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A Comparison of the Ichthyofaunal Trophic Ecology at Selected Limestone Artificial Reef Sites and Adjacent Natural Reef Sites

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

A Comparison of the Ichthyofaunal Trophic Ecology at Selected Limestone Artificial
Reef Sites and Adjacent Natural Reef Sites

By
Joseph R. Hornbeck

Submitted to the Faculty of
Nova Southeastern University
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Biology
Marine Environmental Science

Nova Southeastern University

2017

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Abstract

Artificial reefs may enhance the biological production of reef-associated flora and fauna, but their trophic structure relative to that of natural reefs remains understudied. We assessed trophic dynamics by comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in 43 fish species from artificial and natural reef tracts of Broward County, Florida. We tested the effect of sampling location (artificial, first, and second reef), general feeding strategy (herbivore, omnivore, planktivore, invertivore, and carnivore), phylogeny, and standard length. For all samples, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranged from -19.5 to -13.1‰ and 6.7 to 13.3‰, respectively. Lower trophic level feeding behavior resulted in more depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and higher trophic level feeding behavior resulted in more enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We detected significant effects of both general feeding strategy and phylogeny. We also detected significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ profiles between artificial and natural reefs; however, these differences were not great enough to suggest changes in the feeding strategy or trophic dynamics of individual fish taxa.

Keywords: Stable Isotopes; Artificial Reefs; Trophic Ecology; Reef Fishes.

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Introduction

Globally, reef systems are being degraded by a number of processes, including coastal development, deleterious fishing practices, and climate change (Stone 1985b, Lonnstedt et al. 2014). Unsustainable fishing practices have been shown to reduce biodiversity and modify ecosystem functionality and health (Worm et al. 2009). In the Caribbean, over-harvesting of herbivorous fishes, coupled with the population crash of spiny sea urchin *Diadema antillarum* as a result of disease, potentially released grazing pressure on macroalgae populations. As a result, established coral colonies were smothered by macroalgae, preventing settling and recruitment of coral larvae (Souter and Linden 2000), which in turn led to a Caribbean-wide decrease in reef fish density due to habitat loss and alteration (Paddack et al. 2009, Koeck et al. 2014, Lonnstedt et al. 2014).

Coastal development in tropical and subtropical areas has been linked to the degradation of reef habitat via sedimentation and eutrophication events. The combined removal of mangrove forests and dredging activities lead to increased sediment transportation to coral reef environments (Souter and Linden 2000). The resulting increase in turbidity decreases sunlight availability to symbiotic zooxanthellae, limiting their ability to photosynthesize and ultimately slowing coral growth. Extreme cases of sedimentation can smother corals and result in direct mortality (Souter and Linden 2000, Bellwood et al. 2004). Pollution runoff, as a result of development, can cause eutrophication events and algal blooms. These algal blooms can degrade reef habitat by smothering and directly killing established corals or by preventing the recruitment and establishment of juvenile corals.

Anthropogenic climate change has been linked to ecological shifts and habitat alteration or loss in coral reef environments. Reduced salinity, fluctuations in light intensity, and contamination from pesticides and fertilizers have also been linked to coral bleaching, but increased sea temperature is thought to be the major cause of mass bleaching events, during which the zooxanthellae produce toxic by-products and are expelled by the corals. The loss of the zooxanthellae is not directly lethal, but as the corals rely on food resources provided by the symbionts, bleaching can eventually lead to their death. The loss of reef building corals results in reduced reef coverage and

complexity, directly impacting reef fish habitat and productivity (Souter and Linden 2000).

In the United States, artificial reef construction is overseen at the federal level by the National Marine Fisheries Service (NMFS). Artificial reefs are described by NMFS as “a structure which is constructed or placed in waters covered under this title for the purpose of enhancing fishery resources and commercial and recreational fishing opportunities” (Stone 1985b). In order to provide a framework for the construction and establishment of artificial reefs, NMFS created the National Artificial Reef Plan (NARP) in 1985. Critically, NARP identifies key information gaps that need to be addressed for managers to make informed decisions regarding the use of artificial reefs as management tools (Stone 1985b). Specifically, NARP describes the need for quantitative information regarding the trophodynamics of artificial reefs. The objective of this study was to use stable isotope analysis to quantify and compare the trophodynamics of artificial reef sites located off Broward County, Florida with adjacent natural reef sites.

United States Artificial Reef Program

In the United States, the first recorded effort to construct and establish an artificial reef occurred off of the coast of South Carolina in 1830, using wood logs as the building materials (Stone 1985a). The first large-scale construction of a marine artificial reef occurred in 1935 when four vessels and other materials were intentionally sunk off the coast of New Jersey (*Ibid.*). The 1940s saw limited artificial reef construction due to the United States’ involvement in World War II, but by the 1950s, artificial reef construction experienced a resurgence (see review in McGurrin et al. 1989). Prior to 1985, construction of artificial reefs within the United States primarily used natural materials and man-made scrap, both due to their availability and low costs (*Ibid.*). Driven by concerns over declining fisheries resources, the United States passed the National Fishing Enhancement Act of 1984 and developed the National Artificial Reef Plan (NARP) in 1985 (*Ibid.*). NARP provided managers with a set of goals and guidelines to follow when developing and planning the establishment of an artificial reef. According to the NARP, an artificial reef must be established in a manner that will, “enhance fishery resources to

the maximum extent practicable, facilitate access and use by U.S. recreational and commercial fishermen, minimize conflicts among competing uses of waters covered under this title and the resources in such waters, minimize environmental risks and risks to personal health and property, and be consistent with generally accepted principles of international law and shall not create any unreasonable obstruction to navigation” (Stone 1985b). Various materials have been used to construct artificial reefs, including sunken vessels, boulders, concrete rubble, and metal structures such as derelict oilrigs (see review in Broughton 2012); materials that are no longer in use due to poor stability and short lifespan include: tires, automobiles, and wood structures (*Ibid.*). Although NARP provides guidelines for the construction and establishment of artificial reefs, state agencies are responsible for construction and establishment of artificial reefs in state waters (Stone 1995b).

Studies of the ecological impacts of artificial reefs traditionally used visual surveys (e.g., Bohnsack and Bannerot 1986, Granneman and Steele 2014) of fish species diversity and biomass. Generally, artificial reefs have been found to effectively accumulate fish (Bohnsack and Sutherland 1985), with a positive correlation existing between species abundance and structural height and complexity (Potts and Hulbert 1994, Spieler et al. 2001, Sherman et al. 2002). However, critics of artificial reefs have often claimed that presence does not imply production; namely, that artificial reefs do not increase the biological production of reef-associated fish at a site, but rather act as a production sink from adjacent natural reefs (Bohnsack and Bannerot 1986, Grossman et al. 1997, Carr and Hixon 1997, Lonnstedt et al. 2014).

When discussing biological attraction versus production in terms of the impact of an artificial reef, *attraction* is the net movement of an individual organism from natural to artificial habitats. *Direct production* is characterized as a change in the biomass over time, through births, deaths, growth, immigration, and emigration (Carr and Hixon 1997). *Secondary biomass production* refers to increased food resources, shelter from predation, settling habitat for larval organisms, etc. (see review in Broughton 2012). Arena et al. (2007) compared sunken vessel artificial reefs and natural reef fish assemblages, finding that planktivores composed 55.8% of artificial reef assemblages, whereas the natural reef site fish assemblages were only 22% planktivores. They proposed that this discrepancy in

assemblages was due to certain confounding ecological advantages that the artificial reef provided for planktivores; specifically, the artificial reef had more vertical relief than the natural reef, which provided increased feeding area for planktivores. Artificial reefs may also increase the foraging potential for reef-associated fishes by providing shelter for those foraging fish, giving them access to the meiofaunal community at the site (Posey and Ambrose 1994, Danovaro et al. 2002). By increasing the foraging capacity of meiofaunal feeders, it is possible that an artificial structure could alter the fish assemblages of higher trophic level feeders and also possibly their feeding behavior (Gravina et al. 1989, Danovaro et al. 2002).

Studies have shown that the establishment of an artificial reef has the potential to create new habitat that provides similar ecological functions as natural habitat (Bohnsack and Sutherland 1985, Sheehy and Vik 2010). However, Lindberg et al. (2006) stated that the attraction-production issue may be a “false dichotomy” and that artificial reefs only act as biological sinks because they attract increased fishing pressure, which in turn leads to increased fish mortality. Love et al. (2006) pointed out that most research has focused on only the artificial reefs themselves, and that a direct comparison with adjacent natural reefs is necessary. This was reiterated in a 2012 NOAA report (Broughton 2012), which stated that future studies should compare the ecological functionality of artificial reefs and corresponding natural reefs.

Southeast Florida Reef System

Physical Characteristics

The Florida Reef Tract is the only coral reef system located within the continental United States. The Tract is approximately 577 km in length, spanning from the Dry Tortugas to Stuart, Florida, and can be separated into three sections: Florida Keys, Southeast Florida, and the Eastern Gulf of Mexico. The Southeast Florida section spans approximately 150 km from Miami-Dade to Stuart and is found roughly 1.5 km off the coast. This reef system is described as a non-frame building series of three linear reef tracts formed from Holocene *Acropora palmata* reef complexes, colloquially referred to as the inner, middle, and outer reefs. The Southeast Florida section has three parallel reef

tracts (first reef, second reef, and third reef) with a width of 600 m (inner to outer) and depths from the top of the reef structure ranging from 3 to 30 m. The three reef tracts are separated from one another separated by sedimentary deposits of varying thicknesses (Banks et al. 2008).

The first reef tract is the least uniform of the three, being described as a series of discontinuous reef patches (Banks et al. 2008). The reef crests at depths ranging from 1.8 to 9.1 m. The portion of the first reef tract north of Port Everglades features average depths of 4.4 m and exhibits more coral growth compared to sections south of the port, which average depths of. 5.3 m. Generally, coral growth increases seaward, with the inner reef containing the least amount of coral growth relative to the other tracts (Ferro et al. 2005).

The second reef tract is a mostly continuous feature, extending from South Miami-Dade County northward to the Boca Raton Inlet (Banks et al. 2008). It exhibits the greatest range in depth compared to the other reef tracts. South of Port Everglades, the reef crests at a depth of 10.7 m compared to 5.7 m north of the port (Ferro et al. 2005). The crest of the second reef is characterized as having low structural complexity, consisting mostly of platform-type substrate, with substantial algal cover and little coral or sponge growth (Ferro et al. 2005).

The third reef is the most continuous reef tract, extending northward from Biscayne Bay to latitude N26°43', where it abruptly terminates (Banks et al. 2008). The average depth of the third reef is approximately 16 m below sea level, ranging from 12.1 to 32.4 m. The eastern edge was found to have the most structural complexity, characterized by a well-defined reef border with coral patches and some spur-and-groove formations (Moyer et al. 2003, Ferro et al. 2005).

Florida has the largest number of permitted artificial reefs in the United States (Adams et al. 2006). Broward County alone features 108 artificial reef sites (*Ibid.*) that vary in construction material: limestone boulders, sunken vessels, and prefabricated structures, often of concrete or a concrete-based matrix (Sherman et al. 2001, Sherman et al. 2002, Arena et al. 2007). The depth from sea surface to non-reef seafloor at which these reefs are deployed also varies and has been identified as a key determinant of fish assemblage complexity; shallow sites at 9 m or less from surface to seafloor had a higher

abundance of herbivorous fish, whereas sites deeper than 18 m had a higher presence of planktivorous fish (Arena et al. 2007).

Fish Assemblage and Fisheries

The Florida Reef Tract supports a diverse faunal community, including reef-building hermatypic corals. The community composition of Broward County's subtropical reefs generally resembles that of Caribbean and tropical Atlantic reefs (Banks et al. 2008). Extensive surveys conducted in Broward County waters over 30 m depth have recorded over 350 fish species (Ferro et al. 2005, Banks et al. 2008). Fish assemblages differ slightly among the three reef tracts, with species richness and fish abundance increasing seaward. The nearshore hard bottom of the first reef is dominated by juvenile reef fishes, especially grunts (Family Haemulidae) (Ault et al. 2001, Moyer et al. 2003, Ferro et al. 2005). On deeper reefs, wrasses (Family Labridae), tangs and surgeonfishes (Family Acanthuridae), and damselfishes (Family Pomacanthidae) become more abundant (Ferro et al. 2005).

Many of the reef fishes and invertebrates of southeast Florida support both recreational and commercial industries. Johns et al. (2001) estimated that natural and artificial reef use in 2001 generated \$4.4 billion from fishing and diving activities. The coastal region of southeast Florida accounts for 20% of the recreational saltwater fishing licenses sold within the state of Florida, indicating a high level a recreational fishing pressure (Ault et al. 2001). As a result, many of the commercially and recreationally important fish species, most notably large groupers (Family Serranidae) and snappers (Family Lutjanidae) are characterized as being overharvested (Ferro et al. 2005, Johnson et al. 2007). Other species that are frequently targeted by these reef-associated fisheries include jacks (Family Carangidae) and porgies (Family Sparidae) (Johnson 2007). Between 1990 and 2000, the mean annual harvest of reef, coastal, and pelagic offshore fishes within the southeast Florida region was 9,706.9 metric ton (mt) per year, of which reef fishes accounted for almost one quarter of that total harvest per year (Ault et al. 2001, Ferro et al. 2005).

Stable Isotope Analysis and Trophic Studies

Feeding is one of the most complex and important interactions within the ichthyofaunal community of a reef (Manteifel 1961). Understanding the trophic relationships within ecological communities is key to understanding community structure, including its overall ecological health and resilience (Hooper et al. 2005, Carscallen et al. 2012). The traditional technique used in trophic studies is stomach content analysis, which characterizes the diet of an individual by examining the contents of the stomach (Bowen 1996, Jennings et al. 1997). The stomach of the specimen is removed and its contents emptied; the material is then analyzed and quantified in order to infer feeding preferences and frequencies (Hyslop 1980, Bowen 1996). Certain shortcomings are associated with this method. First, it only allows investigators to see what was consumed immediately before the specimen was sampled (Hyslop 1980, Bowen 1996). Additionally, the digestion rate of prey items within the stomach is not uniform; soft-bodied prey items will digest more rapidly and therefore be harder to detect or identify compared to dense or hard-bodied prey items (Bowen 1996). Both of these issues create the possibility of the underrepresentation of those soft-bodied items and the over-representation of hard-bodied items.

Stable isotope analysis is another technique used in trophic studies. Every element has multiple isotopic forms depending on the number of neutrons in the nucleus. Of the 3100 known isotopes, only 283 are known as “stable” because they do not undergo radioactive decay (Fry 2006). The stable nature of these isotopes allows investigators to map the movement of these elements through the biosphere. The elements specifically used in stable isotope ecology are: carbon (C), nitrogen (N), oxygen (O), sulfur (S), and hydrogen (H) (reviewed in Peterson and Fry 1987, Fry 2006). Nitrogen and carbon are the most frequently used for trophic studies concerning marine fauna (Layman et al. 2012).

Both carbon and nitrogen have a pair of isotopic forms that can be used in trophic studies, C^{12}/C^{13} and N^{14}/N^{15} . In each pair, the isotope with fewer neutrons is referred to as “light” and the isotope with more neutrons is referred to as “heavy.” For both carbon and nitrogen, there is a naturally occurring disproportionate ratio of light and heavy isotopes

with light isotopes accounting for over 95% of all isotopes for either element. This baseline ratio of heavy to light isotopes changes, however, as carbon and nitrogen move through the biosphere via a process known as isotopic fractionation (Fry 2006). For carbon and nitrogen, isotopic fractionation occurs because light isotopes are preferentially used in chemical processes; heavy isotopes form bonds that are harder to make and break relative to light isotopes. Isotopic fractionation results in the sample being either more enriched or depleted in the heavy isotope relative to the standard. The baseline standard used for carbon is PeeDee Belemnite and the standard for nitrogen is atmospheric nitrogen (Hayes 2002 Fry 2006). Comparing the ratio of heavy/light isotopes in a sample to the baseline standard gives a value, which is expressed as a “del” (for delta, the difference between two values, and using the symbol δ) value and measured in parts per thousand (‰).

Certain tissue types offer different insights into the temporal dietary trends of an individual, depending on the elemental turnover rates of the tissue of interest (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Hobson 1999, Fry 2006). Keratinous tissues such as hair and nails are metabolically inert, and maintain an isotopic record reflecting the location and diet of the individual at the moment the tissue was synthesized. Other tissues are metabolically active, and the dietary information obtained will be temporal, ranging from a few days (e.g., blood plasma) to several weeks (e.g., muscle), depending on regeneration (“turnover”) rates (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Hobson 1999). Pinnegar and Polunin (1999) suggest that the use of white (skeletal) muscle tissue is best suited for dietary studies as it shows lower variability in isotopic composition compared to other tissues.

Carbon Isotope Ratios

Trophic studies tend to use $\delta^{13}\text{C}$ as a means of identifying the major sources of carbon for a food web i.e. the primary producers. There is little isotopic fractionation associated with $\delta^{13}\text{C}$ (0.5-1.0‰) between trophic steps (DeNiro and Epstein 1978). During photosynthesis, isotopic fractionation occurs because C^{12} is used more than C^{13} , resulting in the flora having a more depleted $\delta^{13}\text{C}$ relative to the standard. The $\delta^{13}\text{C}$ of the primary producer is affected by its photosynthetic pathway: C3, C4, or CAM (Gannes et

al. 1998). Tissue of C3 flora is more depleted in $\delta^{13}\text{C}$ (-34‰ to -22‰) relative to atmospheric CO_2 (-8‰) and both C4 (-6.0 ‰ to -13‰) and CAM flora (-10.0‰ to -22.0‰) (Bender 1971, Smith and Epstein 1971, Benedict 1978, DeNiro and Epstein 1978, O'Leary 1981, Gannes et al. 1998).

Mangroves, marine algae, and seagrasses are C3 flora yet they all have distinct $\delta^{13}\text{C}$ ranges. Kieckbusch et al. (2004) reported that the dominant primary producers of southeastern Florida are mangroves, benthic macro algae, phytoplankton, and sea grasses. Mangroves, like other C3 plants utilizing atmospheric CO_2 , have $\delta^{13}\text{C}$ range of -30 to -24‰ (Bouillon et al. 2007). Marine benthic algae and phytoplankton use bicarbonate as a source of carbon, which is more enriched in $\delta^{13}\text{C}$ (0‰) compared to atmospheric CO_2 , and exhibit a $\delta^{13}\text{C}$ range of -20 to -10‰. It has been shown that in conditions of decreased water turbulence, diffusion boundary-layer resistance is decreased, resulting in a more enriched $\delta^{13}\text{C}$ and as a result marine benthic algae typically exhibit a $\delta^{13}\text{C}$ range of -17 to -12‰ and phytoplankton -22 to -17‰ (France 1995a, Bouillon et al. 2007). In areas where water movement is greatly reduced, marine benthic algae can be enriched in $\delta^{13}\text{C}$ by as much as 9‰ (France and Holmquist 1997). Conversely, when found growing in mangrove forests, marine benthic algae display greatly depleted $\delta^{13}\text{C}$. Sea grasses also use bicarbonate, but are affected by rate-limiting diffusion barriers that cause their $\delta^{13}\text{C}$ to closely match C4 plants (-13‰ to -6‰) (Lin et al. 1991, Gannes et al. 1998).

Researchers have used the distinct $\delta^{13}\text{C}$ ranges of mangroves, sea grasses, phytoplankton, and marine benthic algae to examine carbon sources within food webs. For example, Cocheret et al. (2003) used $\delta^{13}\text{C}$ as a means of linking individual reef fishes with three different habitat types: mangrove, sea grass, and reef. Establishing these linkages was possible because the dominant flora of each habitat type produced distinct $\delta^{13}\text{C}$ ranges; specifically, mangroves are the most depleted in $\delta^{13}\text{C}$ and sea grasses the most enriched. Studies have also shown that with seaward movement, the $\delta^{13}\text{C}$ of sampled fauna become more depleted as the food web base shifts from benthic algae to phytoplankton (France 1995a, France 1995b, Wyatt et al. 2012).

Nitrogen Isotope Ratios

The two naturally occurring stable nitrogen isotopes used in trophic studies are ^{14}N and ^{15}N . The ratio of ^{15}N to ^{14}N , referred to as the $\delta^{15}\text{N}$, can be used to infer the dietary habits of an individual. Unlike $\delta^{13}\text{C}$, there is an enrichment trend of $\delta^{15}\text{N}$ per trophic step. Metabolic processes preferentially use ^{14}N and in turn increase the ratio of ^{15}N to ^{14}N , a process referred to as metabolic fractionation, so that the $\delta^{15}\text{N}$ of the individual is enriched relative to its food item (Mill et al. 2007). This enrichment trend follows a stepwise pattern as individuals feed at progressively higher trophic levels. Fractionation of $\delta^{15}\text{N}$ has been shown to be consistent at all trophic levels (3-4‰), with the exception of primary consumption (Vander Zanden and Rasumssen 2001, Post 2002, Mill et al. 2007, Cresson et al. 2014).

The $\delta^{15}\text{N}$ of food web bases can vary and should be considered when drawing inferences between an individual's $\delta^{15}\text{N}$ and its trophic dynamics (Post 2002). Additionally, it has been shown that $\delta^{15}\text{N}$ can be anthropogenically enriched in areas where sewage and other pollution runoff are introduced into a marine system (Heikoop et al. 2000, Risk et al. 2009). The $\delta^{15}\text{N}$ of an individual and the $\delta^{15}\text{N}$ of the perceived food web base can be used to calculate an individual's trophic position. Whereas trophic level is a qualitative representation of an individual's energetic interactions, trophic position is a quantitative measurement that describes not only which trophic level that individual occupies but where that individual lies between trophic levels. Individuals do not always feed at discrete trophic levels, making it difficult to classify them as feeding at a definitive trophic level (Carscallen et al. 2012). The trophic position concept is better suited to capture complex feeding interactions, such as omnivory, when compared to the trophic level concept (Paine 1988, Polis and Strong 1996, Vander Zanden and Rasmussen 1999, Post 2002).

Objectives and Hypotheses

This study focused on the reef-associated fish assemblages of artificial and natural reefs in Broward County. The purpose of this study was to improve the understanding of trophic dynamics of reef fish and elucidate any possible differences in the feeding ecology of the artificial and natural reef habitats. Effective management of local fish

stocks depends on a thorough understanding of the trophic dynamics of reef-associated fish at both natural and adjacent artificial reefs.

The specific objectives of this study were to 1) collect and document the reef-associated fish at eight different study sites; 2) using mass spectrometry, analyze muscle tissue in order to obtain the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ s for each individual; 3) use statistical analyses to evaluate whether relationships exist among $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue and feeding strategy; 4) compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue and reef fish community composition between artificial and natural reef sites; and 5) use these data to infer larger patterns of habitat use, fish community, and trophic interactions in artificial versus natural reef environments.

Hypotheses

The main question being asked by this study is: Will reef fish trophic dynamics vary between the artificial sites and natural sites? Because sampled individuals were used to make comparisons between the sites, the first question asked was: Does the community structure of the catch data reflect the community structure of the site? Second, species were assigned to “trophic guilds” based on food resource preference in order to test the a priori assumption that feeding strategy influenced $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Presumably, the $\delta^{15}\text{N}$ of an individual will increase with feeding at a higher trophic level. In contrast, the $\delta^{13}\text{C}$ of individuals will reflect the basal primary producer within the food web, and these values will be used to compare carbon sources. Lastly, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of samples taken from the artificial reef sites were compared to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of samples taken from the first natural reef tract and second natural reef tract. The artificial reef sites being investigated are located equidistant between the first and second natural reef tracts. Studies have shown that the physical characteristics and fish assemblages of the first and second reef tract are different, which may impact the feeding dynamics of those sites. Additionally, it has been shown that with seaward movement, the $\delta^{13}\text{C}$ of sampled fauna will become more depleted (France 1995a, France 1995b, Wyatt et al. 2012) and, therefore, it is expected that the $\delta^{13}\text{C}$ of the first reef sites will be more enriched than the middle reef sites. In order to provide a more comprehensive comparison of the artificial to natural

reef trophic dynamics, the artificial reef sites will be compared to both the first and second reef tracts.

Materials and Methods

Study Sites

All sites were sampled between July 23, 2014 and August 29, 2014. The climate of southeast Florida is described as “Tropical Savanna,” having two distinct seasons: wet and dry (Banks et al. 2008, Misra and DiNapoli 2013). To avoid any possible complications in trophic analysis due to variables stemming from differences between the two seasons, sampling was only conducted during the wet season (June through September).

During October 2009, the Florida Department of Transportation (FDOT) deployed a series of 12 artificial reef concrete boulders off the coast of Broward County Florida (Figure 1). These artificial reefs were deployed on open, sandy bottom areas between the adjacent first and second natural reef tracts, at an average depth of 14 m. A total of eight study sites were chosen and sampled: four artificial sites and four natural sites (Table 1). The study sites were grouped by location: natural first reef (3AN and 6AN), natural second reef (1AN and 5BN), inner artificial (3A and 6A), and outer artificial (1A and 5B). The artificial reef sites chosen were 3A, 1A, 6A, and 5B. Sites 3A and 6A are the innermost sites, with a distance from land of approximately 1.45 km, and have a north-south orientation separated by a distance of approximately 0.13 km. Sites 1A and 5B are the outermost sites, with a distance from land of approximately 1.53 km, and have a north-south orientation of approximately 0.13 km (Figure 1).

Natural sites were chosen from the first and second reef tracts, based primarily on their orientation to the artificial reef sites. The rationale behind sampling both the first and second reef is due to perceived potential differences in the trophodynamics of the first and second reef. For this reason, sites were grouped by their *reef type* (artificial versus natural) and *distance from shore* (inner versus outer). The labels for the natural sites are a combination of the label of the artificial site that the natural site corresponds to and the letter “N” which stands for “natural”. The first reef sites, 3AN and 6AN, are

located approximately 1.13 km from the coastline of Broward County, with a north-south orientation at a distance of 0.13 km. The second reef sites, 1AN and 5BN, are located approximately 1.83 km seaward and also have a north-south orientation at a distance of 0.13 km (Figure 1).

Sampling procedure

As per the requirements of the Nova Southeastern University Oceanographic Center (NSUOC) policy concerning research diving, all participating SCUBA divers were either active or probationary members of the NSUOC Scientific Diving Program. A minimum of one active member supervised and participated in all dives performed with probationary members. Additionally, in preparation for this study, an official dive plan outlining all diving activity was drafted and submitted to the NSUOC Diving Safety Officer (DSO) for review (see Appendix I). This dive plan was reviewed and accepted by the NSUOC DSO.

For all dives, dive teams consisted of at least two and no more than four divers. For this study, enriched air (NITROX) was utilized in order to maximize dive time. Due to the limited amount of vessel time available to this project, a total of four dives occurred during each field event. The average bottom time of each dive was approximately 35 minutes: 15 minutes for the survey and 20 minutes for specimen collection. Each dive team consisted of one diver designated as the survey diver and the other diver(s) as the specimen collection divers. The survey diver was deployed with a dive slate and data sheet to record observed fauna and the collection diver(s) handled the sampling gear.

Survey methodology

As part of the sampling procedure, a visual census of the fish assemblage of each site was conducted. The artificial reef sites are confined by their spatial limitations and immediate termination of reef structure into homogenous sandy bottom and cover less area when compared to the natural reef tracts. Due to the spatial difference in reef cover, performing a roving diver survey would not have offered a comparable survey of the artificial and natural reef sites; thus, the Bohnsack-Bannerot stationary visual census

technique was used instead (Bohnsack and Bannerot 1986). Using the Bohnsack-Bannerot method, the survey diver observed faunal species diversity and abundance for fifteen minutes. The artificial sites have a rough circular shape and a diameter of approximately 20 m, which was used as the diameter of the survey cylinder in order to standardize the survey area between sites. Additionally, the survey cylinder had a height of 5 m based on the relief height of the sites.

Fish species diversity and abundance were recorded using the Reef Environmental Education Foundation (REEF) Fish Survey Project's methodology; counts of observed species were assigned to one of four log₁₀ abundance categories: single (1), few (2-10), many (11-100), and abundant (> 100) (Pattengil-Semmens and Semmens 2003). Density scores were calculated for each species by site using abundance categories and the equation:

$$D = [(nS \times 1) + (nF \times 2) + (nM \times 3) + (nA \times 4)] / (nS + nF + nM + nA)$$

where D is the density score and nS, nF, nM, and nA are the number of times an abundance category was given (Pattengil-Semmens and Semmens 2003). The survey data were used to provide a comparison of fish species surveyed at each of the eight sites studied against the catch composition of each study site after sampling. The purpose of this comparison to determine if the species sampled per site reflected the species present at each site.

Fish collection

Specimen collections were conducted under Florida Fish and Wildlife Conservation Commission (FWC) permit number SAL-13-1537 to sample individual of species that would otherwise be protected, whether by size restrictions, seasons, or other regulatory concerns. Reef fish collection was conducted using a spear gun; collected fish were placed in bags and sent to the surface via lift bags to be retrieved by the surface support crew. Once retrieved by the surface support crew, collected fish were placed in individual sample bags with a tag noting the species, date, and site of collection prior to being placed on ice. Fish collection lasted approximately 20 minutes in order to standardize sampling effort.

Table 1. Global Positioning System (GPS) coordinates for the artificial (3A, 6A, 1A, 5B) and corresponding natural reef (3AN, 6AN, 1AN, 5BN) sites, located off of Broward County, Florida. Visual surveys and sampling of marine fish species were conducted at these sites.

Artificial Reef Sites			Natural Reef Sites		
Site Name	Latitude (North)	Longitude (West)	Site Name	Latitude (North)	Longitude (West)
3A	26°09.1887	80°05.1449	3AN	26°09.1889	80°05.3373
6A	26°09.1148	80°05.1703	6AN	26°09.1158	80°05.3379
1A	26°09.1914	80°05.0944	1AN	26°09.1903	80°04.9324
5B	26°09.1201	80°05.0958	5BN	26°09.1190	80°04.9330

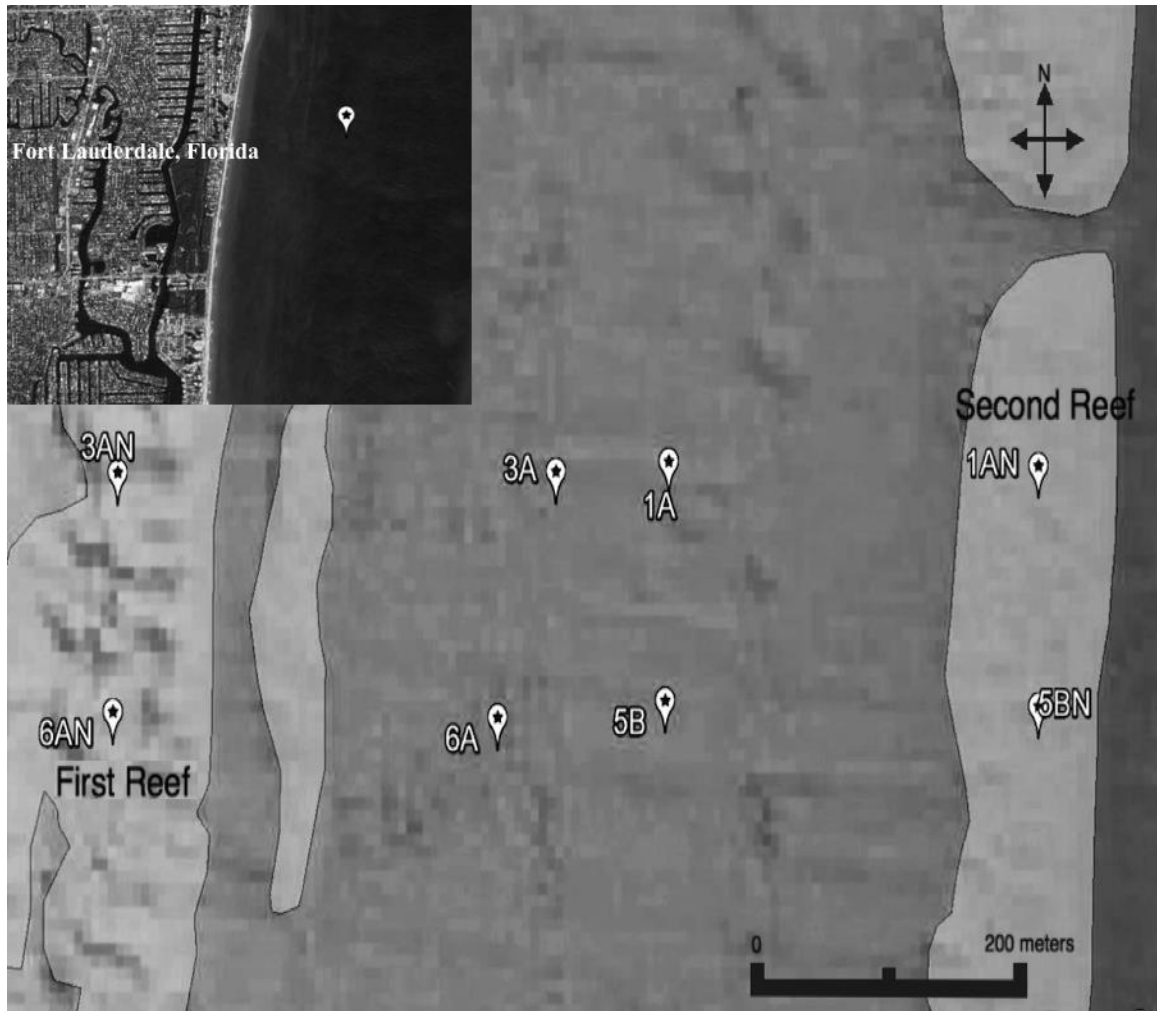


Figure 1. Map showing the position of the limestone boulder artificial reef study sites (3A, 1A, 6A, 5B) and the natural reef study sites located on the first reef (3AN, 6AN) and second reef (1AN, 5BN) tracts. All study sites were located off the coast of Fort Lauderdale, FL

Fish processing

Specimens were catalogued for the sample site, date of collection, date of processing, biological samples taken, sex, and weight/length metrics. This information was recorded on paper data sheets and kept in the NSUOC Fisheries Laboratory; copies were also stored electronically. Using existing National Marine Fisheries Service (NMFS) species codes (NMFS 2010) whenever possible, a three-letter code was assigned to identify each catalogued species and a number assigned to each individual. When a NMFS species code was not available, one was created using the same three-letter format (see Table 3 for a list of the species codes used in this project).

After cataloging an individual sample, the weight of the animal and its morphometrics were recorded, including standard, total, and fork length. Recording multiple length types proved vital, as certain individuals were damaged and therefore a true total length was impossible. For this reason, standard length was chosen to represent the length of each catalogued individual. Based on a review of published literature, the general feeding habits of each species were used to place each species into one of five broad trophic guilds: herbivore, omnivore, planktivore, invertivore, and carnivore (Table 2). To better graphically represent each species within each trophic guild, species were assigned a trophic code consisting of the first letter of the trophic guild (e.g. H for herbivore) and a number (based on the alphabetical order of the species code) in order to differentiate the species within a trophic guild. Species within the trophic guild *herbivore* are those species that are found to have a diet consisting of marine flora. Trophic guild *omnivore* consists of species that are described as having a diet of both marine flora and fauna. The trophic guild *planktivore* consists of species that feed primarily on planktonic invertebrates. The trophic guild *invertivore* consists of species that were found to feed primarily on benthic invertebrates and the trophic guild *carnivore* consists of species that feed on both benthic invertebrates and marine fish.

Table 2. Trophic Guilds (TG) based on the general feeding strategy of each species in this study. Prey items for species of this study were sourced from primary literature. Species within a Trophic Guild (TG) were assigned a guild code (TC).

TG	TC	Species	Prey items	Reference(s)
Herbivore	H1	<i>Acanthurus bahianus</i>	algae, phanerogams	Randall 1967
	H2	<i>Acanthurus chirurgus</i>	algae	Randall 1967
	H3	<i>Acanthurus coeruleus</i>	algae	Randall 1967
	H4	<i>Sparisoma aurofrenatum</i>	sponge, algae, phanerogams	Randall 1967, Dunlap and Pawlik 1998
	H5	<i>Sparisoma chrysopterum</i>	sponge, algae, phanerogams	Randall 1967, Dunlap and Pawlik 1998
	H6	<i>Sparisoma viride</i>	algae, phanerogams	Randall 1967
	H7	<i>Stegastes partitus</i>	algae	Randall 1967, Hixon 1993
Omnivore	O1	<i>Canthigaster valentini</i>	phenerogams, sponge,	Randall 1967
	O2	<i>Holacanthus ciliaris</i>	algae, sponge, tunicates, hydrozoans	Randall 1967
	O3	<i>Holacanthus tricolor</i>	algae, zoantharians, sponge	Randall 1967
	O4	<i>Pomacanthus paru</i>	algae, sponge, tunicates, zoantharians, gorgonians	Randall 1967
	O5	<i>Lactophrys triqueter</i>	annelids, sipunculids, crabs, shrimps, tunicates, sponge	Randall 1967, Dominici- Arosemena and Wolff 2005
	O6	<i>Abudefduf saxatilis</i>	anthozoans, copepods, algae, tunicates	Randall 1967
Planktivore	P1	<i>Clepticus parrae</i>	copepods, shrimps, crabs	Randall 1967
	P2	<i>Chromis multilineata</i>	copepods, tunicates, stomatopods	Randall 1967
Invertivore	I1	<i>Chaetodon capistratus</i>	zoantharians, annelids, gorgonians, tunicates	Randall 1967, Lasker 1985
	I2	<i>Cheatodon sedentarius</i>	annelids, shrimps, amphipods, hydrozoans	Randall 1967
	I3	<i>Diodon holocanthus</i>	gastropods, pelecipods, sea urchins, Crabs	Randall 1967

Table 2. Cont.

TG	TC	Species	Prey items	Reference(s)	
Invertivore	I4	<i>Anisotremus virginicus</i>	sea urchin, crabs, shrimps, annelids, pelecipods	Randall 1967	
	I5	<i>Haemulon album</i>	crabs, shrimps, stematopods, pelecipods, holothurians, sea urchins, annelids	Cummings et al. 1966, Randall 1967, Sierra 1983	
	I6	<i>Haemulon aurolineatum</i>	shrimps, annelids, crabs, amphipods, pelecipods	Randall 1967	
	I7	<i>Haemulon carbonarium</i>	crabs, gastropods, sea urchin, annelids	Randall 1967	
	I8	<i>Haemulon flavolineatum</i>	annelids, crabs, holothurians, shrimps, pelecipods	Randall 1967	
	I9	<i>Balistes capricus</i>	mollusks, crustacea	Goldman et al. 2016	
	I10	<i>Bodianus rufus</i>	crabs, ophiuroids, sea urchins, gastropods	Randall 1967	
	I11	<i>Halichoeres garnoti</i>	crabs, ophiuroids, gastropods, fishes	Randall 1967	
	I12	<i>Lachnolaimus maximus</i>	gastropods, crabs, ophiuroids	Randall 1967, Claro et al. 1989	
	I13	<i>Calamus proridens</i>	crustaceans	Druzhinin 1976	
	I14	<i>Sphoeroides spengleri</i>	crabs, mollusks, annelids, echinoids	Randall 1967	
	Carnivore	C ₁	<i>Carangoides bartholomaei</i>	fishes, cephalopods, shrimps	Randall 1967, Sierra et al. 1986
		C ₂	<i>Caranx crysos</i>	fishes, cephalopods, crabs, stematopods	Randall 1967
		C ₃	<i>Caranx ruber</i>	fishes	Randall 1967, Sierra and Popova 1982
C ₄		<i>Seriola rivoliana</i>	fishes, cephalopods,	Manooch and Haimovici 1983	
C ₅		<i>Haemulon parra</i>	shrimps, crabs, amphipods, gastropods, annelids	Randall 1967	
C ₆		<i>Haemulon plumieri</i>	crabs, annelids, sea urchins, gastropod	Randall 1967, Valdes-Munoz and Silva 1977	

Table 2. Continued.

TG	TC	Species	Prey items	Reference(s)
	C ₇	<i>Haemulon sciuros</i>	crabs, pelecipods, shrimps, sea urchins	Randall 1967, Valdes-Munoz and Silva 1977
	C ₈	<i>Lutjanus griseus</i>	fishes, crabs, shrimps	Starck 1970, Claro 1983a
	C ₉	<i>Lutjanus synagris</i>	fishes, crabs, shrimps	Randall 1967, Claro 1981
	C ₁₀	<i>Ocyurus chrysurus</i>	fishes, crabs, shrimps	Randall 1967, Starck 1970, Claro 1983 b
	C ₁₁	<i>Pseudupeneus maculatus</i>	crabs, shrimps, annelids, mollusks, fishes	Randall 1967
	C ₁₂	<i>Pterios volitans</i>	fishes, shrimps, crabs	Morris 2009
	C ₁₃	<i>Cephalopholis cruenata</i>	fishes, stomatopods, crabs, gastropods	Randall 1967
	C ₁₄	<i>Hypoplectrus unicolor</i>	crustaceans, fishes	Sierra et al. 1994

Stable Isotope Analysis

Approximately 30 grams (g) of white muscle tissue was taken from the anterior dorsal region and processed for stable isotope analysis. Muscle sub-samples were taken and cut into small 3-5 mm² pieces. One sample was placed into a labeled drying tin and put into a 60°C oven for drying while a duplicate sample was labeled and stored at -80°C. The desiccation process lasted between 48-72 hours. Desiccated tissue samples were then pulverized for homogeneity using a Wig-L-Bug MSD model amalgamator (DENTSPLY Rinn; Elgin, IL) and placed in individually labeled glass shell vials. Samples were weighed to approximately 0.6-0.8 milligrams (mg) and pelletized in sterile aluminum tins for stable isotope analysis. Stable isotope analysis was conducted using a Finnigan Delta Plus continuous flow isotope ratio mass spectrometer (CF-IRMS) at the Smithsonian OUSS/MCI Stable Isotope Mass Spectrometry Laboratory (Suitland, MD). All samples were linearly corrected with a two-point linear correction to acetanilide and urea standards calibrated to a V-PDB (Pee Dee Belemnite) standard; Pee Dee Belemnite is the standard used for ¹³C/¹²C, and atmospheric air for ¹⁵N/¹⁴N. Reproducibility was 0.2‰. For all samples, the ratio of the percent carbon to the percent nitrogen (%C/%N) was assessed in order to account for lipid bias. The lipid content of the sample can bias the analysis, resulting in a more depleted δ¹³C (Logan et al. 2008). For this reason, the %C/%N of each sample was first calculated.

The ratio of the heavy to light isotopes for each tissue sample was calculated and expressed using the equation:

$$\delta (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$$

Since the fractionation of carbon isotopes is typically < 1‰ increase per trophic level, the δ¹³C was used to indicate the initial source of carbon (i.e., the food web base) (DeNiro and Epstein 1978, Tieszen 1983, Peterson and Fry 1987, Hentchel 1998). The δ¹⁵N of an individual alone cannot clearly provide insight into the trophic position of that individual due to variation in δ¹⁵N at the base of food webs among ecosystems (Vander Zanden and Rasmussen 2001, Carscallen et al. 2012). For this reason, the trophic position for each individual was calculated using the method of Post (2002):

$$\text{Trophic position} = \lambda + (\delta^{15}\text{N}_{\text{Consumer}} - \delta^{15}\text{N}_{\text{Base}}) / \Delta_n$$

where λ is the trophic level of the organism used as the $\delta^{15}\text{N}_{\text{Base}}$ and Δ_n is the rate of $\delta^{15}\text{N}$ enrichment per trophic interaction. The rate of enrichment used in this equation depends on the nature of the trophic interaction, typically is 3-4‰ (Vander Zanden and Rasmussen 2001, Post 2002, Carscallen et al. 2012). The rate of enrichment (Δ_n) was set at 3.2‰ per Sweetings et al. (2007). As noted by Cresson et al. (2014), an important assumption when calculating trophic position is the $\delta^{15}\text{N}_{\text{Base}}$ value. Trophic positions were calculated using $\delta^{15}\text{N}$ for the four primary producers as $\delta^{15}\text{N}_{\text{Base}}$: benthic macroalgae, phytoplankton, seagrass, and *Rhizophora mangle* red mangrove. Sea grass habitats north of Government Cut in Miami-Dade County, FL., which includes the location of this study, are limited to the Inter-Coastal Waterway (ICW). The $\delta^{15}\text{N}$ of sea grasses (5.6‰) in the ICW of Broward County, Florida were sourced from a study performed by Gabriel et al. (2015). Red mangrove $\delta^{15}\text{N}$ (2.7 ‰) was sourced from the findings of a study performed in Broward County, Florida by Parks (2013). Macroalgae (2.6‰) was sourced from a study performed in southeast Florida by Behringer and Butler (2006) and phytoplankton (1.8‰) from Rau et al. (1990). The calculated $\delta^{15}\text{N}$ -based trophic positions were compared to trophic positions sourced from FishBase, which were based on prey items sourced from published diet studies (Froese and Pauly 2016).

Data Analysis

Survey and Catch Data: characterization of fish community

The software package PRIMER (version 7.0.9; PRIMER-E, Ltd.; Ivybridge, U.K.) was used to calculate among-site Bray-Curtis fish community similarity indices for both survey and collection data. These were used to establish triangular matrices of fish community similarity. To verify that the fish collections accurately reflected fish community composition and structure at each site, the RELATE procedure in PRIMER was used to statistically compare the structure of the matrices generated using the fish collections and the visual surveys. The test statistic for RELATE is P (rho) which ranges from 0 to 1: if P=1, then the two matrices perfectly overlap, indicating that all fish species are equally abundant; as P approaches 0 the matrices differ, indicating that the fish communities have few to no species in common. This analysis tested whether the species collected at each site reflected the fish assemblage present at each site. The collection

data (with species abundances summed by site) were examined with a Permutational Multivariate Analysis of Variance (PERMANOVA) to compare the extent to which the following factors affected the species composition of sites: *reef type* (natural versus artificial), *distance from shore* (inner versus outer), and the interaction of *reef type* by *distance from shore*. Statistical significance was evaluated at the $\alpha=0.05$ level.

Isotope Data

The General Linear Model procedure in JMP (version 10.0; SAS, Cary NC, USA) was used to examine the dependent responses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of individual muscle tissue samples to the following independent factors: *family* (16 levels, see below), *trophic guild* (five levels), *reef type* (two levels: artificial and natural), *distance from shore* (two levels: inner and outer), and *standard length* (continuous). The factors *family*, *trophic guild*, and *size* were used to test a priori assumptions that these factors influence $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The factors *reef type* and *distances from shore* were used in order to elicit any differences in the trophic dynamics of the artificial reefs against the first and second natural reef tracts.

To further compare the trophic dynamics of the first reef, the second reef, and the artificial reefs, the General Linear Model procedure in JMP (version 10.0; SAS, Cary NC, USA) was used to examine the dependent responses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of individual muscle tissue samples to the following independent factors: *trophic guild*, (four levels), *location* (three levels: first reef, second reef, artificial reef), and the interaction term *trophic guild* by *location*. Samples belonging to the *trophic group planktivore* were not used in this analysis because they were not present at all three locations. For $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, tukey-kramer pairwise comparisons were used to compare each *trophic guild* by *location*, in order to determine which *trophic guilds* were significantly different across the three locations.

Results

Specimen Collection and Survey Data

Collection dives took place on natural sites on July 25, 2014 and August 29 2014 and on artificial sites on July 23, 2014 and August 28, 2014. A total of 43 species of fishes belonging to 17 taxonomic families were sampled, for a total of 258 individual reef fish collected. The Family Haemulidae had the highest number of collected individuals, followed in order by the Families Acanthuridae, Scaridae, Carangidae, Labridae, Pomacentridae, Serranidae, Pomacanthidae, Chaetodontidae, Balistidae, Scorpaenidae, Mullidae, Lutjanidae, Tetraodontidae, Diodontidae, Sparidae, and Ostraciidae (Table 3). By size, the largest species sampled was Almaco Jack *Seriola rivoliana* (Family Carangidae; 38.6 ± 2.54 cm), while the smallest species sampled was Sharpnose Pufferfish *Canthigaster valentini* (Family Tetraodontidae; 6.9 ± 0.92 cm), and the species that exhibited the widest range in length was Stoplight Parrotfish *Sparisoma viride* (Family Scaridae; 13.5 ± 30 cm) (Table 3).

The comparison of the Bray-Curtis similarity matrices of the catch data (Tables 4 and 5) and the survey data (Tables 6 and 7) showed significant correlation ($P=0.568$, $p=0.004$) between the species sampled at each site and those surveyed at each site, confirming that the community structure of the collection data is representative of the community structure of the survey data. Using the collection data, the PERMANOVA test showed that the species composition was significantly influenced by *reef type* (artificial sites versus natural) ($df=1$, Psuedo-F=4.471, $p=0.025$). The species composition of sites was not significantly influenced by *distance from shore* ($df=1$, Psuedo-F=1.881, $p=0.105$); however, as an interaction term (reef type by distance from shore) species composition was significantly influenced ($df=1$, Psuedo-F=3.12528, $p=0.022$). Figure 2 illustrates the relationship between the community structure of the eight study sites and both reef type and distance from shore. Haemulid grunts accounted for the most fish sampled at both natural and artificial sites (Tables 4 and 5). Families Diodontidae, Ostraciidae, and Sparidae were only found and sampled on artificial sites. The Spotted Goatfish *Pseudupeneus maculatus* (Family Mullidae) were only found at natural sites.

Stable Isotope Data

A total of 255 muscle tissue samples from 43 reef-associated fish species were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 8). For all samples, the %C/%N of the sample was assessed (3.2 ± 0.001) and lipid content was found to be too low to bias results (Sweetings et al. 2006). The Shapiro-Wilk test indicated normal distribution for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($\delta^{15}\text{N}$: $p=0.0001$; $\delta^{13}\text{C}$: $p=0.0164$). General Linear Models examining the responses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of individual muscle tissue samples to the three *a priori* independent factors (*trophic guild*, *family*, and *standard length*) were both significant ($\delta^{15}\text{N}$: $R^2=0.762$, $p<0.001$; $\delta^{13}\text{C}$: $R^2=0.593$, $p=0.001$). The factor *family* was significant for both $\delta^{15}\text{N}$ ($df=16$, $F=7.086$, $p<0.001$) and $\delta^{13}\text{C}$ ($df=16$, $F=7.946$, $p<0.001$). Figure 3 illustrates for samples cluster by family, based on the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The factor *trophic guild* was significant for both $\delta^{15}\text{N}$ ($df=4$, $F=6.403$, $p<0.001$) and $\delta^{13}\text{C}$ ($df=4$, $F=17.969$, $p<0.001$). *Standard Length* was not a significant factor for either $\delta^{15}\text{N}$ ($df=1$, $F=3.041$, $p=0.083$) or $\delta^{13}\text{C}$ ($df=1$, $F=0.473$, $p=0.492$). $\delta^{15}\text{N}$ -based trophic position estimates were made using the four food web bases (microalgae, phytoplankton, sea grass, and red mangrove) and compared to reported stomach content based-trophic position (Table 9).

The range of $\delta^{15}\text{N}$ for all muscle tissues was 6.7 to 13.3‰. The *trophic guild herbivore* was the least enriched in $\delta^{15}\text{N}$ (7.98 ‰) followed by *omnivore* (9.3 ‰), *planktivore* (9.3 ‰), *invertivore* (10.5 ‰), and *carnivore* (10.7 ‰). The range of $\delta^{13}\text{C}$ for all muscle tissues was -19.5 to -13.1‰. The trophic guild *planktivore* (-17.6 ‰) was the most depleted in $\delta^{13}\text{C}$ followed by *omnivore* (-17.0 ‰), *herbivore* (-16.5 ‰), *carnivore* (-15.5 ‰), and *invertivore* (-15.1 ‰) (Table 8; Figures 5 and 6).

Habitat Type

General Linear Models examining the responses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of individual muscle tissue samples to the independent factors *reef type* and *distance from shore* were significant factors for $\delta^{13}\text{C}$ (reef type: $df=1$, $F=13.677$, $p=0.001$; distance from shore: $df=1$, $F=14.161$, $p<0.001$) but not for $\delta^{15}\text{N}$ (reef type: $df=1$, $F=0.002$, $p=0.975$; distance to shore: $df=1$, $F=1.888$, $p=0.172$). Muscle tissue samples were regrouped by *location* (first reef, second reef, or artificial reef) and *trophic guild*. General Linear Models

examining the responses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of individual muscle tissue samples to the independent factors *location*, *trophic guild*, and the interaction term *trophic guild* by *location* were significant for both: $\delta^{15}\text{N}$ ($R^2=0.743$ $df=11, 244$, $F=61.2165$, $p<0.001$) and $\delta^{13}\text{C}$ ($R^2=0.403519$, $df=11, 244$, $F= 14.3295$, $p < 0.0001$). For $\delta^{15}\text{N}$, the factors *trophic guild* ($df=3$, $F=158.0593$, $p<0.0001$) *location* ($df=2$, $F=6.6793$, $p= 0.0015$), and *trophic guild* by *location* ($df= 6$, $F=5.6114$, $p< 0.0001$) were significant. For $\delta^{13}\text{C}$, the *trophic guild* ($df=3$, $F=24.1257$, $p<0.0001$) *location* ($df=2$, $F=12.0514$, $p< 0.0001$), and *trophic guild* by *location* ($df= 6$, $F=2.2775$, $p=0.0372$) were significant. The tukey-kramer pairwise comparison found that, for $\delta^{15}\text{N}$, *trophic guild herbivore* was not significantly different between *first and second reef* ($p=0.9986$), *artificial reef and first reef* ($p=0.0.7669$), and between *artificial reef and second reef* ($p=0.0.9999$). *Trophic guild omnivore* was not significantly different between *first and second reef* ($p=0.9997$), *artificial reef and first reef* ($p=1.0000$), and *artificial reef and second reef* ($p=0.9973$). *Trophic guild invertivore* was significantly different between *first and second reef* ($p<0.0001$), *first reef and artificial reef* ($p=0.0007$) and significantly different between *artificial reef and second reef* ($p=0.0467$). *Trophic guild carnivore* was not significantly different between *first and second reef* ($p=0.9286$), *artificial reef and first reef* ($p=0.9978$), and between *artificial reef and second reef* ($p=0.4745$).

The tukey-kramer pairwise comparison found that, for $\delta^{13}\text{C}$, *trophic guild herbivore* was significantly different between *first and second reef* ($p=0.0400$) but not significantly different between *artificial reef and first reef* ($p=0.7008$) and between the *artificial reef and second reef* ($p=0.7898$). *Trophic guild omnivore* was not significantly different between *first and second reef* ($p=0.9947$), *artificial and first reef* ($p=1.0000$), and *artificial and second reef* ($p=0.9989$). *Trophic guild invertivore* was significantly different between *first and second reef* ($p<0.0001$) and between *first reef and artificial reef* ($p<0.0001$) but not significantly different between *artificial and second reef* ($p=0.5422$). *Trophic guild carnivore* was not significantly different between *first and second reef* ($p=0.9996$), *artificial and first reef* ($p=0.1215$), and between *artificial and second reef* ($p=0.9940$).

Table 3. Total number (**N**), mean (\bar{x}) standard length in centimeters \pm Standard Deviation (**SD**) for each species collected for this study. For species where only one individual was sampled, standard deviation was not calculated. The three letter species code used to catalogue each fish species collected is also given.

Family	Species	Common Name	Species Code	N	(\bar{x}) Length \pm SD
Acanthuridae	<i>Acanthurus bahianus</i>	Ocean Surgeonfish	OSF	16	20.9 \pm 3.76
	<i>Acanthurus chirurgus</i>	Doctorfish	DOC	6	25.1 \pm 0.39
	<i>Acanthurus coeruleus</i>	Blue Tang	BTN	8	21.3 \pm 3.49
Balistidae	<i>Balistes capricus</i>	Grey Triggerfish	TRG	8	28.2 \pm 1.15
Carangidae	<i>Carangoides bartholomaei</i>	Yellow Jack	YJK	4	17.5 \pm 1.01
	<i>Caranx crysos</i>	Blue Runner	BLU	4	33.4 \pm 3.20
	<i>Caranx ruber</i>	Bar Jack	BRJ	4	35.3 \pm 0.32
	<i>Seriola rivoliana</i>	Almaco Jack	ACJ	8	38.6 \pm 2.54
Chaetodontidae	<i>Chaetodon capistratus</i>	Foureye Butterflyfish	FBF	2	11.4 \pm 0.99
	<i>Cheatodon sedentarius</i>	Reef Butterflyfish	RBF	7	12.5 \pm 0.89
Diodontidae	<i>Diodon holocanthus</i>	Balloonfish	BFP	2	17.3 \pm 0.35
Haemulidae	<i>Anisotremus virginicus</i>	Porkfish	PGY	11	25.9 \pm 2.56
	<i>Haemulon album</i>	White Margate	MAR	1	28.4
	<i>Haemulon aurolineatum</i>	Tomtate	TMT	24	20.2 \pm 1.58
	<i>Haemulon carbonarium</i>	Caesar Grunt	CSG	2	25.0 \pm 2.33
	<i>Haemulon flavolineatum</i>	French Grunt	FRG	20	21.4 \pm 3.42
	<i>Haemulon parra</i>	Sailors Choice	SLC	4	28.0 \pm 2.85

Table 3. Continued

Family	Species	Common Name	Species Code	N	(\bar{x}) Length \pm SD
Haemulidae	<i>Haemulon plumieri</i>	White Grunt	WTG	9	23.2 \pm 3.06
	<i>Haemulon sciuros</i>	Blue Striped grunt	BSG	11	20.3 \pm 2.15
Labridae	<i>Bodianus rufus</i>	Spanish Hogfish	SHG	3	28.3 \pm 5.86
	<i>Clepticus parrae</i>	Creole Wrasse	CRW	3	18.2 \pm 0.71
	<i>Halichoeres garnoti</i>	Yellowhead Wrasse	YHW	3	12.3 \pm 0.75
	<i>Lachnolaimus maximus</i>	Hogfish	HOG	10	35.3 \pm 4.46
Lutjanidae	<i>Lutjanus griseus</i>	Mangrove Snapper	MGS	3	26.2 \pm 1.33
	<i>Lutjanus synagris</i>	Lane Snapper	LNS	1	25.0
	<i>Ocyurus chrysurus</i>	Yellowtail Snapper	YTS	1	30.0
Mullidae	<i>Pseudupeneus maculatus</i>	Spotted Goatfish	SGF	5	17.8 \pm 2.85
Ostraciidae	<i>Lactophrys triqueter</i>	Smooth Trunkfish	SMT	1	11.0
Pomacentridae	<i>Abudefduf saxatilis</i>	Seargent Major	SGM	5	16.0 \pm 0.82
	<i>Chromis multilineata</i>	Brown Chromis	BRC	7	14.2 \pm 0.71
	<i>Stegastes partitus</i>	Bicolor Damsel fish	BCD	5	6.1 \pm 0.87
Pomacanthidae	<i>Holacanthus ciliaris</i>	Queen Angelfish	QUA	1	36.5
	<i>Holacanthus tricolor</i>	Rock Beauty	RKB	3	16.1 \pm 2.40
	<i>Pomacanthus paru</i>	French Angelfish	FAF	5	30.6 \pm 4.58

Table 3. Continued

Family	Species	Common Name	Species Code	N	(\bar{x}) Length \pm SD
Scaridae	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	RBP	12	15.0 \pm 3.52
	<i>Sparisoma chrysopterum</i>	Redtail Parrotfish	RTP	3	23.5 \pm 1.52
	<i>Sparisoma viride</i>	Stoplight Parrotfish	SLP	8	27.9 \pm 8.03
Scorpaenidae	<i>Pterios volitans</i>	Red Lionfish	LNF	7	20.1 \pm 2.13
Serranidae	<i>Cephalopholis cruenata</i>	Graysby	GBY	11	25.1 \pm 3.01
	<i>Hypoplectrus unicolor</i>	Butter Hamlet	BTH	2	12.7 \pm 0.71
Sparidae	<i>Calamus proridens</i>	Littlehead Porgy	LHP	1	31.3
Tetraodontidae	<i>Sphoeroides spengleri</i>	Bandtail Puffer	BTP	1	10.7
	<i>Canthigaster valentini</i>	Sharpnose Puffer	SHP	2	6.9 \pm 0.92

Table 4: Total number of specimens collected during sampling events conducted on all artificial reef sites by family, species, and study site.

Family	Species	Common Name	Site				Total
			3A	6A	1A	5B	
Acanthuridae	<i>Acanthurus coeruleus</i>	Blue Tang	4	0	0	1	5
	<i>Acanthurus chirurgus</i>	Doctorfish	2	0	2	1	5
	<i>Acanthurus bahianus</i>	Ocean Surgeonfish	1	0	4	3	8
Balistidae	<i>Balistes capricus</i>	Grey Triggerfish	5	0	0	0	5
Carangidae	<i>Seriola rivoliana</i>	Almaco Jack	4	0	2	1	7
	<i>Caranx crysos</i>	Blue Runner	3	0	0	0	3
	<i>Caranx ruber</i>	Bar Jack	2	0	0	0	2
	<i>Carangoides bartholomaei</i>	Yellow Jack	1	0	2	1	4
Chaetodontidae	<i>Cheatodon sedentarius</i>	Reef Butterflyfish	0	0	1	1	2
Diodontidae	<i>Diodon holocanthus</i>	Balloonfish	0	0	0	2	2
Haemulidae	<i>Haemulon sciuros</i>	Blue Striped Grunt	0	0	0	8	8
	<i>Haemulon carbonarium</i>	Caesar Grunt	0	0	0	3	3
	<i>Haemulon flavolineatum</i>	French Grunt	0	0	1	1	2
	<i>Haemulon album</i>	White Margate	1	0	1	3	1
	<i>Anisotremus virginicus</i>	Porkfish	4	2	2	1	9
	<i>Haemulon parra</i>	Sailors Choice	1	0	1	3	2
	<i>Haemulon aurolineatum</i>	Tomtate	3	1	10	10	24
	<i>Haemulon plumieri</i>	White Grunt	1	0	1	3	5

Table 4. Continued.

Family	Species	Common Name	Site				Total
			3A	6A	1A	5B	
Labridae	<i>Clepticus parrae</i>	Creole Wrasse	0	0	0	3	3
	<i>Lachnolaimus maximus</i>	Hogfish	1	0	1	3	5
Lutjanidae	<i>Lutjanus synagris</i>	Lane Snapper	1	0	0	0	1
	<i>Lutjanus griseus</i>	Mangrove Snapper	1	2	0	0	3
Pomacanthidae	<i>Holacanthus tricolor</i>	Rock Beauty	0	0	1	0	1
Pomacentridae	<i>Stegastes partitus</i>	Bicolor Damselfish	0	2	3	0	5
	<i>Chromis multilineata</i>	Brown Chromis	0	0	4	0	4
	<i>Abudefduf saxatilis</i>	Sergeant Major	0	0	1	2	3
Scaridae	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	0	1	0	1	2
	<i>Sparisoma chrysopterum</i>	Redtail Parrotfish	0	0	0	2	2
Scorpaenidae	<i>Pterios volitans</i>	Red Lionfish	3	1	0	2	6
Serranidae	<i>Cephalopholis cruenata</i>	Graysby	0	0	1	2	3
Sparidae	<i>Calamus proridens</i>	Littlehead Porgy	1	0	0	0	1
Tetraodontidae	<i>Canthigaster valentini</i>	Sharpnose Puffer	2	0	0	0	2

Table 5: Total number of specimens collected during sampling events conducted on natural reef sites by family, species, and study site.

Family	Species	Common Name	Site				Total
			3AN	6AN	1AN	5BN	
Acanthuridae	<i>Acanthurus bahianus</i>	Ocean Surgeonfish	4	2	2	0	8
	<i>Acanthurus coeruleus</i>	Blue Tang	0	1	1	1	3
	<i>Acanthurus chirurgus</i>	Doctorfish	0	0	1	0	1
Balistidae	<i>Balistes capricus</i>	Grey Triggerfish	0	0	2	1	3
Carangidae	<i>Seriola rivoliana</i>	Almaco Jack	0	0	0	1	1
	<i>Caranx crysos</i>	Blue Runner	0	0	0	1	1
	<i>Caranx ruber</i>	Bar Jack	2	0	0	0	2
	<i>Carangoides bartholomaei</i>	Yellow Jack	0	0	1	0	1
Chaetodontidae	<i>Chaetodon capistratus</i>	Four eye Butterflyfish	1	0	0	1	2
	<i>Cheatodon sedentarius</i>	Reef Butterfly	0	2	0	3	5
Haemulidae	<i>Haemulon sciuros</i>	Blue Striped Grunt	1	2	0	0	3
	<i>Haemulon flavolineatum</i>	French Grunt	11	7	0	0	18
	<i>Anisotremus virginicus</i>	Porkfish	0	2	0	0	2
	<i>Haemulon parra</i>	Sailors Choice	0	1	0	0	1
	<i>Haemulon plumieri</i>	White Grunt	1	2	0	1	4

Table 5. Continued.

Family	Species	Common Name	Site				Total
			3AN	6AN	1AN	5BN	
Labridae	<i>Lachnolaimus maximus</i>	Hogfish	0	0	2	3	5
	<i>Bodianus rufus</i>	Spanish Hogfish	2	1	0	0	3
	<i>Halichoeres garnoti</i>	Yellowhead Wrasse	1	0	1	1	3
Lutjanidae	<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0	1	0	0	1
Mullidae	<i>Pseudupeneus maculatus</i>	Spotted Goatfish	3	1	1	0	5
Ostraciidae	<i>Lactophrys triqueter</i>	Smooth Trunkfish	0	1	0	0	1
Pomacanthidae	<i>Pomacanthus paru</i>	French Angelfish	1	0	1	3	5
	<i>Holacanthus ciliaris</i>	Queen Angelfish	0	0	0	1	1
	<i>Holacanthus tricolor</i>	Rock Beauty	0	0	1	1	2
Pomacentridae	<i>Chromis multilineata</i>	Brown Chromis	0	3	0	0	3
	<i>Abudefduf saxatilis</i>	Sergeant Major	0	2	0	0	2
Scaridae	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	3	3	2	2	10
	<i>Sparisoma chrysopterum</i>	Redtail Parrotfish	0	0	1	0	1
	<i>Sparisoma viride</i>	Stoplight Parrot	3	2	3	0	8
Scorpaenidae	<i>Pterios volitans</i>	Red Lionfish	0	1	0	0	1
Serranidae	<i>Hypoplectrus unicolor</i>	Butter Hamlet	2	0	0	0	2
	<i>Cephalopholis cruenata</i>	Graysby	4	2	0	2	8
Tetraodontidae	<i>Sphoeroides spengleri</i>	Bandtail Puffer	0	0	0	1	1

Table 6. Results of fish surveys conducted on artificial reef sites for this study. Density scores are listed for each species surveyed at each artificial site.

Family	Species	Common Name	Site			
			3A	6A	1A	5B
Acanthuridae	<i>Acanthurus coeruleus</i>	Blue Tang	2	2	1.5	2.5
	<i>Acanthurus chirurgus</i>	Doctorfish	2	2	0	3
	<i>Acanthurus bahianus</i>	Ocean Surgeonfish	2.5	2	2	2.5
Balistidae	<i>Balistes capricus</i>	Grey Triggerfish	2	0	0	0
Carangidae	<i>Almaco Jack</i>	Almaco Jack	1.5	0	1	2
	<i>Caranx ruber</i>	Bar Jack	2	0	2	0
	<i>Caranx crysos</i>	Blue Runner	3	0	0	0
	<i>Seriola dumerili</i>	Greater Amberjack	0	2	0	0
	<i>Carangoides bartholomaei</i>	Yellow Jack	3	0	0	0
Chaetodontidae	<i>Cheatodon sedentarius</i>	Reef Butterflyfish	2	0	0	2
	<i>Chaetodon striatus</i>	Banded Butterflyfish	0	0	2	0
Diodontidae	<i>Diodon holocanthus</i>	Balloonfish	0	1	0	0
Gobiidae	<i>Coryphopterus glaucofraenum</i>	Bridled Goby	0	0	1	2
	<i>Coryphopterus hyalinus</i>	Glass Goby	0	3	0	3
	<i>Elacatinus oceanops</i>	Neon Goby	0	0	0	1
Haemulidae	<i>Haemulon sciuros</i>	Bluestriped grunt	3	1	2	3
	<i>Haemulon melanurum</i>	Cottonwick	0	3	0	3
	<i>Haemulon flavolineatum</i>	French Grunt	2	2	2.5	3

Table 6. Continued.

Family	Species	Common Name	Site			
			3A	6A	1A	5B
Haemulidae	<i>Haemulon</i> sp.	unidentified grunts	0	4	0	4
	<i>Anisotremus virginicus</i>	Porkfish	2	3	2	2
	<i>Haemulon parra</i>	Sailors Choice	2	3	0	0
	<i>Haemulon aurolineatum</i>	Tomtate	4	4	4	4
	<i>Haemulon plumieri</i>	White Grunt	0	2	2	2
	<i>Haemulon album</i>	White Margate	1	2	0	2
Holocentridae	<i>Myripristis jacobus</i>	Blackbar Soldierfish	0	2	0	0
Labridae	<i>Thalassoma amblycephalum</i>	Bluehead Wrasse	2	4	3	3
	<i>Halichoeres maculipinna</i>	Clown Wrasse	0	0	0	3
	<i>Clepticus parrae</i>	Creole Wrasse	2	0	0	0
	<i>Lachnolaimus maximus</i>	Hogfish	1	0	0	2
	<i>Halichoeres radiatus</i>	Puddingwife	0	0	0	1
	<i>Halichoeres bivittatus</i>	Slippery Dick	3	3	2	2.5
	<i>Bodianus rufus</i>	Spanish Hogfish	3	1	0	1
	<i>Halichoeres garnoti</i>	Yellowhead Wrasse	2	2	2	1.5
Labrisomidae	<i>Malacoctenus triangulatus</i>	Saddled Blenny	0	0	0	1
Lutjanidae	<i>Lutjanus buccanella</i>	Blackfin Snapper	0	0	0	1
	<i>Lutjanus synagris</i>	Lane Snapper	0	3	0	0
	<i>Ocyurus chrysurus</i>	Yellowtail Snapper	0	1	0	0

Table 6. Continued.

Family	Species	Common Name	Site			
			3A	6A	1A	5B
Lutjanidae	<i>Lutjanus griseus</i>	Mangrove Snapper	1	2	0	0
Monacanthidae	<i>Cantherhines pullus</i>	Orangespotted Filefish	0	0	0	1
Mullidae	<i>Pseudupeneus maculatus</i>	Spotted Goatfish	2	2	2	2.5
	<i>Mulloidichthys martinicus</i>	Yellow Goatfish	0	2	2	0
Ostraciidae	<i>Acanthostracion polygonius</i>	Honeycomb Cowfish	0	0	0	1
	<i>Lactophrys triqueter</i>	Smooth Trunkfish	0	0	0	0
	<i>Lactophrys bicaudalis</i>	Spotted Trunkfish	0	0	0	1
Pomacanthidae	<i>Holacanthus ciliaris</i>	Queen Angelfish	0	1	1	2
	<i>Holacanthus tricolor</i>	Rock Beauty	0	0	2	1
Pomacentridae	<i>Stegastes leucostictus</i>	Beaugregory	1	2	0	0
	<i>Stegastes partitus</i>	Bicolor Damselfish	1.5	3	2.5	2
	<i>Chromis cyanea</i>	Blue Chromis	3	2	2	2
Pomacentridae	<i>Chromis multilineata</i>	Brown Chromis	2.5	0	2	3
	<i>Stegastes adustus</i>	Dusky Damselfish	0	2	2.5	2
	<i>Chromis scotti</i>	Purple Reeffish	0	3	2	3
	<i>Abudefduf saxatilis</i>	Sergeant Major	2	0	2	2
	<i>Stegastes variabilis</i>	Cocoa Damselfish	0	0	0	2
Scaridae	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	2	2	2	2
	<i>Sparisoma chrysopteron</i>	Redtail Parrotfish	0	0	1	0

Table 6. Continued.

Family	Species	Common Name	Site			
			3A	6A	1A	5B
Scaridae	<i>Sparisoma viride</i>	Stoplight Parrotfish	0	1	0	2
	<i>Sparisoma rubripinne</i>	Yellowtail Parrotfish	0	1	0	1.5
	<i>Scarus iseri</i>	Striped Parrotfish	0	0	0	2
Scorpaenidae	<i>Pterios volitans</i>	Red Lionfish	2	2	1	0
Serranidae	<i>Pomacanthus arcuatus</i>	Gray Angelfish	0	0	1	2
	<i>Cephalopholis cruenata</i>	Graysby	2	0	1.5	2
	<i>Serranus tigrinus</i>	Harlequin Bass	0	1	2	0
Sparidae	<i>Calamus proridens</i>	Littlehead Porgy	0	1	0	0
	<i>Calamus calamus</i>	Saucereye Porgy	0	0	0	1
Synodontidae	<i>Synodus intermedius</i>	Sand Diver	0	1	0	0
Tetraodontidae	<i>Canthigaster valentini</i>	Sharpnose Puffer	2	3	2.5	2.5

Table 7. Results of fish surveys conducted on natural reef sites for this study. Density scores are listed for each species surveyed at each natural reef site.

Family	Species	Common Name	Site			
			3AN	6AN	1AN	5BN
Acanthuridae	<i>Acanthurus coeruleus</i>	Blue Tang	3	2	2	2
	<i>Acanthurus chirurgus</i>	Doctorfish	0	0	2	2
	<i>Acanthurus bahianus</i>	Ocean Surgeonfish	3	2	2	3
Ballistidae	<i>Cephalopholis cruenata</i>	Graysby	0	0	0	3
Carangidae	<i>Caranx crysos</i>	Blue Runner	0	0	0	3
Chaetodontidae	<i>Chaetodon capistratus</i>	Foureye Butterflyfish	2	2	0	2
	<i>Cheatodon sedentarius</i>	Reef Butterflyfish	2	2	2	3
	<i>Chaetodon ocellatus</i>	Spotfin Butterflyfish	2	0	0	2
Ephippidae	<i>Chaetodipterus faber</i>	Atlantic Spadefish	3	0	0	0
Gobiidae	<i>Coryphopterus glaucofraenum</i>	Bridled Goby	3	2	2	3
	<i>Coryphopterus hyalinus</i>	Glass Goby	4	4	4	4
	<i>Elacatinus oceanops</i>	Neon Goby	2	2	0	2
	<i>Gnatholepis thompsoni</i>	Goldspot Goby	0	2	0	3
	<i>Ptereleotris helenae</i>	Hovering Goby	0	0	0	2
Haemulidae	<i>Haemulon sciuros</i>	Bluestriped Grunt	1	0	1	0
	<i>Haemulon carbonarium</i>	Caesar Grunt	2	0	0	0
	<i>Haemulon melanurum</i>	Cottonwick	0	0	0	0
	<i>Haemulon flavolineatum</i>	French Grunt	0	2	1	0

Table 7. Continued.

Family	Species	Common Name	Site			
			3AN	6AN	1AN	5BN
Haemulidae	<i>Haemulon</i> sp.	unidentified grunts	3	0	0	0
	<i>Anisotremus virginicus</i>	Porkfish	0	0	0	1
	<i>Haemulon parra</i>	Sailors choice	1	0	0	0
	<i>Haemulon plumieri</i>	White Grunt	2	1	0	1
	<i>Anisotremus surinamensis</i>	Black Margate	1	1	1	0
Kyphosidae	<i>Kyphosus sectatrix</i>	Bermuda Chub	3	1	0	0
Labridae	<i>Thalassoma amblycephalum</i>	Bluehead Wrasse	3	3	3	3
	<i>Halichoeres maculipinna</i>	Clown Wrasse	3	2	0	2
	<i>Clepticus parrae</i>	Creole Wrasse	2	3	0	0
	<i>Lachnolaimus maximus</i>	Hogfish	0	0	0	1
	<i>Halichoeres bivittatus</i>	Slippery Dick	1	2	0	2
	<i>Bodianus rufus</i>	Spanish Hogfish	1	1	0	0
	<i>Halichoeres garnoti</i>	Yellowhead Wrasse	4	3	2.5	3
	<i>Halichoeres poeyi</i>	Blackear Wrasse	2	0	0	0
Labrisomidae	<i>Malacoctenus triangulatus</i>	Saddled Blenny	1	0	0	0
Lutjanidae	<i>Balistes capricus</i>	Grey Triggerfish	0	0	2	3
	<i>Ocyurus chrysurus</i>	Yellowtail Snapper	2	0	0	0
	<i>Lutjanus griseus</i>	Mangrove Snapper	2	1	0	0
Monacanthidae	<i>Cantherhines pullus</i>	Orangespotted Filefish	2	0	0	0

Table 7. Continued.

Family	Species	Common Name	Site			
			3AN	6AN	1AN	5BN
Monacanthidae	<i>Stephanolepis hispidus</i>	Planehead Filefish	0	0	1	0
	<i>Aluterus monoceros</i>	Unicorn Filefish	0	0	0	2
Mullidae	<i>Pseudupeneus maculatus</i>	Spotted Goatfish	2	2	0	0
	<i>Mulloidichthys martinicus</i>	Yellow Goatfish	0	2	0	2
Ostraciidae	<i>Acanthostracion polygonius</i>	Honeycomb Cowfish	0	1	1	0
Pomacanthidae	<i>Pomacanthus paru</i>	French Angelfish	3	2	0	2
	<i>Holacanthus ciliaris</i>	Queen Angelfish	0	0	0	1
	<i>Holacanthus tricolor</i>	Rock Beauty	0	1	2	2
	<i>Holacanthus bermudensis</i>	Blue Angelfish	0	0	0	1
Pomacentridae	<i>Stegastes leucostictus</i>	Beaugregory	1	0	0	0
	<i>Stegastes partitus</i>	Bicolor Damsel	4	4	3.5	4
	<i>Chromis cyanea</i>	Blue Chromis	3	2	2	0
	<i>Chromis multilineata</i>	Brown Chromis	2	3	0	0
	<i>Stegastes adustus</i>	Dusky Damsel	1	0	0	0
	<i>Chromis scotti</i>	Purple Reef	1	0	0	0
	<i>Abudefduf saxatilis</i>	Sergeant Major	3	2	0	0
	<i>Stegastes variabilis</i>	Cocoa Damsel	2	2	1	0
	<i>Stegastes diencaeus</i>	Longfin Damsel	2	2	0	0
	<i>Microspathodon chrysurus</i>	Yellowtail Damsel	2	0	0	0

Table 7. Continued.

Family	Species	Common Name	Site			
			3AN	6AN	1AN	5BN
Scaridae	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	3	3	2	3
	<i>Sparisoma viride</i>	Stoplight Parrotfish	3	2	0	2
	<i>Sparisoma radians</i>	Bucktooth Parrotfish	2	0	0	2
	<i>Sparisoma atomarium</i>	Greenblotch Parrotfish	3	0	0	3
	<i>Scarus taeniopterus</i>	Princess Parrotfish	0	1	1	0
	<i>Scarus iseri</i>	Striped Parrotfish	3	0	0	2
Serranidae	<i>Butter Hamlet</i>	Butter Hamlet	2	1	0	0
	<i>Pomacanthus arcuatus</i>	Gray Angelfish	0	0	2	2
	<i>Serranus tigrinus</i>	Harlequin Bass	2	1.5	0	2
	<i>Hypoplectrus gemma</i>	Blue Hamlet	1	0	0	0
	<i>Rypticus saponaceus</i>	Greater Soapfish	0	0	1	0
	<i>Serranus baldwini</i>	Lantern Bass	0	0	0	1
	<i>Serranus tabacarius</i>	Tobaccofish	0	2	1	2
Synodontidae	<i>Synodus intermedius</i>	Sand Diver	1	1	0	0
Tetraodontidae	<i>Sphoeroides spengleri</i>	Bandtail Puffer	0	2	1	2
	<i>Canthigaster valentini</i>	Sharpnose Puffer	2	2	1.5	2

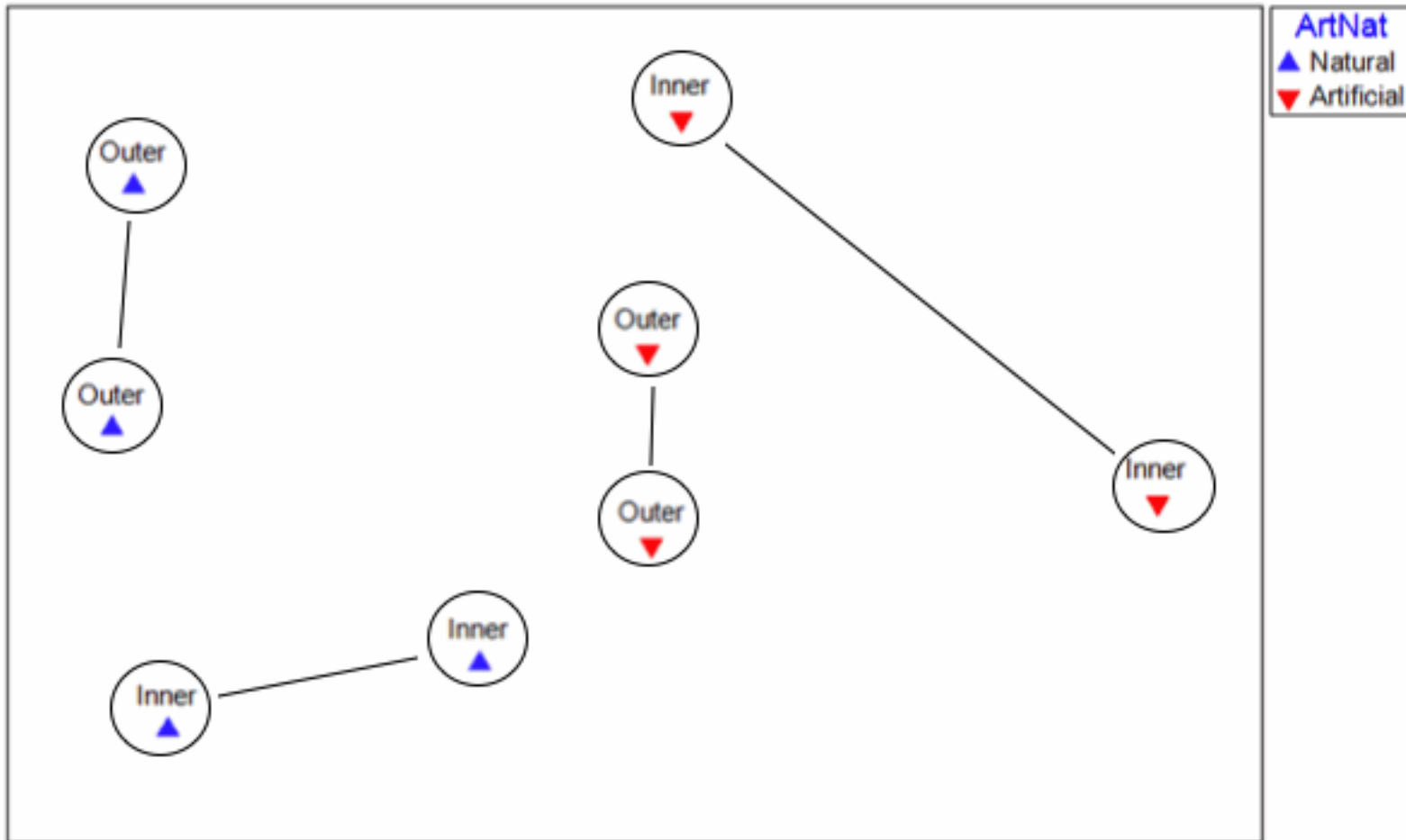


Figure 2. Two-dimensional non-metric multidimensional scaling graph, highlighting the difference between artificial and natural reef fish communities. Circled within the graph are the sites grouped by the interaction term *distance from shore* illustrating that within each reef type, sites group differently based on the interaction term.

Table 8. Species, trophic code (TC), total numbers (N), mean (\bar{x}), standard deviation (SD) and range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. For species where only one individual was sampled, standard deviation was not calculated and the range is listed as not available (n/a).

Trophic Guild	Family	Species	TC	$\delta^{15}\text{N}$ Muscle Data		$\delta^{13}\text{C}$ Muscle Data	
				$\bar{x} \pm \text{SD}$ (‰)	Range (%)	$\bar{x} \pm \text{SD}$ (‰)	Range (%)
Herbivore	Acanthuridae	Ocean surgeonfish	H ₁	8.1 \pm 0.43	7.3 to 8.9	-16.8 \pm 0.46	-17.5 to -15.7
		Doctorfish	H ₂	8.6 \pm 0.27	8.2 to 8.8	-17 \pm 0.70	-17.9 to -15.9
		Blue tang	H ₃	8.0 \pm 0.48	7.5 to 8.4	-17.6 \pm 1.12	-18.8 to -15.4
	Scaridae	Redband Parrotfish	H ₄	7.9 \pm 0.57	7.2 to 8.7	-16.8 \pm 0.97	-17.9 to -15.4
		Redtail Parrotfish	H ₅	8.0 \pm 0.19	7.9 to 8.2	-17.2 \pm 0.67	-17.9 to -16.5
		Stoplight Parrotfish	H ₆	7.3 \pm 0.60	6.7 to 8.4	-15.4 \pm 0.55	-16.0 to -14.7
	Pomacentridae	Bi-Color Damselfish	H ₇	7.2 \pm 0.30	6.8 to 7.5	-14.1 \pm 0.27	-14.5 to -13.7
Omnivore	Tetraodontidae	Sharpnose Puffer	O ₁	9.3 \pm 0.12	9.2 to 9.4	-16.9 \pm 0.1	-17.0 to -16.9
	Pomacanthidae	Queen Angelfish	O ₂	8.6	n/a	-16.6	n/a
		Rock Beauty	O ₃	10.0 \pm 0.69	9.3 to 10.7	-17.5 \pm 0.37	-17.8 to -17.1
		French Angelfish	O ₄	9.0 \pm 0.25	8.7 to 9.2	-17.6 \pm 0.71	-18.5 to -16.6
	Ostraciidae	Smooth Trunkfish	O ₅	10.0	n/a	-14.9	n/a
	Pomacentridae	Sergeant Major	O ₆	9.3 \pm 0.08	9.2 to 9.4	-16.6 \pm 0.6	-17.3 to -16.0
Planktivore	Labridae	Creole Wrasse	P1	9.1 \pm 0.04	9.0 to 9.1	-17.5 \pm 0.28	-17.5 to -17.2
	Pomacentridae	Brown Chromis	P2	9.5 \pm 0.22	9.2 to 9.8	-17.6 \pm 0.53	-18.3 to -17.4
Invertivore	Chaetodontidae	Foureye Butterflyfish	I1	10.2 \pm 0.53	9.8 to 10.5	-15.3 \pm 0.94	-16.0 to -14.6
		Reef Butterflyfish	I2	10.2 \pm 0.45	9.2 to 10.5	-16.3 \pm 0.38	-16.8 to -15.7

Table 8. Continued

TG	Family	Species	TC	$\delta^{15}\text{N}$ Muscle Data		$\delta^{13}\text{C}$ Muscle Data	
				$\bar{x} \pm \text{SD}$ (‰)	Range (‰)	$\bar{x} \pm \text{SD}$ (‰)	Range (‰)
Invertivore	Diodontidae	Balloonfish	I3	9.7 \pm 0.27	9.5 to 9.9	-15.9 \pm 0.39	-16.2 to -15.6
	Haemulidae	Porkfish	I4	10.7 \pm 0.71	9.7 to 12.6	-15.2 \pm 0.58	-15.9 to -14.1
		White Margate	I5	9.9	n/a	-14.8	n/a
		Tomtate	I6	10.5 \pm 0.32	9.8 to 11.1	-15.2 \pm 0.48	-16.4 to -14.2
		Caesar Grunt	I7	11.3 \pm 0.21	11.1 to 11.4	-13.8 \pm 0.03	-13.8 to -13.7
		French Grunt	I8	11.2 \pm 0.30	10.4 to 11.6	-13.7 \pm 0.42	-15.1 to -13.2
	Balistidae	Grey Triggerfish	I9	9.2 \pm 0.27	8.8 to 9.8	-17 \pm 0.76	-17.8 to -15.3
	Labridae	Spanish Hogfish	I10	11 \pm 0.18	10.8 to 11.2	-15.3 \pm 0.21	-15.4 to -15.0
		Yellowhead Wrasse	I11	9.4 \pm 0.11	9.4 to 9.6	-15.6 \pm 0.60	-16.0 to -15.0
		Hogfish	I12	9.9 \pm 0.49	9.0 to 10.7	-15.2 \pm 0.53	-16.5 to -14.7
	Sparidae	Littlehead Porgy	I13	10.2	n/a	-13.7	n/a
	Tetraodontidae	Bandtail Puffer	I14	9.8	n/a	-15.4	n/a

Table 8. Continued

TG	Family	Species	TC	$\delta^{15}\text{N}$ Muscle Data		$\delta^{13}\text{C}$ Muscle	
				$\bar{x} \pm \text{SD}$ (‰)	Range (‰)	$\bar{x} \pm \text{SD}$ (‰)	Range (‰)
Carnivore	Carangidae	Yellow Jack	C1	10.7 \pm 0.41	10.0 to 11.1	-14.7 \pm 0.80	-13.3 to -15.2
		Blue Runner	C2	11.0 \pm 0.83	10.3 to 11.9	-16.5 \pm 0.46	-17.0 to -15.9
		Bar Jack	C3	9.2 \pm 1.29	7.6 to 10.7	-17.5 \pm 1.32	-19.2 to -16.3
		Almaco Jack	C4	9.8 \pm 0.61	8.8 to 10.5	-16.3 \pm 0.81	-17.2 to -14.6
	Haemulidae	Sailors choice	C5	10.9 \pm 0.21	10.8 to 11.0	-14.3 \pm 0.90	-15.2 to -13.2
		White Grunt	C6	11.2 \pm 0.34	10.7 to 11.8	-15.2 \pm 1.23	-16.8 to -13.1
		Bluestriped grunt	C7	11.8 \pm 1.13	10.1 to 13.4	-16.7 \pm 1.92	-19.5 to -13.4
	Lutjanidae	Mangrove Snapper	C8	11.1 \pm 1.13	10.0 to 12.3	-14.2 \pm 0.82	-14.8 to -13.3
		Lane Snapper	C9	11.1	n/a	-14.0	n/a
		Yellowtail Snapper	C10	10.0	n/a	-16.5	n/a
	Mullidae	Spotted Goatfish	C11	9.4 \pm 0.27	9.1 to 9.7	-14.2 \pm 0.31	-14.5 to 13.7
	Scorpaenidae	Red Lionfish	C12	10.6 \pm 0.30	10.2 to 11.1	-15.7 \pm 0.83	-16.6 to 15.0
	Serranidae	Graysby	C13	11.1 \pm 0.53	10.2 to 11.9	-15.4 \pm 0.52	-16.3 to -14.8
		Butter Hamlet	C14	10.5 \pm 0.30	10.3 to 10.7	-14.4 \pm 0.17	-14.5 to -14.3

Table 9. Calculated $\delta^{15}\text{N}$ -based trophic position estimates for each species, listed by trophic guild, using benthic macroalgae (Macro algae), phytoplankton, seagrass, and red mangrove (Mangrove) as the exclusive food web base for that species. Also listed are the stomach content-based trophic position estimates reported by FishBase (Froese and Pauly 2016).

TG	Common Name	TC	Micro algae	Phytoplankton	Seagrass	Mangrove	Stomach Contents
Herbivore	Ocean Surgeonfish	H1	2.7	3.0	1.8	2.7	2
	Doctorfish	H2	2.9	3.1	1.9	2.8	2
	Blue Tang	H3	2.7	2.9	1.7	2.6	2
	Redband Parrotfish	H4	2.7	3.0	1.8	2.7	2
	Redtail Parrotfish	H5	2.7	2.9	1.8	2.6	2
	Stoplight Parrotfish	H6	2.5	2.7	1.5	2.4	2
	Bi-Color Damsel	H7	2.6	2.9	1.7	2.6	2
Omnivore	Sharpnose Puffer	O1	3.1	3.3	2.2	3.0	3.3
	Queen Angelfish	O2	2.9	3.1	1.9	2.8	3
	Rock Beauty	O3	3.3	3.6	2.4	3.3	3
	French Angelfish	O4	2.7	3.0	1.8	2.7	3.1
	Smooth Trunkfish	O5	3.3	3.6	2.4	3.2	3.3
	Sergeant Major	O6	3.1	3.3	2.1	3.0	3.8
Planktivore	Creole Wrasse	P1	3.2	3.4	2.2	3.1	3.7
	Brown Chromis	P2	2.7	3.0	1.8	2.7	3.0
Invertivore	Foureye Butterflyfish	I1	3.4	3.6	2.4	3.3	3.4
	Reef Butterflyfish	I2	3.4	3.6	2.4	3.3	3.9

Table 9. Continued.

TG	Common Name	TC	Macro algae	Phytoplankton	Seagrass	Mangrove	Stomach Contents
Invertivore	Balloonfish	I3	3.2	3.5	2.3	3.2	3.3
	Porkfish	I4	3.5	3.8	2.6	3.5	3.6
	White Margate	I5	3.3	3.5	2.3	3.2	3.3
	Tomtate	I6	3.5	3.7	2.5	3.4	4.4
	Ceasar Grunt	I7	3.7	4.0	2.8	3.7	3.7
	French Grunt	I8	3.7	3.9	2.8	3.6	3.4
	Spanish Hogfish	I10	3.6	3.9	2.7	3.6	3.7
	Yellowhead wrasse	I11	3.1	3.4	2.2	3.1	3.7
	Hogfish	I12	3.3	3.5	2.3	3.2	4.2
	Littlehead Porgy	I13	3.4	3.6	2.4	3.3	3.4
	BandTail Puffer	I14	3.3	3.5	2.3	3.2	3.5
	Tomtate	I6	3.5	3.7	2.5	3.4	4.4
	Ceasar Grunt	I7	3.7	4.0	2.8	3.7	3.7
	French Grunt	I8	3.7	3.9	2.8	3.6	3.4
	Grey Triggerfish	I9	3.1	3.3	2.1	3.0	4.1
	Spanish Hogfish	I10	3.6	3.9	2.7	3.6	3.7
	Yellowhead wrasse	I11	3.1	3.4	2.2	3.1	3.7
Hogfish	I12	3.3	3.5	2.3	3.2	4.2	

Table 9. Continued.

TG	Common Name	TC	Macro algae	Phytoplankton	Sea grass	Mangrove	Stomach Contents
Invertivore	Littlehead Porgy	I13	3.4	3.6	2.4	3.3	3.4
	BandTail Puffer	I14	3.3	3.5	2.3	3.2	3.5
Carnivore	Yellow Jack	C1	3.5	3.8	2.6	3.5	4.5
	Blue Runner	C2	3.6	3.9	2.7	3.6	3.6
	Bar Jack	C3	3.1	3.3	2.1	3.0	3.8
	Almaco Jack	C4	3.3	3.5	2.3	3.2	4.5
	Sailors Choice	C5	3.6	3.8	2.7	3.5	3.5
	White Grunt	C6	3.7	3.9	2.8	3.6	3.8
	Bluestriped Grunt	C7	3.8	4.0	2.8	3.7	3.5
	Mangrove Snapper	C8	3.7	3.9	2.7	3.6	4.2
	Lane Snapper	C9	3.7	3.9	2.7	3.6	3.8
	Yellowtail Snapper	C10	3.3	3.6	2.4	3.3	4
	Spotted Goatfish	C11	3.1	3.4	2.2	3.1	3.7
	Red Lionfish	C12	3.5	3.8	2.6	3.4	4.4
	Graysby	C13	3.7	3.9	2.7	3.6	4.3
Butter Hamlet	C14	3.5	3.7	2.5	3.4	4	

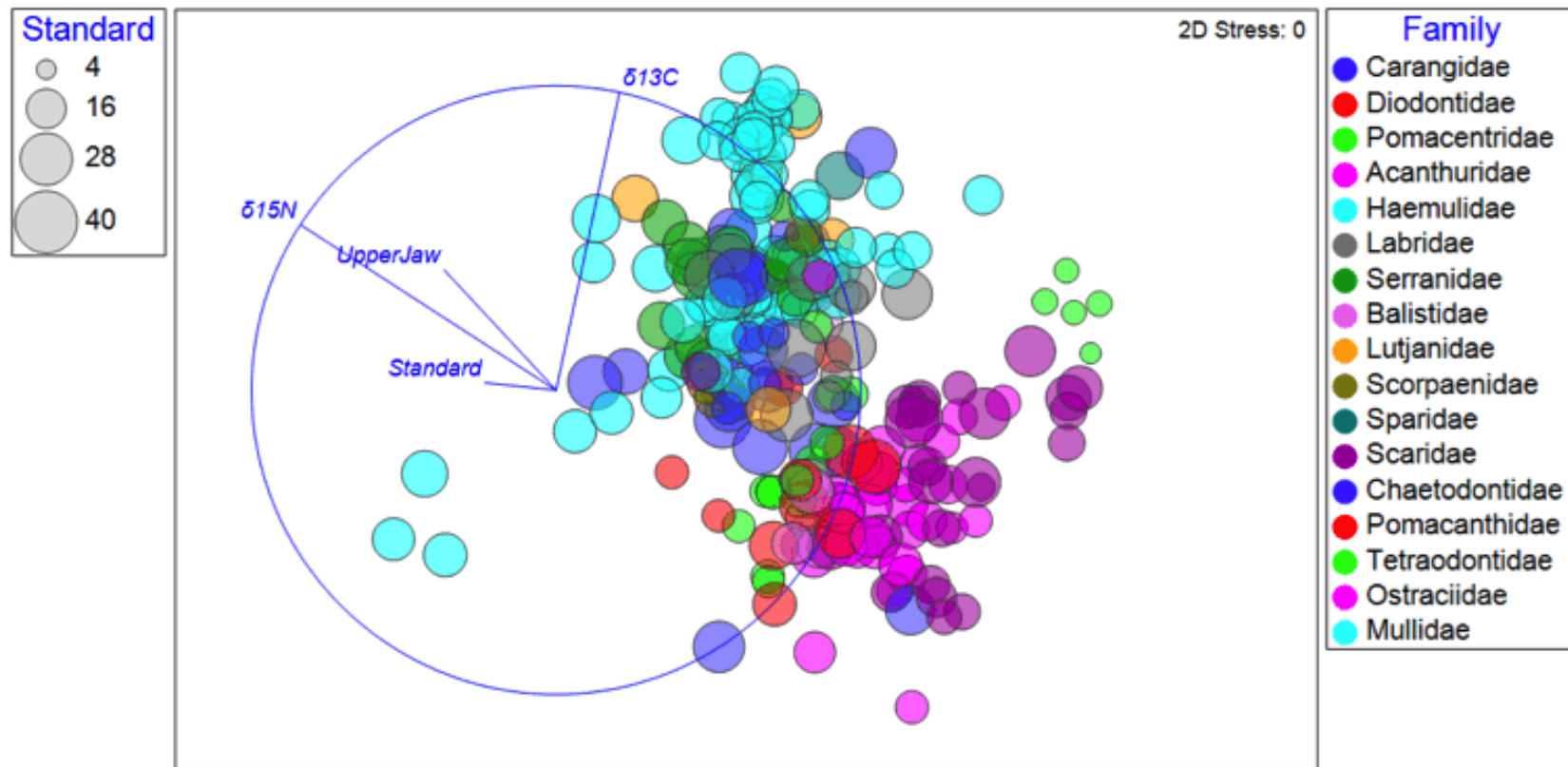


Figure 3. Non-metric multidimensional scaling graph highlighting how the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of samples cluster by taxonomic family. Note also that the vectors show correlation between fish size and $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$. Probably should mention that these are Spearman correlation vectors, that the bubbles

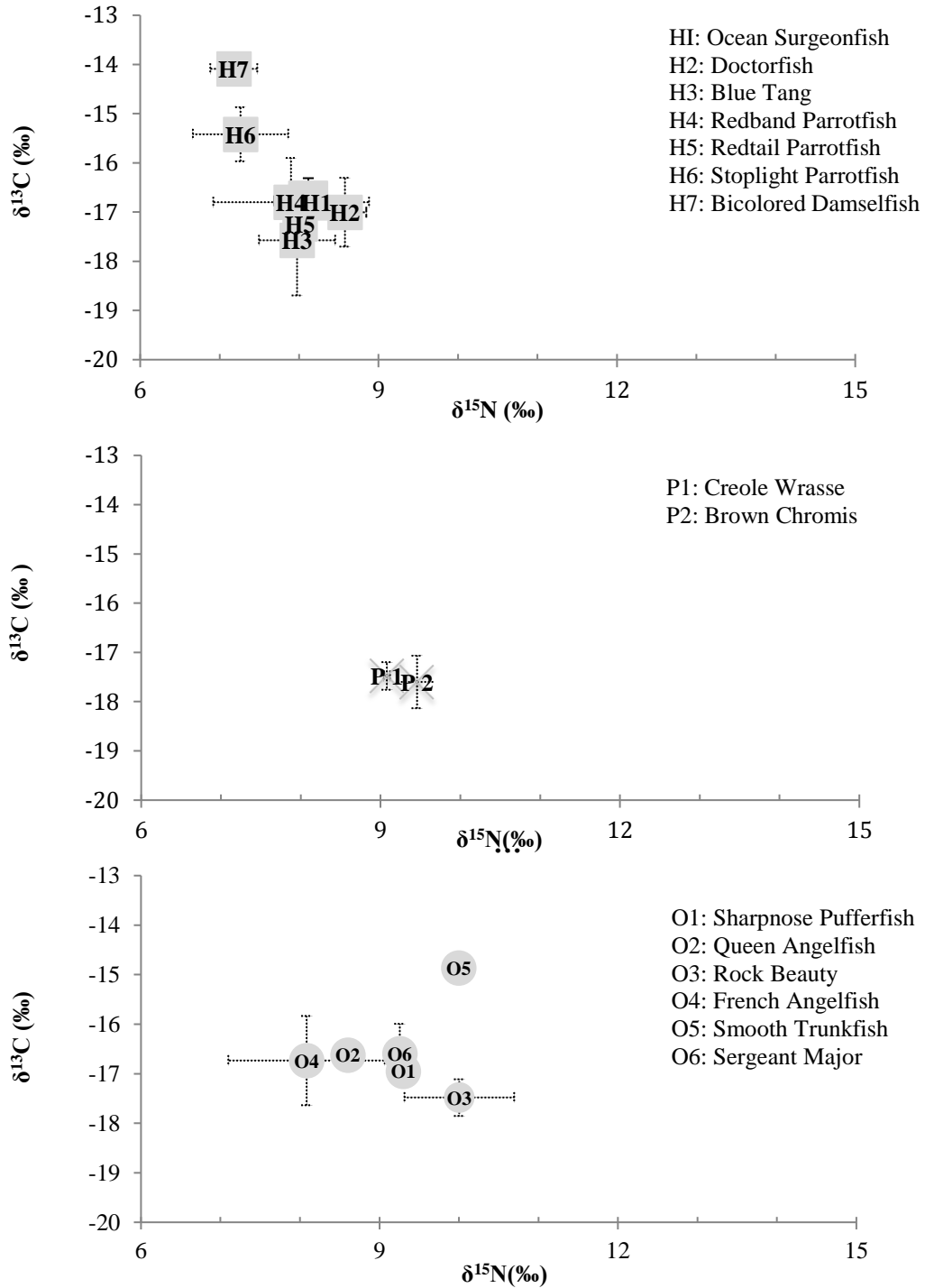


Figure 4. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with standard deviation represented by error bars of the sampled fish species of the trophic guilds herbivore (H), planktivore (P), and omnivore (O).

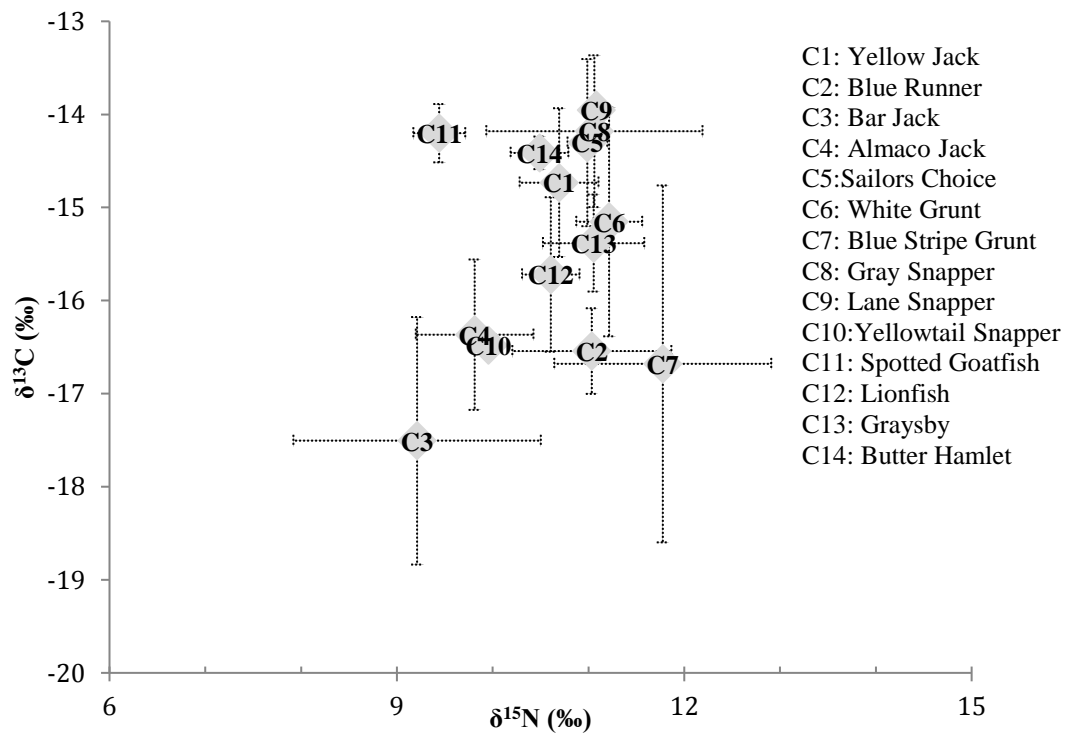
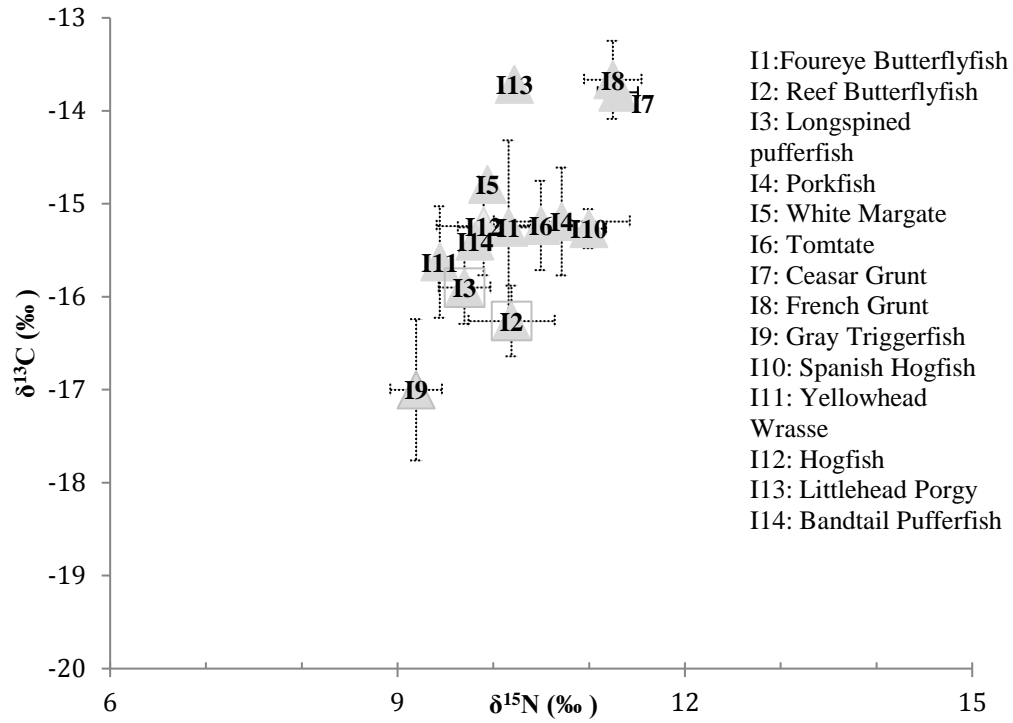


Figure 5. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with standard deviation represented by error bars of the sampled fish species of the trophic guilds invertivore (I) and carnivore (C).

Table 10. List of fish sampled at habitat type Inner Natural Reef, includes Trophic Guild (TG), Guild Code (GC), species Common Name, number sampled (N), mean (\bar{x}), $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm$ Standard Deviation (SD).

TG	TC	Species	N	(\bar{x}) $\delta^{15}\text{N}$ \pm (SD)	(\bar{x}) $\delta^{13}\text{C}$ \pm (SD)
Herbivore	H1	Ocean surgeonfish	6	7.8 \pm 0.36	-16.4 \pm 0.45
	H3	Blue tang	1	7.5	-15.4
	H4	Redband Parrotfish	6	8.1 \pm 0.46	-16.2 \pm 0.48
	H6	Stoplight Parrotfish	5	6.9 \pm 0.31	-15.1 \pm 0.30
Omnivore	O4	French Angelfish	1	9.3	-17.9
	O5	Smooth Trunkfish	1	10.0	-14.9
	O6	Sergeant Major	2	9.3 \pm 0.10	-16.8 \pm 0.37
Planktivore	P2	Brown Chromis	3	9.5 \pm 0.18	-17.2 \pm 0.28
Invertivore	I1	Foureye Butterflyfish	1	10.5	-14.6
	I2	Reef Butterflyfish	2	10.4 \pm 0.18	-15.7 \pm 0.11
	I4	Porkfish	2	10.7 \pm 0.41	-14.1 \pm 0.04
	I7	Caesar Grunt	2	11.3 \pm 0.21	-13.8 \pm 0.03
	I8	French Grunt	18	11.3 \pm 0.22	-13.6 \pm 0.23
	I10	Spanish Hogfish	3	11.0 \pm 0.18	-15.3 \pm 0.21
	I11	Yellowhead Wrasse	1	9.6	-14.9
Carnivore	C3	Bar Jack	2	8.5 \pm 1.30	-18.6 \pm 0.86
	C5	Sailors Choice	1	11.3	-13.1
	C6	White Grunt	3	11.3 \pm 0.37	-13.7 \pm 0.63
	C7	Blue Striped Grunt	3	12.1 \pm 1.11	-15.9 \pm 2.44
	C10	Yellowtail Snapper	1	10.0	-16.5
	C11	Spotted Goatfish	4	9.5 \pm 0.31	\pm 14.2 \pm 0.36
	C12	Red Lionfish	1	10.3	-14.5
	C13	Graysby	6	11.3 \pm 0.48	-15.1 \pm 0.18
	C14	Butter Hamlet	2	10.5 \pm 0.30	-14.4 \pm 0.17

Table 11. List of fish sampled at habitat type Outer Natural Reef, includes Trophic Guild (TG), Guild Code (GC), Species (Common name), number sampled (N), mean (\bar{x}), $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm$ Standard Deviation (SD).

TG	TC	Species	N	(\bar{x}) $\delta^{15}\text{N}$ \pm (SD)	(\bar{x}) $\delta^{13}\text{C}$ \pm (SD)
Herbivore	H1	Ocean surgeonfish	2	8.1 \pm 0.30	-17.5 \pm 0.12
	H2	Doctorfish	1	8.7	-17.2
	H3	Blue Tang	2	8.5 \pm 0.10	-18.2 \pm 0.89
	H4	Redband Parrotfish	4	7.4 \pm 0.33	-17.5 \pm 0.55
	H5	Redtail Parrotfish	1	7.9	-16.5
	H6	Stoplight Parrotfish	3	7.8 \pm 0.49	-16.0 \pm 0.38
Omnivore	O2	Queen Angelfish	1	8.6	-16.6
	O3	Rock Beauty	2	9.7 \pm 0.50	-17.4 \pm 0.52
	O4	French Angelfish	4	8.9 \pm 0.21	-17.5 \pm 0.79
Invertivore	I1	Foureye Butterflyfish	1	9.8	-15.9
	I2	Reef Butterflyfish	3	9.9 \pm 0.64	-16.3 \pm 0.28
	I9	Grey Triggerfish	3	9.2 \pm 0.05	-17.3 \pm 0.40
	I11	Yellowhead Wrasse	2	9.4 \pm 0.01	-16.0 \pm 0.17
	I12	Hogfish	5	9.8 \pm 0.28	-15.5 \pm 0.66
	I14	Bandtail Puffer	1	9.8	-15.4
Carnivore	C1	Yellow Jack	1	10.8	-15.2
	C2	Blue Runner	1	10.3	-15.9
	C4	Almaco Jack	1	9.9	-16.9
	C6	White Grunt	1	10.9	-15.5
	C11	Spotted Goatfish	1	9.4	-14.3
	C13	Graysby	2	10.3 \pm 0.18	-15.0 \pm 0.25

Table 12. List of fish sampled at habitat type Inner Artificial Reef, includes Trophic Guild (TG), Guild Code (GC), Species (Common name), number sampled (N), mean (\bar{x}), $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm$ Standard Deviation (SD).

TG	TC	Species	N	(\bar{x}) $\delta^{15}\text{N}$ \pm (SD)	(\bar{x}) $\delta^{13}\text{C}$ \pm (SD)
Herbivore	H1	Ocean Surgeonfish	1	8.5	-16.7
	H2	Doctorfish	2	8.7 \pm 0.18	-17.1 \pm 0.99
	H3	Blue Tang	4	7.9 \pm 0.52	-17.7 \pm 0.86
	H4	Redband Parrotfish	1	8.0	-15.4
	H7	Bi-Color Damsel	2	7.2 \pm 0.41	-14.1 \pm 0.15
Omnivore	O1	Sharpnose Puffer	2	9.3 \pm 0.12	-16.9 \pm 0.10
Invertivore	I4	Porkfish	6	10.5 \pm 0.43	-15.4 \pm 0.25
	I5	White Margate	1	9.9	-14.8
	I6	Tomtate	4	10.6 \pm 0.16	-14.9 \pm 0.49
	I9	Grey Triggerfish	5	9.2 \pm 0.36	-16.8 \pm 0.9
	I12	Hogfish	1	10.3	-14.9
	I13	Littlehead Porgy	1	10.2	-13.7
Carnivore	C1	Yellow Jack	1	10.8	-15.1
	C2	Blue Runner	3	11.3 \pm 0.81	-16.8 \pm 0.17
	C3	Bar Jack	2	9.9 \pm 1.18	-16.4 \pm 0.26
	C4	Almaco Jack	4	9.5 \pm 0.72	-16.6 \pm 0.47
	C5	Sailors Choice	2	11 \pm 0.04	-14.5 \pm 0.29
	C6	White Grunt	1	11.3	-15.2
	C8	Mangrove Snapper	3	11.1 \pm 1.13	-14.2 \pm 0.82
	C9	Lane Snapper	1	11.1	-14.0
	C12	Red Lionfish	4	10.7 \pm 0.29	-15.8 \pm 0.83

Table 13 List of fish sampled at habitat type Outer Artificial Reef, includes Trophic Guild (TG), Guild Code (GC), Species (Common name), number sampled (N), mean (\bar{x}), $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm$ Standard Deviation (SD).

TG	TC	Species	N	(\bar{x}) $\delta^{15}\text{N}$ \pm (SD)	(\bar{x}) $\delta^{13}\text{C}$ \pm (SD)
Herbivore	H1	Ocean Surgeonfish	7	8.3 \pm 0.46	-16.9 \pm 0.25
	H2	Doctorfish	3	8.4 \pm 0.28	-16.9 \pm 0.81
	H3	Blue Tang	1	7.8	-17.8
	H4	Redband Parrotfish	1	8.7	-17.7
	H5	Redtail Parrotfish	2	8.0 \pm 0.25	-17.6 \pm 0.38
	H7	Bi-Color Damsel	3	7.1 \pm 0.30	-14.1 \pm 0.36
Omnivore	O3	Rock Beauty	1	10.7	-17.6
	O6	Sergeant Major	3	9.2 \pm 0.09	-16.4 \pm 0.75
Planktivore	P1	Creole Wrasse	3	9.1 \pm 0.04	-17.5 \pm 0.28
	P2	Brown Cromis	4	9.4 \pm 0.27	-17.9 \pm 0.45
Invertivore	I2	Reef Butterflyfish	2	10.4 \pm 0.14	-16.5 \pm 0.07
	I3	Balloonfish	2	9.7 \pm 0.27	-15.9 \pm 0.39
	I4	Porkfish	3	11.2 \pm 1.17	-15.4 \pm 0.39
	I6	Tomtate	20	10.5 \pm 0.35	-15.3 \pm 0.47
	I8	French Grunt	2	10.8 \pm 0.56	-14.6 \pm 0.72
	I12	Hogfish	4	10.0 \pm 0.72	-15.0 \pm 0.27
Carnivore	C1	Yellow Jack	3	10.6 \pm 0.55	-14.4 \pm 0.96
	C4	Almaco Jack	3	10.2 \pm 0.16	-15.9 \pm 1.15
	C5	Sailors Choice	1	10.8	-15.2
	C6	White Grunt	4	11.2 \pm 0.42	-16.1 \pm 0.57
	C7	Bluestriped Grunt	7	11.7 \pm 1.19	-17.0 \pm 1.78
	C12	Red Lionfish	2	10.5 \pm 0.32	-16.1 \pm 0.48
	C13	Graysby	3	11.1 \pm 0.26	-16.2 \pm 0.10

Table 14. The mean (\bar{x}) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of for each trophic guild found at the four location types.

Trophic Guild	$(\bar{x}) \delta^{15}\text{N}$ by location				$(\bar{x}) \delta^{13}\text{C}$ by location			
	Inner Natural	Inner Artificial	Outer Artificial	Outer Natural	Inner Natural	Inner Artificial	Outer Artificial	Outer Natural
Herbivore	7.6	8.2	8.1	8.1	-15.8	-17.3	-16.2	-16.8
Omnivore	9.5	9.3	9.9	9.1	-16.5	-17.2	-16.9	-16.9
Planktivore	9.5	N/A	9.3	N/A	-17.2	N/A	-17.7	N/A
Invertivore	10.7	10.1	10.4	9.6	-14.6	-16.1	-15.1	-15.5
Carnivore	10.5	11.1	10.9	10.3	-15.1	-15.5	-15.4	-15.8

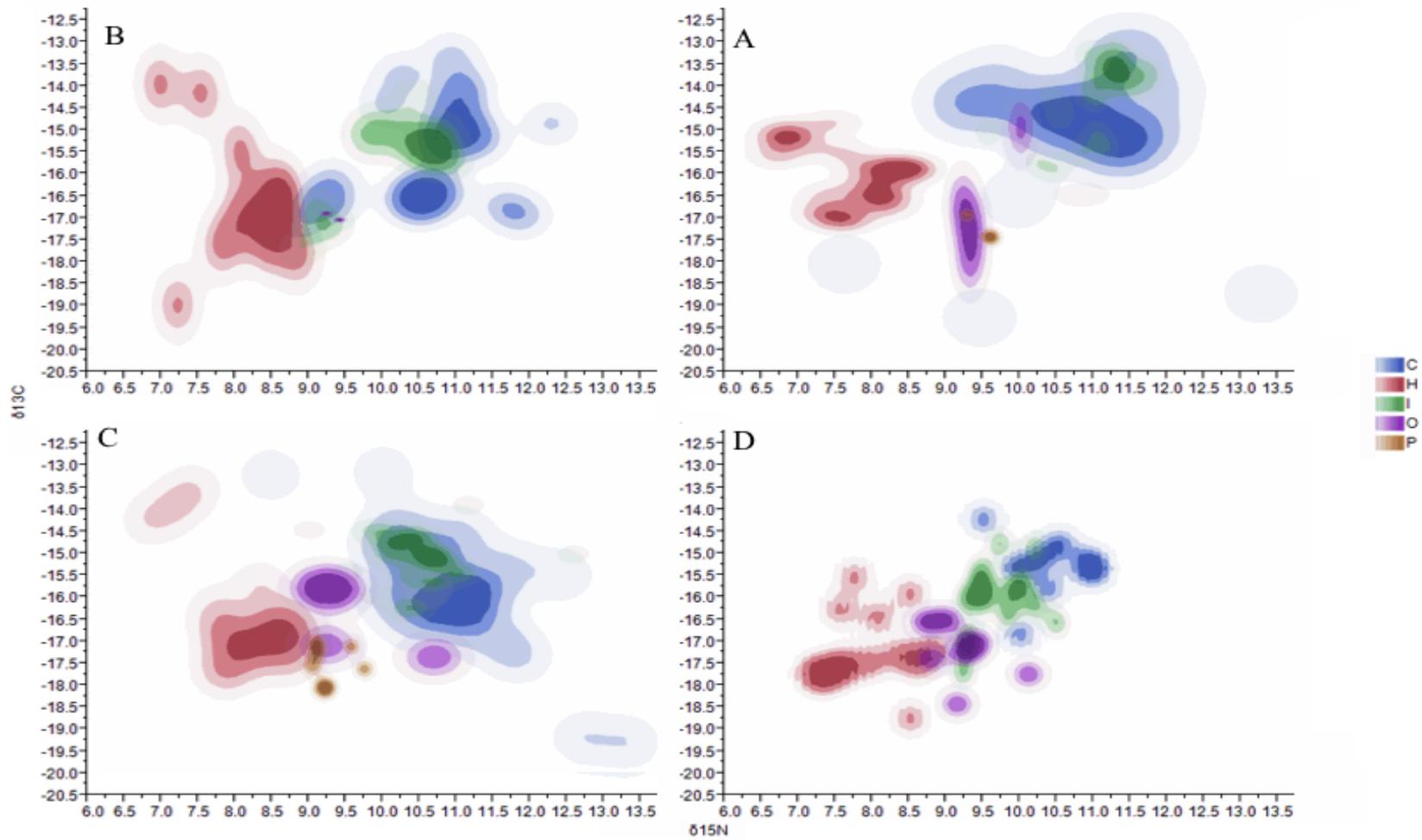


Figure 6. Density plot displaying the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ profiles of the five trophic guilds: carnivore (C), herbivore (H), invertivore (I), omnivore (O), and planktivore (P) by A) First Reef, B) Inner Artificial, C) Outer Artificial, D) Second Reef. Data are presented as heat maps rather than points for clarity and to highlight general trends.

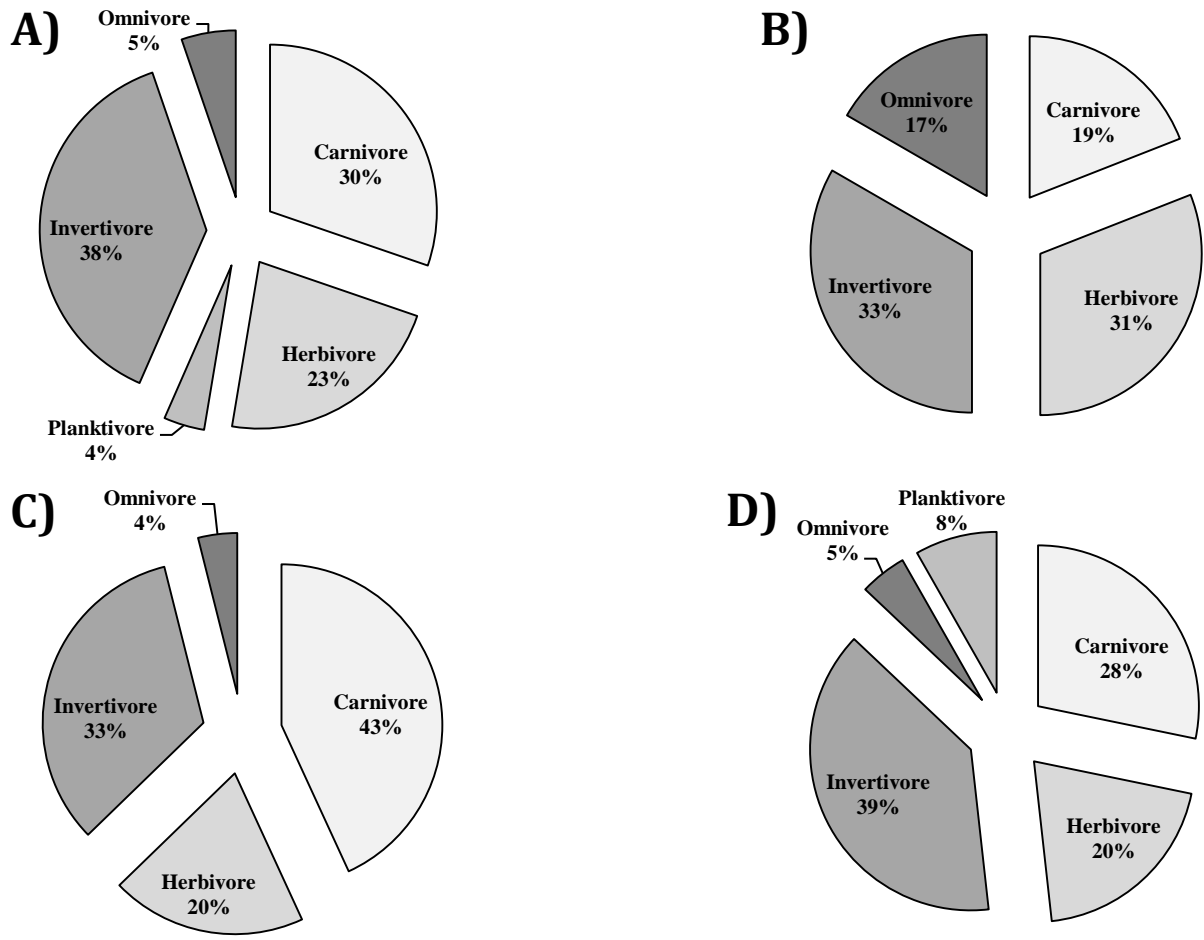


Figure 7. Catch composition of individual samples grouped by trophic guild for the site locations A) First Reef, B) Second Reef, C) Inner artificial, and D) Outer artificial locations.

Discussion

In the present study, reef-associated fish were sampled and their muscle tissue processed for stable isotope analysis in order to answer the main question raised in this study: Will reef fish trophic dynamics vary between the artificial sites and natural sites? The comparative analysis of the catch and survey data confirmed that the species sampled per site reflected the species present and that the community structure of the artificial and natural reefs was significantly different. This study found that the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of an individual influenced by its trophic guild (i.e., feeding strategy) but not by its presence on the first reef, second reef, or artificial reef.

Catch and Survey Data

Fish surveys were conducted at each site prior to sample collection in order to detect sample biases. It was considered that certain species might not be readily sampled due to their evasiveness, size, or regulatory status. Since this study is directly comparing the artificial and natural reef trophic dynamics, it was important to account for any biases that might have occurred during sampling. Comparisons of the survey data and the catch data showed a significant correlation, suggesting that the species composition of the samples taken from each site was representative of the species composition of those fish occupying the site.

The results of the PERMANOVA found that species composition was significantly influenced by *reef type*, suggesting that the fish communities of the artificial reef sites and natural reef sites were significantly different. The interaction term *distance from shore* found that the species composition of each *reef type* was significantly influenced suggesting that the species composition of the natural first reef, natural second reef, and artificial reef sites were significantly different. Studies have shown that the fish assemblages of the first and second reef tracts are different (Ault et al. 2001, Moyer et al. 2003, Ferro et al. 2005). Additionally, it has been shown that the depth at which artificial reefs are deployed, as well as structural complexity and relief height, can influence the resulting fish assemblages (Sherman et al. 2000, Walker et al. 2001, Arena et al. 2007).

Stable Isotope Data

The results of the GLM analysis showed that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue were significantly influenced by the *a priori* factors *family* and *trophic guild*, but not by body size. Figure 3 illustrates the relationship between taxonomic family and an individual's $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$; samples cluster together, based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, by taxonomic family. For this study, the literature review found that species within a taxonomic family shared similar food resources, which would explain why taxonomic family influenced the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue.

Body size has been shown to influence an individual's diet through such secondary factors as gape dimensions and swimming speed (see review by Greenwood et al. 2010). Additionally, diet shifts correlated to body size have been observed in numerous marine fish species (Jennings et al. 2001). For this reason, body length – specifically, standard length – was considered *a priori* as a factor potentially influencing the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue samples. However, body size was not a significant factor for either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ for the fishes in this study. Al-Habsi et al. (2008) reported similar findings regarding a lack of relationship between body size and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in a demersal fish community in the Arabian Sea. For this study, it is likely that body size was not a significant factor influencing the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue samples because of the similar size ranges between trophic guilds. Additionally, it is likely that, for all species sampled, any ontogenetic shift would occur outside of the size range sampled.

In the present study, individual fish belonging to the trophic guild herbivore were the most depleted in $\delta^{15}\text{N}$, which is consistent with other studies that show that primary consumption tends to result in more depleted $\delta^{15}\text{N}$, relative to higher trophic level feeders. The average $\delta^{13}\text{C}$ for the *trophic guild herbivore* was -16.5‰, which is within the known $\delta^{13}\text{C}$ range for marine benthic marine algae (France 1995a). For individuals within the trophic guild Herbivore, $\delta^{15}\text{N}$ -based trophic position estimates calculated using marine benthic algae more closely match the stomach content-based trophic position estimates, making benthic marine algae the most likely food source. The $\delta^{15}\text{N}$ -based trophic position estimates were slightly higher than the stomach content-based trophic position estimates, which is consistent with the findings of Cresson et al. (2014). The slightly $\delta^{15}\text{N}$ -based trophic position estimates may be a result of detritus consumption or

simply that the fractionation rate may be different between herbivores and higher trophic level feeders due to slight differences in their respective enzymatic and digestive systems (Mill et al. 2007).

Of the other three primary producers considered, the $\delta^{13}\text{C}$ range of phytoplankton (-22 to -17‰) most closely resembles the $\delta^{13}\text{C}$ of benthic marine algae, which makes it difficult to distinguish the two primary producers (France 1995a, Kieckbusch et al. 2004). It is unlikely, however, that phytoplankton is the dominant source of carbon for individuals within the *trophic guild herbivore* as these fish species predominantly graze on benthic marine algae. Mangroves exhibit a more depleted range of $\delta^{13}\text{C}$ relative to marine benthic algae (-30‰ to -24‰), thus excluding them as a possible food source for these reef-associated fishes.

Seagrasses were also considered as a possible food source, but their known $\delta^{13}\text{C}$ range (-13‰ to -7) is much more enriched than the herbivores collected in this study, with the exception of the Bicolor Damselfish. Herbivorous fishes, such as the Bicolor Damselfish, should display more depleted $\delta^{13}\text{C}$. The fact that these fishes were the most enriched in $\delta^{13}\text{C}$ in this study suggests that there is some discrepancy between their basal carbon source and the other fishes of this study. However, seagrass beds of Broward County, Florida are limited to the Inter-Coastal Waterway (ICW) (Walker 2012) and, as Gabriel et al. (2015) found, seagrasses within the ICW had a mean $\delta^{15}\text{N}$ of 5.6‰, result in trophic position calculations that were much lower than expected. France and Holmquist (1997) found that in areas with decreased water movement, benthic marine algae can be enriched in $\delta^{13}\text{C}$ by as much as 9‰. It may be that the complex structure of the artificial reef piles, where the Bicolor Damselfish were sampled, reduced water movement enough to cause the algal food source to become more enriched in $\delta^{13}\text{C}$.

Species of the *trophic guild omnivore* were slightly more enriched in $\delta^{15}\text{N}$ ($9.3\text{‰} \pm 0.5$) and more depleted in $\delta^{13}\text{C}$ ($-17.0\text{‰} \pm 0.85$) when compared to those in the *trophic guild herbivore*. The *trophic guild planktivore* had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ that were similar to those of the *trophic guild omnivore*, suggesting that they utilize similar food sources (Table 8; Figure 4). The $\delta^{13}\text{C}$ ($-17.6\text{‰} \pm 0.46$) of *trophic guild planktivore* suggests that phytoplankton is the source of primary production in the diet of these species.

Additionally, the $\delta^{15}\text{N}$ -based trophic position estimates using phytoplankton as the food

web base more closely matches the stomach content-based trophic position when compared to the other primary producers.. Phytoplankton tends to exhibit $\delta^{15}\text{N}$ that are less enriched when compared to marine benthic algae (Cresson et al. 2014), which would explain why the mean $\delta^{15}\text{N}$ of the *trophic guild planktivore* are not as enriched as the *trophic guild invertivore* (Table 8; Figure 4).

The *trophic guild invertivore* was more enriched in $\delta^{15}\text{N}$ ($10.5\text{‰} \pm 0.74$) relative to the other trophic guilds in this study, with the exception of the *trophic guild carnivore*, which is consistent with higher trophic level feeding habits relative to the other *trophic guilds* of this study. Species within *trophic guild invertivore* are known to feed primarily on marine invertebrate fauna, and Behringer and Butler (2006) found that marine benthic algae is an important food resource for benthic invertebrates on the reef systems of Southeast Florida. For this trophic guild, $\delta^{15}\text{N}$ -based trophic position estimates using marine benthic algae as the food web base were closest to the stomach content-based trophic positions.

The *trophic guild carnivore* consists of reef-associated fish species that exhibit a diet of both marine invertebrates and teleost fishes. Piscivory (exclusive consumption of fishes) is associated with higher trophic level feeding, and it was expected for this reason that individuals within this guild would exhibit the highest levels of enrichment in $\delta^{15}\text{N}$ (Cresson et al. 2014). While this *trophic guild* does exhibit the highest mean enrichment in $\delta^{15}\text{N}$ ($10.7\text{‰} \pm 1.01$), it is only slightly more enriched compared to the mean $\delta^{15}\text{N}$ of the *trophic guild invertivore* ($10.5\text{‰} \pm 0.74$). Additionally, the mean $\delta^{13}\text{C}$ of the *trophic guild carnivore* ($15.5\text{‰} \pm 1.4$) is similar to the mean $\delta^{13}\text{C}$ of the *trophic guild invertivore* ($15.1\text{‰} \pm 1.07$) suggesting that the individuals of these two trophic guilds share similar feeding habits. The mean $\delta^{13}\text{C}$ of species within this guild suggest that marine benthic algae are the major carbon source for their diets.

With the exception of the Blue Runner, all of the three remaining jack species (Bar Jack, Almaco Jack, Yellow Jack) exhibited $\delta^{15}\text{N}$ -based trophic position estimates that were much lower than the reported stomach content-based trophic position estimates (Froese and Pauly 2016). The reported stomach content-based trophic positions for these three jacks (Bar Jack, Almaco Jack, Yellow Jack) were made using data from studies that found that fishes were the most common prey type (Randall 1967, Sierra and Popova

1982, Manooch and Haimovici 1983, Sierra et al. 1986). However, at sizes similar to those sampled for this study, jacks will feed on a combination of fishes and marine invertebrates such as crustaceans and mollusks (Randall 1967, Sierra and Popova 1982), which would explain why their $\delta^{15}\text{N}$ -based trophic position calculations were closer to other members of the trophic guild carnivore than they were to the reported stomach content-based based trophic positions.

The Bluestriped Grunt was the only species in this trophic guild to exhibit $\delta^{15}\text{N}$ -based trophic position calculations that were considerably higher than the stomach content-based trophic position. Bluestriped Grunts displayed the most enriched $\delta^{15}\text{N}$ and most depleted $\delta^{13}\text{C}$ of all samples within this study. This is the opposite of the enrichment trend that would be expected and suggests that the carbon source for these three individual Bluestriped Grunts is different from the other sampled fish. It has been shown that marine benthic algae in the presence of mangroves display a more depleted $\delta^{13}\text{C}$ than is to be expected due to the dissolved inorganic carbon in the water originating from mangrove detritus (Boullion et al. 2008). In addition, Parks (2013) found that the microalgae present near mangroves was more enriched in $\delta^{15}\text{N}$ (5.6‰), which is most likely due to anthropogenic enrichment stemming from runoff (Heikoop et al. 2000). This would explain why these three individuals exhibited such enriched $\delta^{15}\text{N}$ and such depleted $\delta^{13}\text{C}$.

$\delta^{13}\text{C}$ by habitat type

The GLM found that the $\delta^{13}\text{C}$ of muscle tissue samples were significantly influenced by *reef type* (artificial versus natural) and distance from shore (inner versus outer). The mean $\delta^{13}\text{C}$ for these locations (natural first reef: -15.1‰, natural second reef: -16.5‰, inner artificial: -15.8‰, outer artificial: -16.0‰) increased slightly with seaward movement. Studies have shown that with seaward movement and depth, the $\delta^{13}\text{C}$ of sampled fauna will become more depleted (France 1995a, France 1995b, Bouillon et al. 2007, Wyatt et al. 2012).

Alternatively, it may be that transitory movement between the first and second reef is the root cause for samples from the artificial reefs having intermediate $\delta^{13}\text{C}$. With the exception of Pomacentrids, which display territorial behavior, the fishes of this study

are active foragers and grazers, moving over reef in search of food (Valdés-Munoz and Mochek 2001). As an example, this study found Bluestriped Grunts on the first reef and artificial reef sites that had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ that suggested that they were feeding in inshore mangrove forests. As Lindberg et al. (2006) found, artificial reefs can be utilized solely as shelter and it may be that the fishes of this study are utilizing the artificial reef piles as shelter as they transition between the first and second reef. If these fishes were feeding on both the first and second reef, isotopic mixing would explain why these fishes displayed intermediate $\delta^{13}\text{C}$.

The re-analysis of the data found that $\delta^{13}\text{C}$ of *trophic guilds* was significantly influenced by *location* (i.e. presence on the first reef, second reef, or artificial reef). The tukey-kramer pairwise comparison showed, however, that the $\delta^{13}\text{C}$ of the *trophic guilds* were mostly not significantly different across the three locations except that *trophic guild invertivore* on the first reef were significantly different from the *invertivores* of the second and artificial reefs and *trophic guild herbivore* was significantly different between the first reef and second reef. In both instances, the trophic guilds of the first reef were only enriched by 1‰, which is not large enough to assume any difference in the basal carbon source.

$\delta^{15}\text{N}$ by habitat type

The GLM found that the $\delta^{15}\text{N}$ of muscle tissue were not significantly influenced by either reef type (artificial versus natural) or distance from shore (inner versus outer sites). The mean $\delta^{15}\text{N}$ of these locations (natural first reef: 10.0‰, natural second reef: 9.1‰, inner artificial: 9.9‰, outer artificial: 10.0‰) were similar. Additionally, the mean $\delta^{15}\text{N}$ of each trophic guild were similar across the four groups (Table 14, Figure 6). The re-analysis of the data found that $\delta^{15}\text{N}$ of *trophic guilds* was significantly influenced by *location* (i.e. presence on the first reef, second reef, or artificial reef). The tukey-kramer pairwise comparison showed, however, that the $\delta^{15}\text{N}$ of the *trophic guilds* were mostly not significantly different across the three locations except that *trophic guild invertivore*, which was significantly different across all three locations. The mean $\delta^{15}\text{N}$ of the trophic guild invertivore only differed by 1‰ between the first and second reef and even less

between the artificial sites and the first and second reef (Table 14) suggesting that feeding behavior did not change due to location.

Conclusion

Artificial reefs are used as a means of supplementing natural benthic habitat for the purpose of enhancing biological production of marine life. The goal of this study was to compare the feeding dynamics of reef associated fishes at both artificial limestone boulder habitats and natural reef habitats through the use of stable isotope ecology.

Reef-associated fishes were sampled and documented from the first and second natural reef tracts and limestone boulder artificial reefs. Although the community structure of the fish species differed between the artificial and natural reefs, this did not impact the trophodynamics of these sites. This study found that the general diet of the species significantly influenced the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of white muscle tissues, derived from isotopic analysis. Species that generally follow low trophic level feeding strategies (i.e., herbivory) had the lowest $\delta^{15}\text{N}$, with $\delta^{15}\text{N}$ increasing with higher trophic level feeding. For the sampled reef-associated fish, trophic dynamics did not change a result of their presence on natural or artificial habitat.

Overall, this study found that the trophodynamics of the artificial reefs were similar to the natural reef sites, which suggests that these artificial reef sites offered similar food resources compared to the natural reefs. In the context of their construction and placement, it would seem that these artificial reefs were effective in supplementing natural reef habitat.

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