopod	6.67 (6.67)	0	0	0	0	0
Halimeda	0.1 (0.1)	0.01 (0.01)	0	2.2 (2.2)	0	0
Sand	0	0	4.35 (4.35)	0	3.57 (3.57)	3.13 (3.13)
Snail	0	0	0	0	0.18 (0.18)	0.02 (0.02)
Unknown	0	7.64 (4.21)	2.39 (2.39)	6.45 (4.49)	0.05 (0.05)	1.14 (0.98)

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