Stable Isotopes Reveal Trophic Relationships and Diet of Consumers in Temperate Kelp Forest and Coral Reef Ecosystems

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ABSTRACT. We explored the use of stable nitrogen (N) isotope analysis to assess trophic position of consumers in two marine ecosystems: the kelp forests of southern California and a coral atoll in the tropical Pacific. The $\delta^{15}N$ values of consumers in both ecosystems increased from known herbivores (invertebrates and fish) to higher-level consumers (predatory invertebrates and fish). In the absence of data on trophic enrichment in ^{15}N for our study species, we used the oft-cited value of +3.4‰ increase in $\delta^{15}N$ value per trophic level and estimates of the $\delta^{15}N$ producer baseline value to estimate trophic position. The trophic position of consumers computed using N isotopes compared favorably to published observations of diet. Nitrogen isotope analysis revealed that some of our higher-level fish consumers from rocky reefs (i.e., some rockfish) were feeding largely on invertebrates rather than on fish, as is often assumed. Our analysis also suggests that higher-level consumers on coral reefs may consume more herbivorous prey (i.e., both fishes and invertebrates) than previously reported. Our data support the use of nitrogen isotope values to assess trophic position and, thus, their utility as one metric with which to explore the effects of short- and longer-term natural and human-induced changes on kelp forest and coral reef food webs.

INTRODUCTION

Food webs and the factors controlling their structures are among the more intensively studied areas in the field of ecology (e.g., Post, 2002; Byrnes et al., 2011; Moore and de Ruiter, 2012). This interest is stimulated by the need to test theory pertaining to processes that structure ecological communities and food webs (Moore and De Ruiter, 2012) and to better understand and manage the impacts of anthropogenic and natural changes to the world's ecosystems (Naiman et al., 2012). In marine ecosystems, research is underway to assess the potential ramifications of disturbance-induced short- and long-term changes in habitat structure on food web complexity (Adam et al., 2011; Byrnes et al., 2011), to evaluate how the removal of top-level predators through fishing influences ecosystem function (Steneck et al., 2004; McCauley et al., 2010; Rosenblatt et al., 2013, in this issue), and, conversely, to explore how shifts in trophic position associated with changes in the availability of prey resulting from climatic change or other factors influence the performance of individuals and populations of higher-level consumers (e.g., Lindegren et al., 2010).

Kelp forests and coral reefs are among the most productive ecosystems in the ocean (Hatcher, 1988; Mann, 2000). They support a high diversity of species and complex food webs, and both are subject to changes induced by natural and anthropogenic drivers. Kelp forests are highly dynamic ecosystems, with seasonal and interannual variability in their abundance driven by physical disturbance, grazing, and longer-term nutrient regimes such as those caused by El Niño-Southern Oscillation (ENSO) events (Dayton et al., 1999; Reed et al., 2011). Similarly, in coral reef ecosystems, the cover of live coral can change rapidly in response to disturbances such as coral bleaching events, large waves associated with cyclones, or outbreaks of natural enemies such as the crown-of-thorns sea star, and these effects can be long lasting (Adjeroud et al., 2009; Adam et al., 2011; Kayal et al., 2012).

One metric that can be used to assess the effects of natural and anthropogenic drivers on the structure of kelp forest and coral reef food webs is the trophic positions of the constituent consumers (Fredriksen, 2003; Jack and Wing, 2011). Trophic position can be defined as the location of an organism within a food web, which can be used to characterize variation in the diet of component species in time and space and in food chain length (Post et al., 2000; Post, 2002). In order to assign trophic position, it is necessary to acquire information on consumer diet. Assessment of diet items can be inferred from a snapshot analysis of stomach or gut contents and/or from observations of feeding in the field or in the laboratory. These assessments are invaluable in describing specific items ingested, but their identification can be challenging due to maceration and digestion (Carassou et al., 2008; Wyatt, 2012), and assimilation of different foods may vary (Olive et al., 2003; Wyatt, 2010). Laboratory studies of feeding or food preference (e.g., Sweeting et al., 2007) may not translate to the field where consumers have a broader choice of prey. Finally, because diet can vary in time and space, or during ontogeny, one-time observations of stomach contents may not accurately describe the diet integrated over time (de la Morinière et al., 2003).

STABLE ISOTOPES OF N AND THE INFERENCE OF TROPHIC POSITION

An additional approach, which has received considerable attention in recent years, involves using variation in the stable isotopes of nitrogen (N) to assess trophic position (Fry, 1988; Cabana and Rasmussen, 1996; Post et al., 2000; Vander Zanden and Rasmussen, 2001; Post, 2002). This approach is based on the presence of two naturally occurring stable N isotopes in nature, the more abundant "lighter" ^{14}N (99.632% of atmospheric N) and the "heavier" ^{15}N. A faster loss of ^{14}N than ^{15}N through metabolic activity and excretion generally leaves consumers with a ratio of ^{15}N to ^{14}N that is higher than that of their diet, a process known as trophic "fractionation" or "enrichment." By convention, isotopic ratios are expressed per mil (‰) and represent the relative abundance of the two stable N isotopes to one another in a particular sample compared with the same ratio in atmospheric N. Higher $\delta^{15}N$ values indicate enrichment of the sample in the rare isotope ^{15}N relative to the standard and forms the basis for the use of stable isotopes in food web ecology (Peterson and Fry, 1987; Fry, 2006).

A meta-analysis of trophic enrichment factors (n = 56 examples) found an overall increase in the mean $\delta^{15}N$ value of consumers relative to their diet of +3.4 ± 1.0‰ (± 1 SD), with no significant difference in this value between herbivores and carnivores (Post, 2002). This mean trophic enrichment value was identical to that (+3.4 ± 1.1‰) previously reported by Minagawa and Wada (1984). Because of the stepwise increase in the $\delta^{15}N$ value of a consumer relative to its diet, the possibility exists for estimating relative trophic position using the $\delta^{15}N$ value of the consumer. In order to make an assessment of trophic position, it is necessary to estimate the baseline $\delta^{15}N$ of the producer(s) (trophic level 1) or a producer proxy (trophic level 2) to which the $\delta^{15}N$ values of the higher-level consumers can be compared (Hobson and Welch, 1992; Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 2001; Post, 2002).

CONSIDERATIONS IN THE USE OF N ISOTOPES TO INFER TROPHIC POSITION

Stable N isotope values reflect consumer diet integrated over time and thus may reveal trophic relationships not evident from the inspection of gut contents. Nitrogen isotope analysis may be particularly informative in evaluating the trophic position of omnivorous species that feed across trophic levels and whose diet may reflect spatial and temporal variability in community structure and thus the types of food available (Jack and Wing, 2011). Nitrogen isotope analysis also may provide insight into the timing or stage of development of ontogenetic-related shifts in diet and how these vary in time and space (Hentschel, 1998; de la Morinière et al., 2003).

However, conclusions derived from the use of N isotopes to assign trophic position can be influenced by the selected baseline $\delta^{15}N$ values, against which the value of higher-level consumers are compared, and the trophic enrichment factor. Post (2002) and others (e.g., Cabana and Rasmussen, 1996) discuss approaches for obtaining $\delta^{15}N$ baseline values to use in the assessment of trophic position. The accuracy of the baseline $\delta^{15}N$ values of the producers can be influenced by spatial and temporal variability in producer $\delta^{15}N$ values and by the presence of two or more sources of production that have differing $\delta^{15}N$ values. A trophic enrichment factor of 3.4‰ is widely accepted and often used in isotope mixing models, but this factor is known to vary (McCutchan et al., 2003; Caut et al., 2009; Layman et al., 2012). Its applicability, and the use of nitrogen isotopes in general to assess trophic position, need to be evaluated in marine systems (Wyatt et al., 2010).

Here, we illustrate that stable N isotope analysis is a promising tool for assessing trophic positions of consumers in marine ecosystems by using two case studies: the kelp forests of southern

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California and a coral atoll in the tropical Pacific. For both the kelp forest and coral reef ecosystems, we show that the trophic position of consumers computed from N isotope values compares favorably to published observations of diet. Further, using estimates of trophic position based on δ^{15}N values, we explore whether selected kelp forest suspension feeders consume appreciable quantities of zooplankton and the extent to which the diet of species commonly considered omnivorous might vary across kelp forests and coral reefs. Finally, we identify the degree of spatial variability and ontogenetic shifts in trophic position and diet for selected reef fish in a Pacific coral reef ecosystem.

N ISOTOPES AND THE TROPHIC POSITION OF KELP FOREST CONSUMERS

During a four-year study, we measured the stable N isotope values (and C, not discussed here) of a range of invertebrate consumers known to include herbivores, omnivores, and predators from four subtidal rocky reefs in the Santa Barbara Channel (Page et al., 2008). These reefs are study sites of the Santa Barbara Coastal Long Term Ecological Research (SBC LTER) project. We supplement these data with the N isotope values of common kelp forest fishes sampled more recently (2011) from one of these reefs (Mohawk Reef; recent work of author Koenigs and colleagues). The information on diet that we used to compare with our estimates of trophic position was obtained from Morris et al. (1980), a review of the diet of kelp forest consumers provided as supplemental material (Table S1) in Byrnes et al. (2011), and recent work of author Koenigs and colleagues. To set the average producer baseline N isotope values for comparison with higher-level consumer values, we used the average of the N isotope values of the main sources of primary production supporting the kelp forest food web obtained by Page et al. (2008): the giant kelp *Macrocystis pyrifera*, four species of other benthic macroalgae, and suspended particulate organic matter (POM). Trophic position was calculated as $T = (\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta N$, where ΔN is the enrichment in δ^{15}N per trophic level. Averaged POM and macroalgal values used as the producer baseline ranged from 7.9–8.7‰ across our study reefs.

The N isotope values of kelp forest invertebrates and fishes, shown for Mohawk Reef (the only reef for which fish data are available), ranged from lows for the gastropod *Lithopoma undosa* and the purple urchin *Strongylocentrotus purpuratus* to highs for the strawberry anemone *Corynactis californica* and two species of sea stars, *Pisaster giganteus* and *Asterina miniata*. N isotope values for the sampled fish were similar to or greater than the values of the strawberry anemone (Figure 1).

The computed trophic position values of kelp forest consumers reflect the integrated energy transfers from food to consumer and thus are continuous, rather than the discrete integer values

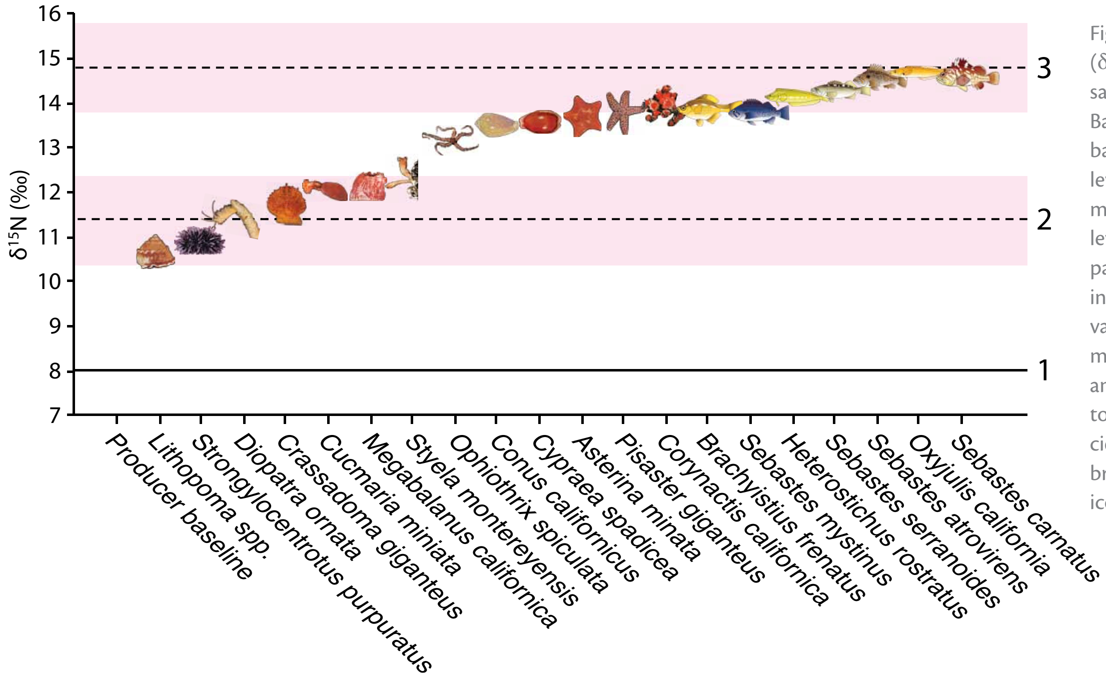


Figure 1. Nitrogen isotope values (δ^{15}N) of invertebrates and fishes sampled from Mohawk Reef, Santa Barbara Channel. The producer baseline and position of trophic levels 2 and 3, assuming an enrichment factor of +3.4‰ per trophic level, are also shown for comparison with the δ^{15}N values of the invertebrates and fishes. Mean δ^{15}N values computed from approximately 20 specimens of each alga and invertebrate species and three to 10 specimens of each fish species. Standard errors for invertebrates and fish are covered by the icons. Shaded area indicates ±1‰ standard deviation values from Minagawa and Wada (1984) and Post (2002).

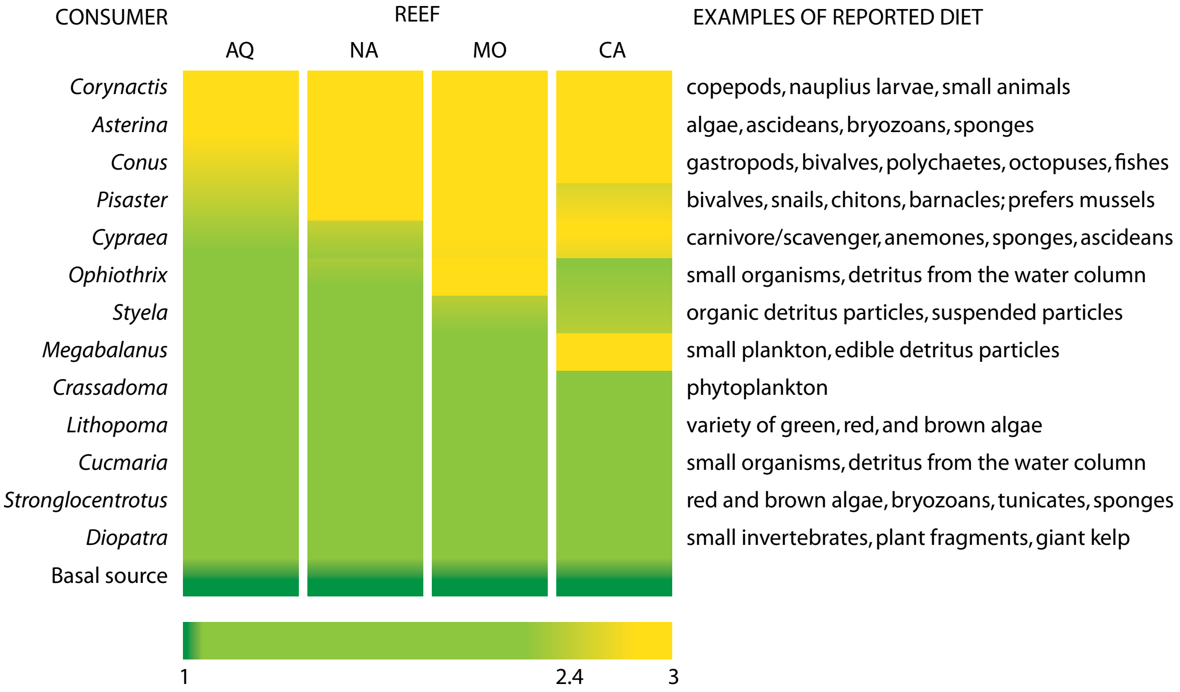
that are often assigned based on gut content studies or feeding observations (Vander Zanden and Rasmussen, 2001). Our trophic position estimates agree with reported dietary information and provide insight on the diet of consumers for which less information is available. Most of the suspension feeders fall within the standard deviation of the mean for level 2, indicating that these species are feeding on suspended POM without significant use of zooplankton as food. The strawberry anemone *Corynactis*, in contrast, was positioned similarly to the two sea star species as a top invertebrate predator. Thus, the isotope data support observations that these anemones, with their large nematocysts, are feeding on copepods, planktonic larvae, and other small zooplankton, rather than on phytoplankton (Morris et al., 1980).

The brittlestar *Ophiothrix spiculata*, a suspension feeder, is positioned between levels 2 and 3, suggesting an omnivorous diet. This conclusion is supported by the little dietary information available on this invertebrate, which can often be seen with arms raised into the water column, apparently for suspension feeding, but it is also reported to feed on small benthic organisms (Morris et al., 1980). The purple urchin *Strongylocentrotus purpuratus*, though capable of omnivorous feeding, is positioned near the mean of level 2, suggesting a diet largely consisting of macroalgae, as has been generally reported (Leighton, 1966; Duggins, 1981). In contrast, the bat star *Asterina* is reported as an omnivore, but the N isotope data suggest that it feeds primarily as a carnivore on the study reefs.

The seven species of kelp forest fish that we analyzed were positioned at or near level 3, as expected, based on published dietary information for these species. However, published reports also indicate that some of the rockfish (*Sebastes* spp.) and the giant kelp fish (*Heterostichus rostratus*) can feed across trophic levels, consuming smaller fish. Indeed, trophic position values for some species (*Sebastes atrovirens*, *S. serranoides*, *Heterostichus rostratus*, *Brachyistius frenatus*) reviewed on the comprehensive database "FishBase" range from 3.4 to 3.9 (Froese and Pauly, 2013), suggesting significant piscivory. The N isotope data indicated that our sampled fish were primarily feeding on invertebrates, and the stomach contents of these species, which consisted primarily of isopods, amphipods, hydroids, gastropods, and bryozoans, supported this conclusion (recent work of author Koenigs and colleagues).

SPATIAL PATTERNS IN N ISOTOPE VALUES— KELP FOREST

Trophic position estimates for the invertebrate consumers can be compared across reefs (Figure 2). Trophic position



CONSUMER	EXAMPLES OF REPORTED DIET
Corynactis	copepods, nauplius larvae, small animals
Asterina	algae, ascideans, bryozoans, sponges
Conus	gastropods, bivalves, polychaetes, octopuses, fishes
Pisaster	bivalves, snails, chitons, barnacles; prefers mussels
Cypraea	carnivore/scavenger, anemones, sponges, ascideans
Ophiothrix	small organisms, detritus from the water column
Styela	organic detritus particles, suspended particles
Megabalanus	small plankton, edible detritus particles
Crassadoma	phytoplankton
Lithopoma	variety of green, red, and brown algae
Cucmaria	small organisms, detritus from the water column
Stronglocentrotus	red and brown algae, bryozoans, tunicates, sponges
Diopatra	small invertebrates, plant fragments, giant kelp
Basal source	

Figure 2. Comparison of trophic position of the invertebrates sampled annually from 2002–2005 across four reefs. Color shading represents trophic position values from primary (green) to secondary (yellow) consumer with species feeding across trophic levels in between. Method of calculation of trophic position from consumer δ^{15}N values provided in text.

values were computed as above and standardized across reefs using N isotope baseline values computed for each reef derived from Page et al. (2008). To facilitate this comparison, trophic position is compared across reefs arranged from west to east and relative to the westernmost reef, Arroyo Quemado. Invertebrates characterized as primary consumers at Arroyo Quemado were similarly characterized at the other three reefs. However, the lower position of some omnivorous and predatory invertebrates at Arroyo Quemado (*Ophiothrix spiculata, Conus californicus*, *Cypraea spadicea, Pisaster giganteus*), in comparison to the other rocky reefs (Mohawk Reef in particular), suggested that the diet of these species at Arroyo Quemado contained a greater proportion of lower-level prey, a possibility that could be further evaluated through surveys of the diets of these consumers in the field.

N ISOTOPES AND THE TROPHIC POSITION OF CORAL REEF CONSUMERS

We collected a total of 2,097 individuals representing 214 species and 43 families of reef fishes from Mururoa Atoll during a collaborative research effort conducted by personnel affiliated with the Moorea Coral Reef (MCR) LTER site, the French Institute for Research and Development (Institut de Recherche pour le Développement) and the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE). The French government has prohibited fishing in the waters around Mururoa since the mid-1970s and, as a result, the fish community present in the atoll's lagoon displays a trophic structure reflective of a less-disturbed coral reef ecosystem (Planes et al., 2005). Fishes were collected using a variety of methods, including rotenone, small nets, and hook and line from 13 different locations within the lagoon during a single sampling trip in June 2006. Additional samples of dietary components (e.g., macroalgae, reef turf, zooplankton, and coral) also were collected at each sampling location. Estimates of fish species trophic positions were made using δ^{15}N values of dorsal muscle tissue. The average of the δ^{15}N values for the main sources of primary production supporting the coral reef food web (several species of macro- and turf algae) was used to determine the producer baseline N isotope value at each location (overall island mean 2.8‰ ± 0.3 SE).

The δ^{15}N values of coral reef fishes sampled ranged from lows of 5.5–5.7‰ for two genera of herbivorous parrotfishes (*Chlorurus, Scarus*) and three genera of scorpionfish/unicornfish (*Acanthurus, Ctenochaetus*, *Naso*) to highs exceeding 10‰ for several genera of large piscivores (moray eels *Gymnothorax*, snappers *Lutjanus,* and groupers *Epinephelus*;

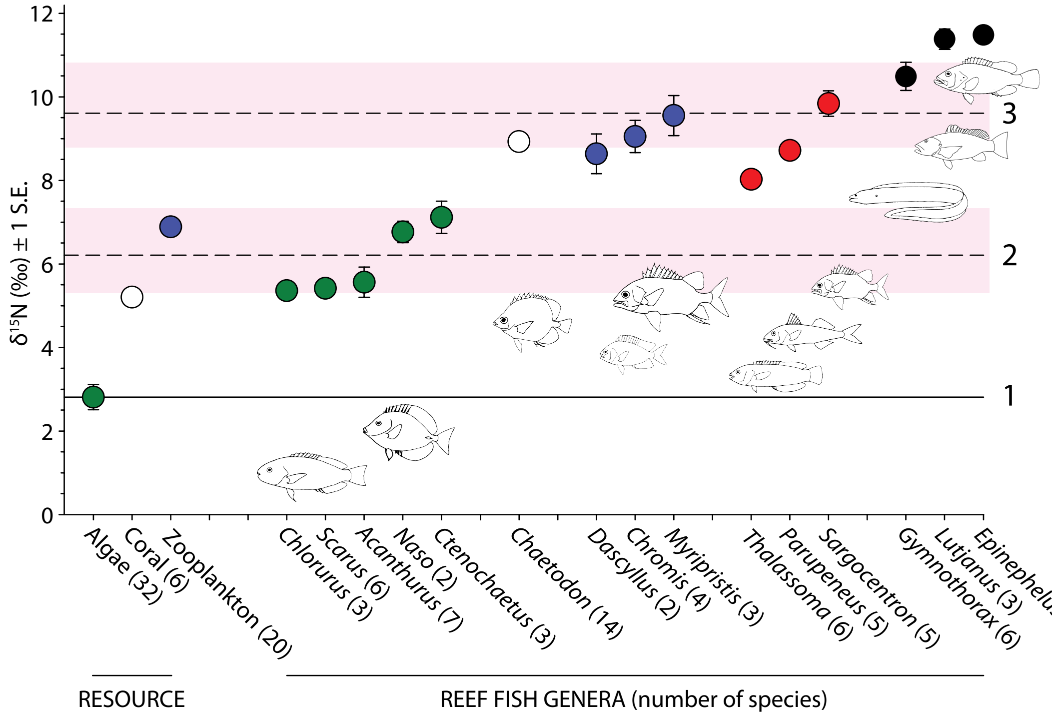


Figure 3. The nitrogen isotope values (δ^{15}N) of resource base and fishes sampled from Mururoa Atoll, French Polynesia. The resource baseline and position of trophic levels 2 and 3, assuming an enrichment factor of +3.4‰ per trophic level, are also shown for comparison with the δ^{15}N values of the fishes. The number of species analyzed within the genus appears in parentheses. Mean δ^{15}N values and standard errors (SE) are calculated across genera. Shaded area indicates ±1‰ standard deviation values.

Figure 3). Corallivorous butterflyfishes (*Chaetodon*), planktivorous damselfishes (*Dascyllus* and *Chromis*), and several genera of meso-carnivores (squirrelfish *Sargocentron,* soldierfish *Myripristis*, goatfish *Parupeneus*, and wrasses *Thalassoma*) fell in between these values (Figure 3). The computed trophic position estimates agree with reported dietary information for these genera (Parrish, 1987; Kulbicki et al., 2005; Randall, 2005; Froese and Pauly, 2013). Similar to the estimates for kelp forest consumers, trophic position values calculated using N isotopes suggest that some genera are feeding across trophic levels. In particular, the average trophic position of the six species of wrasses in the genus *Thalassoma* is intermediate between levels 2 and 3, suggesting a diet consisting of a mix of algae and invertebrates, while δ^{15}N values for the two species of planktivorous *Dascyllus* indicate that the diet for these species likely also includes algae in addition to zooplankton (Wyatt et al., 2010).

It is of interest to compare estimates of trophic position from the current N isotope analysis to those based on analysis of gut contents (Froese and Pauley, 2013). In general, there was good agreement between these two methods for the largely herbivorous fishes (parrotfish, surgeonfish, and unicornfish; FishBase values 2.0–2.3), as well as for the major genera of planktivorous pomacentrids (*Dascyllus*, 2.5–2.8; *Chromis*, 2.5–3.1). Estimates based on gut contents, however, tended to overestimate trophic positions for fishes feeding at higher trophic levels when compared to trophic levels estimated using δ^{15}N (*Gymnothorax*, 3.3 vs. 4.2; *Lutjanus*, 3.5 vs. 4.1; and *Epinephelus*, 3.6 vs. 4.1). This suggests a larger contribution of herbivorous invertebrates or fishes, as opposed to predatory species (e.g., planktivores), to the diets of this group than suggested by analysis of gut contents.

N ISOTOPES AND ONTOGENETIC SHIFTS IN TROPHIC POSITION

Many species of coral reef fishes display ontogenetic shifts in habitat use (Lecchini et al., 2012) that are typically accompanied by shifts in diet (de la Morinière et al., 2003; Kulbicki et al., 2005; Pratchett et al., 2008). Nitrogen isotope values can be useful in assessing changes in diet and trophic position during growth and development (Galván et al., 2010). Such changes were evident for some of our coral reef fish. Two species, the white cheek surgeonfish *Acanthurus nigrofuscus* and the orange spine unicornfish *Naso literatus*, feed at a higher trophic position when small, possibly on zooplankton or small benthic invertebrates, and switch to benthic algae as they grow (Figure 4). The opposite pattern occurred for the hexagon grouper *Epinephelus hexagonatus* and bigscale soldierfish *Myripristis berndti*. For these species, δ^{15}N values increased with increase in fish size,

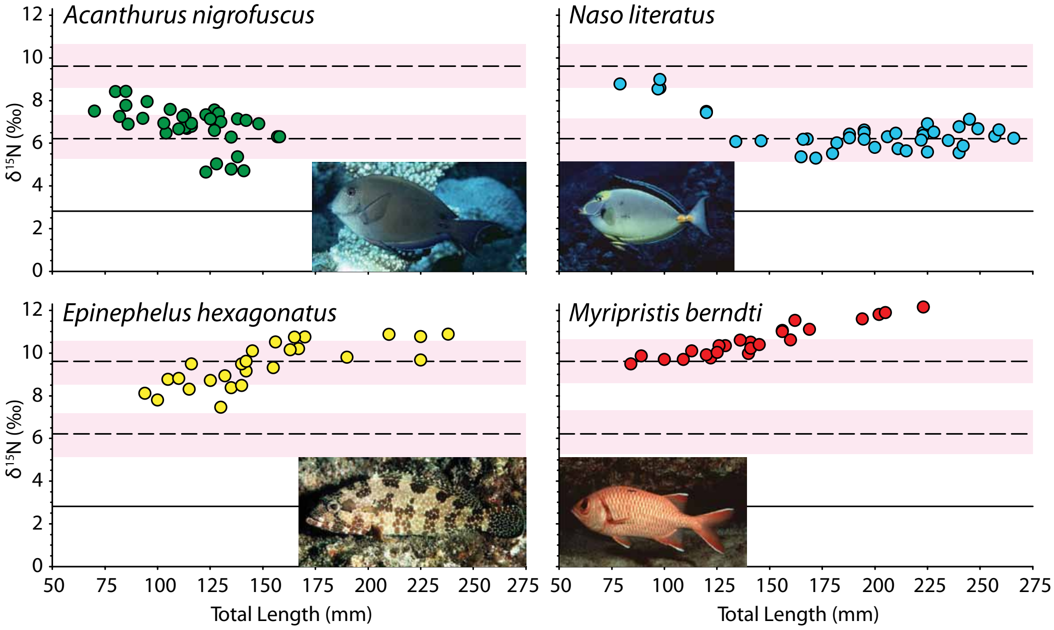


Figure 4. Relationship between δ^{15}N values of selected coral reef fishes and fish total length. The primary producer baselines and positions of trophic levels 2 and 3 are also shown.

suggesting an ontogenetic switch in diet to one that includes more high-level invertebrate or fish prey.

SPATIAL PATTERNS IN N ISOTOPE VALUES— CORAL REEF

Spatial differences in the relative contributions of oceanic versus reef-based nutrients can affect the $\delta^{15}N$ values of reef consumers (Hanson, 2011; Wyatt et al., 2012). We grouped the 13 locations sampled within Mururoa Atoll into four geographic regions (North, South, East, and West), and we compared the trophic position of selected coral reef fish across these four regions. Producer baseline values of $\delta^{15}N$ from the more oceanic western region of the atoll were higher than baseline values of $\delta^{15}N$ from the more lagoonal southern regions (Figure 5). When fish $\delta^{15}N$ values are converted to trophic position using the location-specific baseline values, this comparison reveals that moray eel (*Gymnothorax javanicus*), sable squirrelfish (*Sargocentron spiniferum*), and hexagon grouper (*Epinephelus hexagonatus*) could be feeding at slightly higher trophic levels in these more oceanic locations compared to individuals sampled in other regions throughout the lagoon. As in other studies (Wyatt et al., 2012), the reported diets for several species of corallivores (*Chaetodon auriga*, *C. trifascialis*) and the herbivorous *Stegastes fasciolatus* indicate that these species may feed omnivorously and that variability in trophic position across locations may reflect the availability of different prey.

SUMMARY AND CONCLUSIONS

Nitrogen isotope analysis can be an informative approach for evaluating the trophic position of consumers in kelp forest and coral atoll food webs. The $\delta^{15}N$ values of consumers increased from known herbivores (invertebrates and fish) to higher-level consumers (predatory invertebrates and fish). In the absence of data on trophic enrichment in ^{15}N for our study species, we used the oft-cited value of +3.4‰ per trophic level. Despite the potential for interspecific variation in this value, our estimates of trophic position generally agreed with published dietary information. Nevertheless, these estimates can be refined with measurements of actual trophic enrichment in ^{15}N. Nitrogen isotope analysis may be particularly useful for

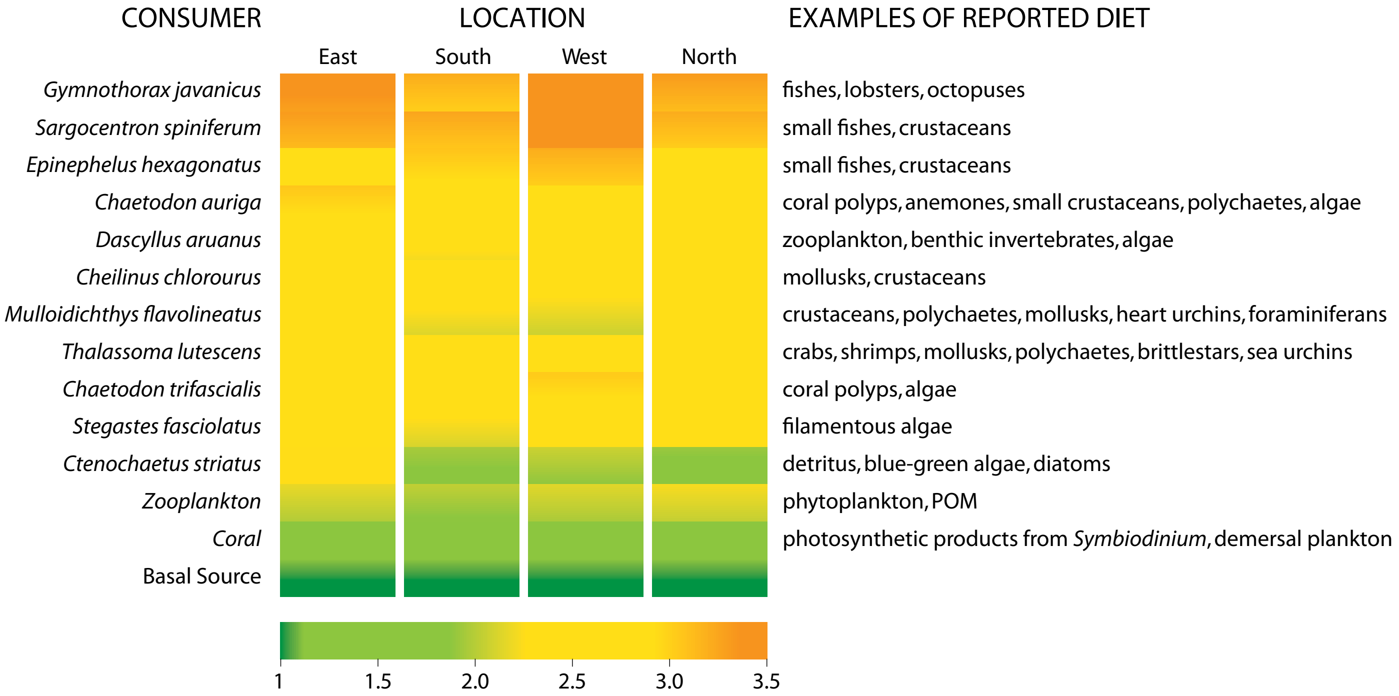


Figure 5. Comparison of trophic positions of coral reef fishes sampled from Mururoa Atoll across four locations. Color shading represents trophic position values from primary (green), to secondary (yellow), to tertiary (orange) consumer, with species feeding across trophic levels shaded in between. Method of calculation of trophic position from consumer $\delta^{15}N$ values as above.

comparing the diets of species capable of feeding omnivorously (Post et al., 2000; Jack and Wing, 2011). Notably, diet studies on some of our higher-level fish consumers (i.e., rockfish from the rocky reef) report both invertebrates and fish as prey. Trophic position estimates suggested that these fish were feeding predominately on lower-level invertebrates rather than as piscivores.

> “OUR DATA SUPPORT THE USE OF NITROGEN ISOTOPE VALUES TO ASSESS TROPHIC POSITION AND, THUS, THEIR UTILITY AS ONE METRIC WITH WHICH TO EXPLORE THE EFFECTS OF SHORT- AND LONGER-TERM NATURAL AND HUMAN-INDUCED CHANGES ON KELP FOREST AND CORAL REEF FOOD WEBS.”

There are few studies that have used N isotopes to explore trophic position in marine systems. In one exception, Jack and Wing (2011) reported rock lobsters feeding at a higher average trophic level inside than outside of kelp beds, which may have reflected the availability of different types of prey between these locations. Our data support the use of N isotopes to assess trophic position, and thus their potential utility as one metric with which to investigate the effects of short- and longer-term natural and human-induced changes on kelp forest and coral reef food webs.

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