

David D. Chagaris. DIET ANALYSIS OF SELECTED FISHES IN A BELIZEAN CORAL REEF ECOSYSTEM AND DEVELOPMENT OF AN EOCPTH FOOD WEB MODEL. (Under the direction of Dr. Joseph J. Luczkovich). Department of Biology, May 2006.

The diets of selected fish from the coral reef ecosystem at Calabash Caye, Belize have been analyzed through stomach content analysis. These diets have been compared to literature values from the West Indies (Randall 1967) using regular equivalence, which gives insight not only into the variation in prey items, but also to the different roles each species occupies in its own ecosystem. The diets from Belize and the West Indies were found to be similar in cases where sufficient samples were taken. Regular equivalence and multi-dimensional scaling have been employed to categorize the food web at Calabash Caye. This method reveals trophic structure and trophic niche of organisms in this community. These diets were then incorporated into an Ecopath model to analyze the flow of energy through the system. Analyses of the Ecopath outputs reveal that primary production is high and that a large percentage of energy in the system moves through short cycles in the lower trophic levels. Comparisons were made between the outputs of this model with that of an Ecopath model of the U.S. Virgin Islands - Puerto Rico reef area. The higher levels of production suggest that Calabash Caye is either more disturbed or at less mature developmental stage than the U.S. Virgin Islands - Puerto Rico reef area. Ultimately, simulations can be applied to the Calabash Caye Ecopath model to predict the changes that take place in the food web as biomass and abundance of fish and invertebrates changes due to fishing pressure, marine protected areas, or natural perturbations. This preliminary Ecopath model is designed to be used by the Belize Fisheries Department for developing management strategies for their marine resources.

DIET ANALYSIS OF SELECTED FISHES IN A BELIZEAN
CORAL REEF ECOSYSTEM AND DEVELOPMENT OF AN
ECOPATH FOOD WEB MODEL

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David D. Chagaris

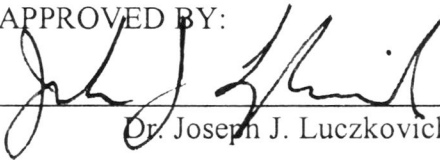
May 2006

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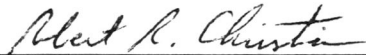
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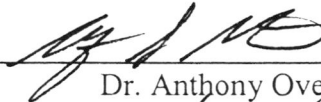
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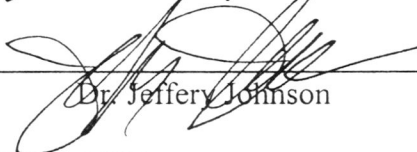
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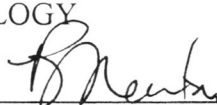
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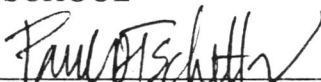

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List of Fish Species

Southern stingray	<i>Dasyatis</i>	<i>americana</i>
Spotted eagle ray	<i>Aetobatus</i>	<i>narinari</i>
Blacktip shark	<i>Carcharhinus</i>	<i>limbatus</i>
Permit	<i>Trachinotus</i>	<i>falcutus</i>
Yellow jack	<i>Caranx</i>	<i>bartholomaei</i>
Horse-eye jack	<i>Caranx</i>	<i>latus</i>
Bar jack	<i>Caranx</i>	<i>ruber</i>
Palometa	<i>Trachinotus</i>	<i>goodei</i>
Bonefish	<i>Albula</i>	<i>vulpes</i>
Mutton snapper	<i>Lutjanus</i>	<i>analis</i>
Schoolmaster	<i>Lutjanus</i>	<i>apodus</i>
Black margate	<i>Anisotremus</i>	<i>surinamensis</i>
Yellowtail snapper	<i>Ocyurus</i>	<i>chrysurus</i>
Gray angelfish	<i>Pomacanthus</i>	<i>arcuatus</i>
Redfin needlefish	<i>Strongylura</i>	<i>notata</i>
False pilchard	<i>Harengula</i>	<i>culpeola</i>
Red-ear sardine	<i>Harengula</i>	<i>humeralis</i>
Atlantic thread herring	<i>Opisthonema</i>	<i>oglinum</i>
Longsnout butterflyfish	<i>Chaetodon</i>	<i>aculeatus</i>
Foureye butterflyfish	<i>Chaetodon</i>	<i>capistratus</i>
Banded butterflyfish	<i>Chaetodon</i>	<i>striatus</i>
Silver mojarra	<i>Eucinostomus</i>	<i>aregenteus</i>
Yellowfin mojarra	<i>Gerres</i>	<i>cinereus</i>
Porkfish	<i>Anisotremus</i>	<i>virginicus</i>
Tomtate	<i>Haemulon</i>	<i>aurolineatum</i>
French grunt	<i>Haemulon</i>	<i>flavolineatum</i>
Bluestriped grunt	<i>Haemulon</i>	<i>sciurus</i>
Reef squirrelfish	<i>Holocentrus</i>	<i>ascensionis</i>
Longspine squirrelfish	<i>Holocentrus</i>	<i>rufus</i>
Gray snapper	<i>Lutjanus</i>	<i>griseus</i>
Mahagony snapper	<i>Lutjanus</i>	<i>mohagoni</i>
Lane snapper	<i>Lutjanus</i>	<i>synagris</i>
Yellow goatfish	<i>Mulloidichthys</i>	<i>martinicus</i>
Spotted goatfish	<i>Pseudupeneus</i>	<i>maculatus</i>
Sergeant major	<i>Abudefduf</i>	<i>saxatilis</i>
Saucereye porgy	<i>Calamus</i>	<i>calamus</i>
Yellow sea chub	<i>Kyphosus</i>	<i>incisor</i>
Bermuda chub	<i>Kyphosus</i>	<i>sectatrix</i>
Ocean surgeonfish	<i>Acanthurus</i>	<i>bahianus</i>
Doctorfish	<i>Acanthurus</i>	<i>chirurgus</i>
Doctorfish juvenile	<i>Acanthurus</i>	<i>chirurgus</i>
Blue tang	<i>Acanthurus</i>	<i>coeruleus</i>

Black durgon	<i>Melichthys</i>	<i>niger</i>
Yellowtail damselfish	<i>Microspathodon</i>	<i>chrysurus</i>
Great barracuda	<i>Sphyraena</i>	<i>barracuda</i>
Hogfish	<i>Lachnolaimus</i>	<i>maximus</i>
Cubera snapper	<i>Lutjanus</i>	<i>cyanopterus</i>
Green moray	<i>Gymnothorax</i>	<i>funnebris</i>
Nassau grouper	<i>Epinephelus</i>	<i>striatus</i>
Trumpetfish	<i>Aulostomus</i>	<i>maculatus</i>
Peacock flounder	<i>Bothus</i>	<i>lunatus</i>
Spanish hogfish	<i>Bodianus</i>	<i>rufus</i>
Creole wrasse	<i>Clepticus</i>	<i>parrae</i>
Puddingwife	<i>Halichoeres</i>	<i>radiatus</i>
Sand tilefish	<i>Malacanthus</i>	<i>plumieri</i>
Honeycomb cowfish	<i>Acanthostracion</i>	<i>polygonius</i>
Grasby	<i>Cephalopholis</i>	<i>cruentata</i>
Coney	<i>Cephalopholis</i>	<i>fulva</i>
Rock hind	<i>Epinephelus</i>	<i>adscensionis</i>
Red hind	<i>Epinephelus</i>	<i>guttatus</i>
Slippery dick	<i>Halichoeres</i>	<i>bivittatus</i>
Yellowhead wrasse	<i>Halichoeres</i>	<i>garnoti</i>
Black-ear wrasse	<i>Halichoeres</i>	<i>poeyi</i>
Blue chromis	<i>Chromis</i>	<i>cyanea</i>
Barred hamlet	<i>Hypoplectrus</i>	<i>puella</i>
Island frillfin	<i>Bathygobius</i>	<i>mystacium</i>
Green razorfish	<i>Xyrichtys</i>	<i>splendens</i>
Reef silversides	<i>Allanetta</i>	<i>harringtonensis</i>
Hardhead silversides	<i>Atherinomorus</i>	<i>stipes</i>
Dwarf herring	<i>Jenkinsia</i>	<i>lamprotaenia</i>
Striped anchovy	<i>Anchoa</i>	<i>hepsetus</i>
Dusky anchovy	<i>Anchoa</i>	<i>lyolepis</i>
Fairy basslet	<i>Grama</i>	<i>loreto</i>
Clown wrasse	<i>Halichoeres</i>	<i>maculipinna</i>
Harlequin bass	<i>Serranus</i>	<i>tigrinus</i>
Whitespotted filefish	<i>Cantherines</i>	<i>macroceros</i>
Queen angelfish	<i>Holacanthus</i>	<i>ciliaris</i>
Rock beauty	<i>Holacanthus</i>	<i>tricolor</i>
French angelfish	<i>Pomacanthus</i>	<i>paru</i>
Dusky damselfish	<i>Stegastes</i>	<i>fuscus</i>
Cocoa damselfish	<i>Stegastes</i>	<i>variabilis</i>
Orangespotted filefish	<i>Cantherhines</i>	<i>pullus</i>
Beau gregory	<i>Stegastes</i>	<i>leucostictus</i>
Yellow damselfish	<i>Stegastes</i>	<i>planifrons</i>
Sharpnose puffer	<i>Canthigaster</i>	<i>rostrata</i>
Goldspot goby	<i>Gnatholepis</i>	<i>thompsoni</i>

Princess parrotfish	<i>Scarus</i>	<i>taeniopterus</i>
Redfin parrotfish	<i>Sparisoma</i>	<i>rubripinne</i>
Stoplight parrotfish	<i>Sparisoma</i>	<i>viride</i>
Striped parrotfish	<i>Scarus</i>	<i>iserti</i>
Redband parrotfish	<i>Sparisoma</i>	<i>aurofrenatum</i>
Redlip blenny	<i>Ophioblennius</i>	<i>atlanticus</i>

Introduction

The legitimate concern for the declining status of coral reefs worldwide arises from their critical importance for ecosystem goods and services they provide to coastal tropical nations. An estimated 30% of coral reefs are already severely damaged, and close to 60% may be lost by 2030 (Wilkinson 2002). Coral reefs are being threatened by fishery over-harvests (Hughes 1994; Roberts 1995), pollution (Tomascik and Sander 1987; Hughes and Connell, 1999), coastal development (Hawkins et. al., 1999), exploitation (Hawkins et. al., 1999), disease (Gladfelter 1982), and global warming (Glynn, 1993). Natural phenomena such as hurricanes cause more acute, localized damage to coral reefs (Woodley et al. 1981).

At a meeting on the global status of coral reefs, overfishing was deemed one of the three most serious threats to reefs (Roberts 1993). Because species have unique trophic roles, the excess removal or harvest of one species will have an impact on other organisms in the community. For example, Hughes (1994) showed that over-harvesting of herbivorous fishes in Jamaica resulted in matted algal overgrowth and mass mortality of hard corals. This well documented phenomenon was a result of “fishing down the food web” (Pauly et al. 1998) in which the trophic level of fish harvested in Jamaica declined over time due to the excess removal of top predator fish species. Sharks, snappers, jacks, triggerfish, and groupers have virtually disappeared from Jamaican reefs over the last three to four decades. Following the demise of these apex species, the fisheries in Jamaica began to put more pressure on herbivorous fishes such as parrotfish and surgeonfish. Despite the removal of these large herbivorous fish, there was relatively

little matted algal growth on the coral around Jamaica until a mass die-off of the echinoid *Diadema antillarum* occurred from 1982 to 1984 due to a species-specific pathogen. Densities of *Diadema antillarum* were reduced by 99% and no significant recovery occurred in the following 10 years. With the continued harvests of herbivorous fishes and the lack of algae-grazing invertebrates such as *Diadema*, the entire reef system at Jamaica has undergone a widespread benthic algal bloom. To prevent catastrophic phase-shifts in community structure like the one that occurred in Jamaica, resource managers are recognizing the importance of a multi-species approach and food webs in managing their fisheries. One method of accomplishing this is through ecosystem modeling.

Belize Coral Reefs and Food Webs

Gillet (2003) divided the Belize fishery into six categories: lobster and conch, inshore artisanal, deep slope and bank, inshore pelagic and shark, inshore commercial trawl, and marine aquarium fisheries. The fishing industry has increased from 25.0 \$BZ million in 1994 to 98.1 \$BZ million in 2003, exports of the fishing industry (excluding aquaculture) were valued at 18.38 \$BZ million in 2003 (Central Statistical Office of Belize 2004). However, when reviewing these figures, it is important to consider that the levels of sustenance and artisanal fishing as well as recreational fishing is high throughout Belize and one must assume that substantial catches go unreported. The growth of the Belize fishery industry is evident above from the increasing value over the previous ten years, yet this economic growth of fisheries can result in negative effects on the ecosystem similar to the one described above. The Belize Fisheries Department is

concerned that the removal of predator species will force fishers to harvest herbivorous fishes that graze algae off the coral heads resulting in algal overgrowth. By modeling the trophic interactions of ecosystems, this food web related phenomenon can be predicted and possibly prevented.

In order to preserve their fisheries resources, the Belize Fisheries Department has designated large areas of their coastline as marine protected areas (MPA). The goals of MPAs are to maintain a sample marine ecosystem in its natural state, provide recreational and tourism services, preserve the value of the area for fisheries, and provide an area for education and research (World Commission on Protected Areas 2005). Belize has 13 MPAs that are well established including Hol Chan, Half Moon Caye, Glovers Reef, and Lighthouse Reef reserves (Belize Coastal Zone Management Authority, 2000) but will be establishing more. Turneffe Atoll Islands and Calabash Caye have been nominated as a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage site (UNESCO 1998 and Eden Garcia, personal communication). These UNESCO World Heritage sites are worthy of preservation and considered to be of outstanding natural and cultural value to humanity. The proposal of a UNESCO World Heritage site at Calabash Caye was the motivation behind the development of this project. Trophic interactions of the species at Calabash Caye are expected to change throughout the food web over time as sizes and abundance of species are altered and competition for prey items changes over time. The pre-reserve data I have gathered for this study will provide a baseline condition showing the current trophic relationships at

Calabash Caye and can be used to model any changes that may occur, if the marine protected area is established.

By using an ecosystem modeling approach managers can predict ecosystem changes caused by the alteration of fish and coral structure, and determine optimal management strategies to preserve biodiversity. The proposed network model will help to predict top-down scenarios that may cause any catastrophic “phase shifts” in community structure such as that which occurred in Jamaica from 1982 to 1984 and can be used to determine the best strategy for managing fisheries while preserving the biodiversity of Belizean coral reefs.

Food Web Models

Food web models are representations of what organisms in a community are eating and are effective in identifying the complex relationships of species and their functional roles in the ecosystem. Food webs are an essential phase to understanding an ecosystem as a whole because all organisms consume or are themselves consumed or recycled as detritus, so that every organism is a part of the food web. Network models, a subset of food web models, trace the amounts of energy, usually in the form of carbon, that flow through the ecosystem via trophic interactions. Ecosystems, and coral reefs in particular, are extremely complex, thus to model the flows of energy in network models, species are assigned to compartments in which energy or materials pass from one compartment to another via links in the food chain (Baird and Ulanowicz 1989). The grouping of species into compartments reduces complexity and can be based upon the similarities of any combination of characteristics such as their diet (Luczkovich et al.

2002), maximum length, or aspect ratio (Opitz 1996). A stomach analysis (Carr and Adams 1972, Luczkovich et al. 2002) is the best method to acquire the necessary dietary information, which is then expressed as a diet matrix of compartments representing the material or energy flows in the model.

By determining the diets of fishes at Calabash Caye, Belize, and inserting them into a diet matrix, I can employ regular equivalence (Luczkovich et al., 2002b) and cluster analyses to designate and group organisms into their unique trophic roles (compartments). Regular equivalence (REGE) reduces complexity by designating species that occupy the same position of the food web into “isotrophic” classes (Luczkovich et al. 2003). An isotrophic class consists of “trophically analogous” species that have the same relations to both predator and prey of other species (Johnson et al. 2001). These classes are determined by relating species on the basis that they obtain energy from the same trophic group and are preyed upon by organisms of the same trophic group. Structural equivalence matches nodes that have incoming and outgoing ties to the exact same nodes (Everett and Borgatti 1991). Unlike structural equivalence models, regular equivalence will distribute species into similar groups based on their ecological roles even if they do not consume the same prey or are not eaten by the same predators. Regular equivalence has been a successful approach to aggregate taxa in food webs (Luczkovich et. al., 2003). Regular equivalence can also be used to measure similarity in trophic relations of two or more species and to compare food webs across geographic locations (Luczkovich et. al., 2003). UCInet with NetDraw (Borgatti et al. 2002) are programs that implement regular equivalence to provide a way to visualize

trophic position, trophic group, and trophic niche, through a three-dimensional food web based on statistical measures of similarity.

Multi-dimensional scaling (MDS) is a non-metric spatial model that attempts to arrange objects graphically in space based on their similarities. MDS computes coordinates for a set of points in two or more dimensions so that distances between points fit to some measured similarities (distances) between corresponding sets of objects. In this case, fish species that have similar prey and similar predators will be placed close together. Luczkovich et al. (2003) employed MDS using REGE coefficients of similarity to determine the trophic role of species in a seagrass food web at St. Marks Wildlife Refuge, Florida.

Ecological Network Analyses

Ecological network analyses (ENA) models were derived from economic models that trace the flow of money or materials through theoretical regions (developed or undeveloped) and large industries by the use of input-output analyses (Leontief 1974). Leontief viewed the world economy as a system of interdependent processes that depend on each other directly, indirectly, or both. Network analysis is built on formulations of matrix algebra and is used to study how system components are tied to a larger web of interactions (Fath 2004). The components in the system are represented as a network of nodes and their connections correspond to the amount of some form of “currency” (materials, money, or energy) that move into and out of compartments. Network analyses are widely implemented by social scientists to study how individual lives are affected by their social interactions.

Ecological network analyses model the flow of energy or matter, in the form of carbon, nitrogen, or phosphorus, between organisms in a community. These models allow us to understand the role each member of the community occupies in the system as well as the system dynamics as a whole. Fath and Patten (1999) reported that early ENA (or input-output analyses) have been used to: determine total energy flows that link components of an ecosystem (Hannon 1973), compare functions such as exergy, ascendancy, and emergy to which define the relative amounts of available energy or information in a system (Herendeen 1989), calculate trophic level distribution (Levine 1980), determine effects on a harvested ecosystem (Levine 1988), investigate mixed trophic impact levels and interactions between system components (Ulanowicz and Kemp 1979, Ulanowicz and Puccia 1990), and identify control in an ecosystem (Hannon 1986, Baird and Ulanowicz 1989). Acceptance of ecological network analyses to answer important questions about the connectivity of system components is growing with the advancement of ecosystem modeling software.

Ecopath Software

Ecopath is a mass-balanced ecological modeling software program designed specifically for fishery purposes and uses carbon, nitrogen, or phosphorus as its currency. The first Ecopath was developed by Polovina (1984a, 1984b) and Polovina and Ow (1983) for modeling a coral reef at the French Frigate Shoals, Hawaii. This initial model was a simplified, steady state, biomass budget approach that used a system of simultaneous linear biomass budget equations to balance biomass production and loss (Polovina 1993). Christensen and Pauly (1992), to make it more user-friendly and

accessible to modelers across the world, then developed Ecopath II. This new version of Ecopath combines the steady-state approach of Polovina (1984) for estimating biomass and food consumption with network analysis theory used by Ulanowicz (1986) for analyzing flows between compartments. A model is built for a particular period of time, usually a year, but can be constructed for a season, as in the winter's seagrass foodweb of St. Marks National Wildlife Refuge, Florida built by Christian and Luczkovich (1999) using Ecopath II.

For this research, I used Ecopath 5.0 (Christensen et al. 2005) which is an updated software package that no longer assumes steady state and is composed of three main components. Ecopath is the mass-balanced “snapshot” of an ecosystem that uses Ecospace to adjust for habitat type and Ecosim as a time dynamic module that accounts for seasonal effects and can be a tool for policy exploration (Pauly et al., 2000). By knowing the biomass, production per unit biomass, consumption per unit biomass, and ecotrophic efficiency for compartments of any system, along with a diet matrix of the ecosystem, Ecopath 5.0 can be used to derive a wide array of outputs. Such outputs are effective trophic levels (Odum and Heald, 1975), omnivory indices, total system throughput, total primary production, primary production to respiration ratio, primary production to biomass ratio, net system production, respiration to biomass ratio, connectance, niche overlap, ascendancy, overhead, capacity, Finn cycling index, flows through trophic levels, transfer efficiencies, and proportion of total flow originating from detritus.

Ecopath is currently used by the WorldFish Center (formerly ICLARM) to compile and manage a database of network models (Fath 2004) and allow researchers access to important information regarding a variety of ecosystems around the world. In addition, Ecopath and Fishbase (www.fishbase.org) have been integrated so that many requirements for an Ecopath model are provided and readily available over the World Wide Web. Because of the growing acceptance of network analysis theory in describing and managing ecosystems and the increasing availability of data for Ecopath models, there are now 2,252 registered users in 126 countries worldwide (Christensen et al. 2005). The most promising application of Ecopath driving this global interest in ecosystem modeling is that it can be used to address sustainability issues of combined human-natural ecosystems.

The ability to address each of the 'rate' or 'state' changes in populations and communities altered by fishing was rated on a four-point scale to assess the capacity of 24 ecosystem models, six of the top eight highest scoring models were of the ECOPATH with Ecosim family (Robinson and Frid, 2002). Simulations of an Ecopath model of the Huizache-Caimanero lagoon in Mexico suggested optimal fishing strategies that would increase economic profits by ten percent based on economic, social, and ecological criteria (Zetina-Rejon et al, 2001). Watson et al. (2000) used the Ecopath with Ecosim (Christensen and Pauly 2005) (discussed later) approach to investigate the possible effects that may occur from establishing a marine protected area in ecosystems already defined by Ecopath models. This was done through simulation of the model by changing biomass and catch over a range of years. Results of the simulations showed that an

increase in biomass would occur for all groups after 10 years of protection. Both fishing and MPAs are currently topics of discussion for Belize officials, thus an Ecopath model will be beneficial to decision makers.

Trophic levels (TL), as assigned by Ecopath, are effective and fractional as suggested by Odum and Heald (1975). Effective trophic levels allow us to statistically group organisms into their unique trophic roles. Because consumers feed across several trophic levels, effective trophic levels are calculated on a continuous scale rather than an integer scale. Ecopath is a commonly used software package capable of calculating effective trophic level. The Ecopath approach to determining trophic levels uses a routine that assigns primary producers and detritus a trophic level of 1, and to consumers, a trophic level of $1 + \text{the weighted average of the preys' trophic level}$ (Christensen et al. 2005). For example, if 40% of a consumer's diet comes from that of TL 1 and 60 % comes from TL 2 then it will have a $TL = 1 + [0.4(1) + 0.6(2)] = 2.6$. Christian and Luczkovich (1999) used Ecopath II to determine effective trophic level and organize a winter's seagrass food web of Goose Creek Bay, St. Marks National Wildlife Refuge, FL. In this study, fish-eating birds had an effective TL of 4.00, Red drums' TL was 3.39, and Blue crabs' TL was 3.22.

The omnivory index (OI) (Pauly et al., 1993) is the variance of the trophic level of a consumer's prey groups (Christensen et al. 2005). An omnivory index of zero indicates that the consumer in question is specialized, i.e. only feeding on a single trophic level. A large value indicates that the consumer feeds on many trophic levels. The system omnivory index is the average OI for all consumers weighted by the logarithm of each

consumer's food intake. It is a measure of how the feeding habits of consumers are distributed between trophic levels and is used to characterize the extent to which a system displays web-like features. The connectance index is similar to the system OI because it also gives an indication to the extent of web-like features of a given food web.

Total system throughput represents the size of the entire system in terms of flow (Ulanowicz, 1986) and is the sum of all flows in a system. It is expressed as the sum of four flow components: total consumption, total export, total respiration, and total flows to detritus. Growth of a system can be translated into an increase in the total system throughput. The primary production/respiration ratio (P_p/R), P_p to biomass ratio (P_p/B), net system production, and respiration to biomass ratio (R/B) all provide a quantitative measure of system maturity and growth (Odum 1969). The ratio between total primary production (P_p) and total respiration (R) is important when describing the maturity of an ecosystem (Odum 1969, 1971). In a "young" ecosystem, production is expected to exceed respiration ($P_p/R > 1$), in a mature system the ratio should approach one. P_p/B and net system production are also expected to be large in developing systems while R/B will be low in an immature ecosystem (Odum 1969).

Niche overlap is an index for quantifying how species overlap using the diet matrix. A value of zero suggests that the two species do not share resources and a value of one would suggest that species completely overlap, intermediate values show partial overlap in resource utilization. Niche overlap is best visualized by plotting the compartments which exhibit some level of overlap on a two dimensional graph. If two compartments have a high predator overlap index (x-axis) then they have similar

predators, if they have a high prey overlap index (y-axis) then they have similar prey. If two compartments have a high overlap of both predators and prey, they may be candidates for aggregation into a single group.

Ascendency, overhead, and capacity represent the amount of information (or limits to the amount of information) in a system. Ascendency is a measure of the average mutual information (AMI) in the system scaled by TST. AMI relates to the uncertainty of the paths that a unit of energy may flow through when it enters the system. The capacity is the estimated amount of AMI that can be held in a system and the overhead is the difference between capacity and ascendency. The overhead provides limits on how much the ascendency can increase and reflects its “strength in reserve” should it be faced with unexpected perturbations (Christensen and Pauly 2005).

The Finn cycling index (FCI) is the fraction of an ecosystems throughput that is recycled and correlates with system maturity (Odum 1971). For all living groups, transfer efficiencies for successive discrete trophic groups can be calculated as a ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput on the trophic level. Transfer efficiencies are presented as percentages per trophic level.

Comparing Ecosystems Using Network Analyses

Ecological network analyses (ENA), such as Ecopath and Network IV, have been used to compare trophic structures among ecosystems over different temporal and spatial scales. A thorough comparison of ecosystems was done by Christensen (1995) to determine differences in system maturity using Ecopath. Christian et al. (2005)

investigated the use of ENA in comparing estuarine ecosystems. The ENA approach is favored because the trophic interactions are weighted so that they represent rates, and not amounts, which can be misleading. Because ecosystems have inherent differences, Christian et al. (2005) used indices from network analyses to compare the trophic structure of several estuaries. The indices used were total system throughput, Finn cycling index, transfer efficiency, and ascendancy/developmental capacity. Christian et al. (2005) found these indices of food webs, from network analyses, to correspond with their understanding of levels of complexity and stress in estuarine systems.

The most detailed description of a network model involving a Caribbean coral reef was achieved by Silvia Opitz (1996). Ecopath II was used to model the U.S. Virgin Island-Puerto Rico (USVI-PR) coral reef area based on data from the literature. Five separate compartment models were created: one 50-box model, two 20-box models, and two 11-box models. The number of fish species was reduced using cluster analysis and invertebrates were grouped based on appropriate energetic criteria. Opitz (1996) determined from her model that the USVI-PR coral reef area has short cycles and that most of the net primary production is being recycled directly to detritus. Transfer efficiencies between trophic levels were also found to be low. She compared the outputs from the model to those constructed for coral reefs at French Frigate Shoals, Hawaii and Bolinao, Philippines and found that the Caribbean ecosystem was at an intermediate maturity level relative to the others. Gastropods and crustaceans also had larger ecotrophic efficiency in the Caribbean than on Pacific coral reefs resulting from higher predation pressure and overexploitation of conch and lobster. This Caribbean coral reef

model will be used as a resource for a majority of the missing data in the model of Calabash Caye and as a tool for comparing ecosystems.

Building a Belize Ecopath Model

In July 2003 and June 2004, sampling took place to analyze the stomach contents of fishes from Calabash Caye, Belize in order to gather dietary data for a food web model. Although dietary information is available for these species of fishes, the literature is decades old (Randall 1967) and was obtained from the West Indies, on the eastern rim of the Caribbean Sea. Thus, in order to obtain an accurate representation of the trophic interactions at Calabash Caye I conducted a dietary study. Should the diets of fish from Calabash Caye show variation from those that are reported in the literature, it will provide grounds for further stomach analysis studies in Belize. Where sufficient studies have already been conducted, and reported in the literature, researchers interested in creating network models should refrain from collecting redundant dietary data because diet analyses of fish is a destructive method of understanding the trophic interactions in marine food webs. Also in June 2004 and again in June 2005, fellow graduate student Deirdre Barry and PhD student Becky Deehr collected biomass of fishes and invertebrates. The data has been compiled to build a network model using Ecopath 5.0 that gives insight into system characteristics as well as information about the components of the system at Calabash Caye and how they interact. The Ecopath food web model describes the current state of Calabash Caye that can be viewed as a baseline condition should changes in ecosystem structure occur in the future.

One objective of this project is to establish dietary intake patterns for selected species from the families: Acanthuridae, Alopidae, Atherinidae, Belontiidae, Carangidae, Dasyatidae, Gerreidae, Haemulidae, Holocentridae, Labridae, Lutjanidae, Pomacentridae, and Sphyraenidae at or around the Calabash Caye reef. A second objective is to use these data to group organisms into “isotrophic” classes based on the similarity coefficient, regular equivalence, and visualize the food web using NetDraw. Thirdly, the diets of fishes from this study have been compared with diets of the same fish species as reported by Randall (1967) from the West Indies to determine any differences in prey items over time and across geographic locations, again using the regular equivalence routine. The diet analyses were also used as part of an Ecopath network model of the reef ecosystem at Calabash Caye based on field data or available data from the literature. A fourth objective is to compare and contrast selected indices from network analyses of the Calabash Caye model and the model of the U.S. Virgin Island - Puerto Rico reef area (Opitz 1996) to investigate the differences in effective trophic levels, omnivory indices, total system throughput, various ratios of primary production, respiration, and biomass, cycling indices, and transfer efficiencies. By comparing these systems, we can determine if outputs from the Ecopath models are consistent with what is known about coral reefs. Regular equivalence has been employed in prior food web studies, but this study will relate the interpretations obtained through regular equivalence with those generated by network analysis in Ecopath. Ultimately, the food web model resulting from this research can be used by the Belize Fisheries Department to assess and predict the impact of tourism, recreational fishing, commercial harvests, natural and human induced

perturbations, and marine protected areas. This network model will benefit fisheries managers and assist in their aim to sustain biodiversity and preserve the coral reefs of Belize.

Materials and Methods

Site Description

Calabash Caye is a part of the Turneffe Islands Atoll, Belize and is the site of the University College of Belize Institute for Marine Studies (UCBIMS). Turneffe Atoll is located about 51 km off the coast of Belize in the Caribbean Sea (Figure 1). At its longest point, Turneffe Atoll stretches 50 km north to south and is 16 km across at its widest part. These islands are about 10-16 km east of the barrier reef with a 275-300 meter deep channel between them. On the eastern side of the atoll, there is a well-defined yet segmented reef (Garcia and Holtermann 1998).

Located on the southeastern rim of Turneffe Atoll and positioned parallel to the reef is a small sandy caye, Calabash Caye (Figures 2 and 3). A central, interior lagoon is approximately 500 m long and is characterized as having high salinities and little flushing. The vegetation on Calabash Caye is described as either a strand-plain system dominated by caye and coccol forest or a saline-swamp land system dominated by mangrove species. Mangrove species (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) cover most of the western and northern areas of the island. Humans have inhabited Calabash Caye since the early 20th century. Originally, it was established as an outpost for the sponge and then coconut industries but was completely devastated by Hurricane Hattie in 1962 (Garcia and Holtermann 1998). The small island is now used primarily by the University of Belize and their staff and visiting researchers to the marine laboratory.

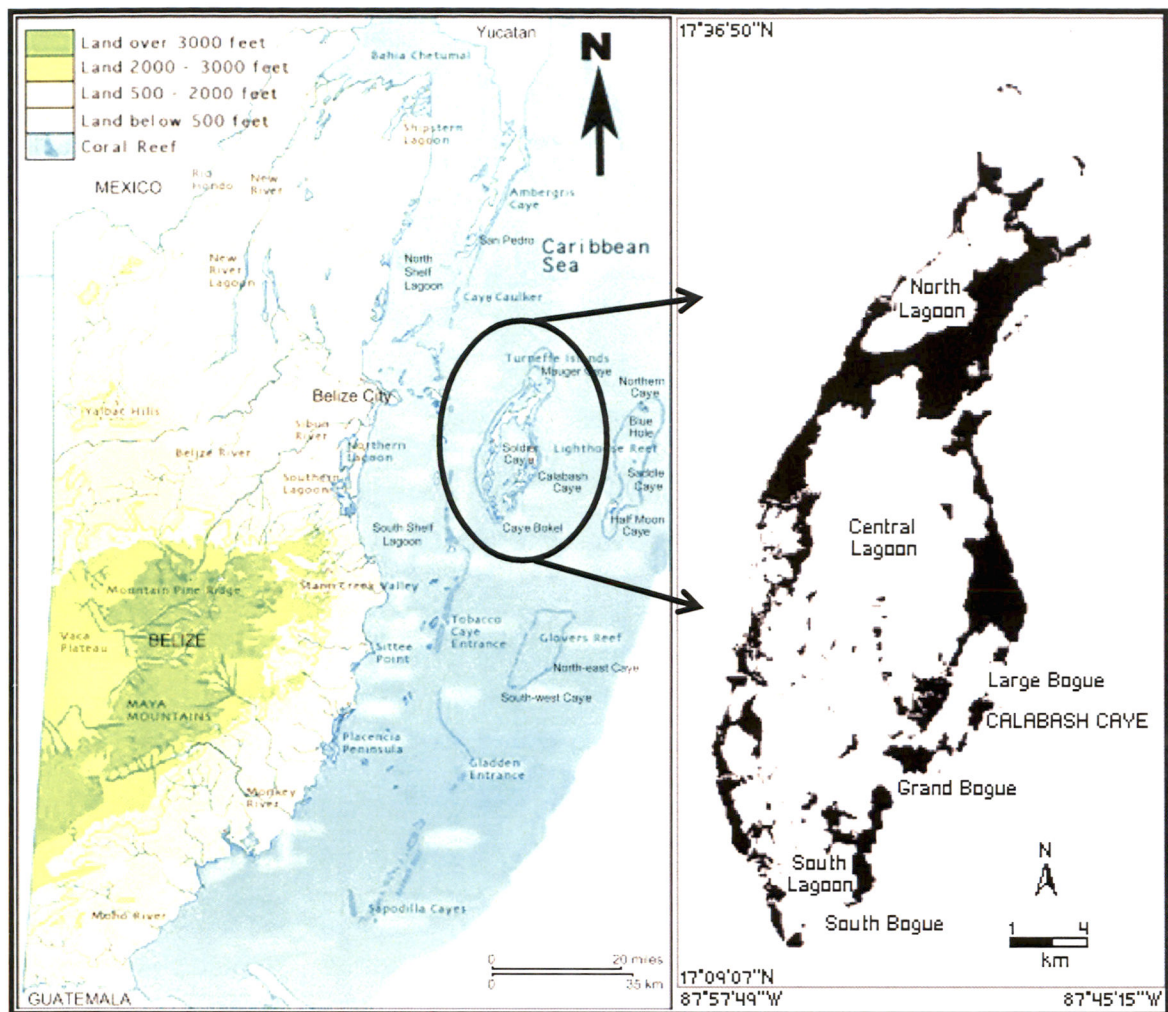


Figure 1. Map of Belize and Turneffe Atoll

Fish Diet Sampling Locations at Calabash Caye

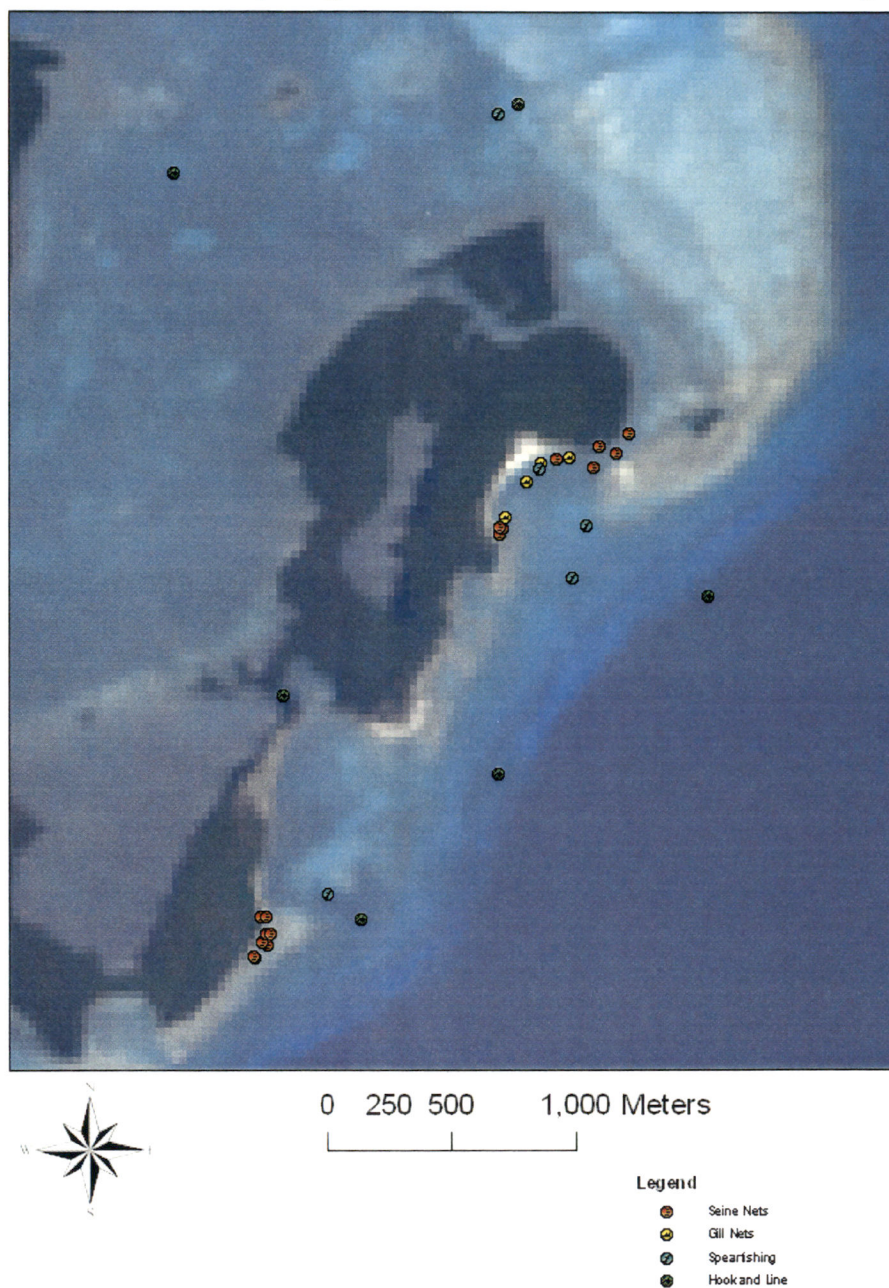


Figure 2. Landsat image of Calabash Caye, Belize showing the locations of samples taken for the diet study.



Figure 3. Aerial photograph of Calabash Caye, Belize from the Coral Caye Conservation.

The climate of Turneffe Atoll and the western Caribbean does not vary much throughout the year. In Belize, there is a rainy season from June to December with steady winds from the east for most of the year. The normal tidal range at Calabash Caye is 0.5 meters (Garcia and Holtermann 1998), the average water temperature is approximately 28.0° C and salinity is between 35.0 – 37.0 ppt. Currents usually run parallel to the sandy beach from north to south and are influenced more by winds than tides.

The majority of fish were collected in either seagrass habitat or coral reef habitat. A typical seagrass bed at Calabash Caye is bordered by mangrove on the landward side and coral reef on the seaward side. *Thalassia testudinum* and *Syringodium filiforme* are the dominant species of sub-aquatic vegetation (SAV) while *Halodule wrightii* is present, yet less abundant. Sediment in the seagrass areas is characterized as a compact sandy bottom mixed with shells. The seagrass areas of Turneffe Atoll and Calabash Caye are important foraging areas for commercially important species of fish and invertebrates such as conch, lobster, and shrimp (Hain 1987, 1988).

The coral reef ecosystem at Turneffe Atoll possesses a typical windward West Indian coral reef zonation pattern (Garcia and Holtermann 1998). This pattern consists of a backreef, reef crest, spur-and-grove zone, mixed zone, forereef terrace, escarpment, forereef, and deep forereef. Dustan et al. (1992) surveyed the hard coral on the reef at Calabash Caye and recorded 29 species of scleractinian coral. Algal cover and sea urchin abundance were also surveyed in the same study. Belize coral reefs were somewhat spared of the coral bleaching events in the early 1990's. The first report of coral

bleaching in Belize came following elevated sea temperatures in the Western Caribbean basin from August to October of 1995 as detected by NOAA satellites (Stout 1995). A later bleaching event occurred worldwide in 1998 and affected the reefs of Belize (Aaronson et al. 2000).

Specimen Collection

Fish were collected using both active and passive sampling techniques in areas around Calabash Caye (Figure 2). For this study, I used experimental gill nets that are 38.10 m long, 1.83 m deep, and are composed of five 7.62 m sections with increasing mesh size from 2.5 - 12.7 cm stretch mesh monofilament. These nets were set at dusk and hauled in just after dawn. A 15 m bag seine with 0.64 cm ace mesh netting was used to sample the fish community present in the seagrass areas just along the shoreline. A 1.8 m pole spear and hook and line were all used to sample the fishes within the reef. All spear fishing was done while snorkeling. Once the fish were captured, they were placed into a transport box and anesthetized using MS 222. Catch data for each net has been recorded, the fish have been enumerated by species and each individual measured to obtain their standard length and total length in mm as well as weight in g. After the measurements were taken, the gastro-intestinal tract was then removed and placed into small vials or whirl-pack bags with 10% formalin and assigned an individual alphanumeric code. These were then transported back to Greenville, NC in heat sealed biological grade bags for laboratory analysis.

Stomach Content Analysis

A sieve fractionation technique was used as described by Adams and Carr (1982), Luczkovich and Stellwag (1993), Luczkovich et al., (2002), and Christian and Luczkovich (1999) to perform stomach analysis and quantify each individual's diet as percent dry mass. Only contents from the stomach were considered. Any material that lies in the intestinal tract posterior to the pyloric caeca was not included in the stomach analysis. This was done so as not to bias the diet towards the hard, non-digestible prey items. Stomach contents were pooled together prior to passing them through the sieves only in cases where there were fish of the same species and the same size class caught at the same time and at the same location.

In this sieve fractionation method, stomach contents of individual fish (or pooled contents) were passed through a series of six nested sieves of sizes 2000, 850, 425, 250, 150, and 75 micrometers. Each sieve's contents were analyzed separately using light microscopy to identify and count the number of food items in the stomach and data were recorded onto a pre-printed data sheet. Dried aluminum dishes were numbered and weighed. Each sieve's contents were transferred to an aluminum dish and then placed in a drying oven at 60°C for 48 hours. Once the samples dried for the required amount of time, they were removed from the oven and the aluminum dishes with the dried stomach contents were weighed again. The difference in weight of the aluminum dish (prior to adding contents and drying) and the aluminum dish plus the dried contents is the dry weight of prey material for each sieve. The data were entered into a Microsoft Excel worksheet and percent dry mass for each prey item was calculated using the numerical

abundance of each prey taxon within a sieve fraction to apportion dry mass to taxa.

Weight was measured to 0.00001 grams using a Mettler H51 precision balance. Fish with empty stomachs were not analyzed.

Diet Matrix Composition

A 137 by 137 square diet matrix consisting of 96 fish species and 41 non-fish groups was constructed in Microsoft excel using dietary data from this study, Randall (1967), Fishbase (www.fishbase.org), and Opitz (1996). Within each cell of the matrix, the proportion of each prey consumed by each predator was entered. The 96 fish species represent a combination of those observed at Calabash Caye during visual transects conducted by Deirdre Barry and those that were collected for this study using the various sampling gear described above. Non-fish groups were determined based on the stomach content analyses of West Indian reef fishes by Randall (1967). Although the diets in this study are presented as percent of dry mass and those of the West Indies (Randall 1967) are presented as percent of volume, they both represent percent diet and thus approximate the relative amounts of energy extracted from various system components. The taxonomic levels of organisms identified from stomach contents in this study and Randall (1967) varied from species to families and higher categories, with most invertebrates grouped under high taxonomic categories. The non-fish prey aggregations used by Opitz (1996) allowed for representation of all prey items in the diet matrix.

Fishes found in the stomach contents of this study were identified mostly to the species or generic level with percent of dry mass of the single species or genera. Randall (1967), on the other hand, gave no indication of percentage volume of the single species

or genera of fishes to the diet of the consumer. Rather, he reported the percent of volume of all fishes combined and listed the species or genera that made up this percentage. For the construction of this matrix, the percentages of “fish” listed by Randall (1967) were divided into equal parts between all the species listed as prey for each consumer. When fish were identified only to family or genera by me or Randall (1967), the respective percent of mass or volume was distributed evenly over all species of the family or the genus that are represented in the matrix.

When the prey item “fish” or “small fish” was the highest level of identification, the percentage was divided into equal parts over selected fish species in the diet matrix as described by Opitz (1996). Using this method, it was assumed that when part of the diet was stated to be “fish” or “small fish” every fish species in the system had the same probability of being preyed upon with exclusions given to those that were (1) larger than the predator under consideration and (2) those that were known to inhabit small reef crevices. For example, a large animal such as a shark would most likely not manage to extract small gobies, blennies, or damselfishes from between coral heads and other crevices. However, for predators such as the trumpetfish whose mouth morphology allows them to capture small fish from within reef heads and other crevices, the second exclusion did not apply and a third restriction was included that excluded small pelagic schooling fish such as small jacks and scombrids from their diets.

Unidentified stomach contents were assigned to the identified parts according the relative abundance of known prey items. A variety of organisms such as eggs and larvae were assigned to zooplankton as determined by Opitz (1996). A list of the items

represented as zooplankton is given in Table 1. In Randall's study (1967), "algae and organic detritus" were often listed as one combined prey item. During the composition of the diet matrix, the relative contribution was divided into two equal parts. In cases where an organisms diet included "corals", the corresponding percentage was divided into two groups with 60% of that percentage going towards symbiotic algae (plant tissue) and the other 40% assigned to corals (animal tissue) as described in Opitz (1996). These dietary data for non-fish taxa was taken directly from the diet composition matrix in USVI-PR Ecopath model (Opitz 1996). These data were obtained for that study from a search of the Aquatic Sciences and Fisheries Abstracts (ASFA). Quantitative diet information of coral reef invertebrates is scarce thus the quantitative diet composition of each non-fish group was estimated from qualitative reports and/or was transferred from ecosystems other than coral reefs (Opitz 1996).

Regular Equivalence and Food Web Visualizations

To analyze similarities in the 137 by 137 diet matrix presented above, I used the regular equivalence (REGE) algorithm in UCINET 6 with NetDraw network analysis software package (Borgatti et al. 2002). The program accepts input as any real-valued square matrix (species-by-species) and converts it to a matrix of REGE coefficients ranging from zero to one for each pair of species. This is computed through a series of iterations with the maximum number of iterations equal to the number of species or compartments. Within each iteration, a search is implemented to optimize a matching function. The result of this procedure is a symmetric matrix of similarity measures of regular equivalence.

Table 1. Items included in "zooplankton" for the diet matrix composition as determined by Opitz (1996).

Taxon	Item
Arthropoda	insects
Annelida	Polychaete larvae
Cnidaria	Scyphozoans (medusae) Siphonophores (medusae)
Crustacea	Barnacle larvae Copepods Crab larvae Euphausids Hermit crab larvae Isopod larvae Mysids Ostracods Scyllarid larvae Shrimp larvae Stomatopod larvae
Ctenophora	Ctenophores (medusae)
Mollusca	Bivalve larvae Cephalopod larvae Gastropod larvae Heteropods Mollusc eggs Pteropods
Tunicata	Appendicularians Salps
Unidentified	Fish eggs Fish larvae

To visualize patterns of similarities arising from the REGE procedure, I submitted the similarity matrix to a non-metric multi-dimensional scaling (MDS) routine to represent similarities as distances in two or three-dimensional space. The program UCInet with NetDraw finds a set of points in k-dimensional space such that the Euclidean distances among these points corresponds to similarities in the diets and predator relations based on the REGE coefficients (Borgatti et al. 2002). The resulting food web diagram presented in NetDraw consists of nodes (species) and edges (connections) based on the original diet matrix and spatially arranged according to their regular equivalence in non-metric multidimensional space.

Nodes in the food web diagram were then colored based on their regular equivalence and assigned different shapes for fish, non-fish, invertebrates, primary producers, and nonliving groups. In order to determine the number of colors needed to color the diagram, I repetitively implemented an optimization clustering on the square REGE matrix to compute similarities of all taxa within a cluster using average Pearson correlation in UCInet. In this optimization procedure, the number of clusters is specified and species are placed into a cluster such that the average similarities are maximized within the cluster. As the number of clusters is changed with each run of the optimization procedure, the ratio of similarity within cluster to similarity between cluster changes and total similarity within all clusters either increases or decreases and is measured by the R^2 value. By plotting R^2 against the number of clusters, I obtained a plot that revealed the greatest within to between cluster similarities at the peak R^2 . The least number of clusters with the highest R^2 value was used to color the food web diagram so

that members of different clusters are assigned a different color. This was done separately for fish and non-fish heterotrophs so that a fish and a non-fish would not be clustered together and primary producers and detritus can be assigned a separate color. This routine was repeated on a 50 by 50 diet matrix that was composed by collapsing the 137 by 137 matrix into the compartments (Opitz 1996) used in the Ecopath model (described below).

Diet Comparisons

To compare the diets of fish from this study against those from the West Indies during the 1960's (Randall 1967) I again used the regular equivalence routine described above. The 137 by 137 diet matrix was expanded to 157 by 157 to include the dietary data of the 20 species of fishes from the West Indies during the 1960's but were observed in this study from Calabash Caye, Belize during 2003 and 2004. Juvenile stages of fish from Belize were not compared with adult stages of fish from the West Indies, thus only 20 species of fish were eligible for comparisons. The columns represent a species as prey, so for each newly added species, the column was made identical to that of the entry from Calabash Caye, Belize. This is so that the predators of these fishes are the same and only their prey items differ and any differences in trophic position based on regular equivalence is due solely to the different diets reported in the two studies and not their predators. The REGE coefficients are measures of similarity based on what prey the fishes consume and what predators consume them. By repeating the methods described above with the expanded diet matrix, I compared not only the similarity of diets across temporal and geographic locations using REGE coefficients but also visualized the

similarity in trophic niche using MDS and NetDraw. The cluster optimization procedure has also been repeated with the expanded matrix to determine if the fishes under consideration cluster into separate “isotrophic” classes due to differences in diets over time and geographic locations.

The ECOPATH Model

Model Construction. To develop a model of Calabash Caye, Belize that can be compared with the model of the U.S. Virgin Island - Puerto Rico system, a 50-compartment model was built using the same aggregations of species as that by Opitz (1996) (Table 2). By keeping the model structure the same, we assume that any differences in the outputs are a result of input values alone. Thus, the 137 by 137 diet matrix described above was collapsed into 50 compartments by averaging the diets of taxa in each compartment described by Opitz (1996).

The four basic input requirements other than the diet matrix for Ecopath are biomass, production/biomass ratio, consumption/biomass ratio, and ecotrophic efficiency (Pauly et al, 2000). A fifth input, the fraction of unassimilated food, can be entered, but was left at the default value of 0.200 until the balancing began. The habitat area fraction is set to 1.0 for all compartments assuming a uniform habitat throughout the sampling area. Biomass in habitat area (B) is the average biomass per unit area calculated in gWW/m^2 (WW = wet weight) for each species. For fish, the values were estimated from catch data and visual census surveys by Deirdre Barry at Calabash Caye (Barry unpublished thesis East Carolina University). Becky Deeher provided abundance and biomass data for benthic macro-invertebrates using a suction dredge technique (Brook

Table 2. Fifty compartments used in this study for the Ecopath model as determined by Opitz (1996).

Compartment Number	Compartment Name	Representative Members
1	large sharks/rays, carnivorous	southern stingray, eagle ray, blacktip shark, nurse shark
2	sharks/scombrids, carnivorous	sharpnose shark, bonnethead, mackerel, tunny
3	large jacks, carnivorous	permit, jacks
4	intermediate jacks, carnivorous	palometa, bar jack, yellow jack, horse-eye jack, blue runner
5	small jacks, carnivorous	scad, ladyfish
6	intermediate reef fish, carnivorous 1	bonefish, mutton snapper, schoolmaster, black margate, angelfish
7	large to intermediate schooling fish, pelagic	needlefish, herrings
8	intermediate reef fish, carnivorous 2	butterflyfish, mojarra, grunts, squirrelfish, porgy, goatfish, sergeant major, lane/mohogany/gray snapper
9	hemiramphidae, herbivorous	halfbeaks
10	kyphosidae, herbivorous	sea chubs
11	intermediate reef fish, herbivorous	surgeonfish, doctorfish, tang, Surge wrasse
12	large reef fish, carnivorous	barracuda, hogfish, cubera snapper, moray eel
13	intermediate reef fish, carnivorous 3	trumpetfish, flounder, creole wrasse, tilefish, coney, graysby, rock hind, red hind
14	small reef fish, carnivorous 1	yellowhead wrasse, chromis, hamlet, razorfish
15	small schooling fish, pelagic	silversides
16	engraulidae, herbivorous	anchovies
17	small reef fish, carnivorous 2	fairy basslet, clown wrasse, harlequin bass
18	large groupers, carnivorous	black grouper, itajara
19	intermediate reef fish, carnivorous 4	filefish, angelfish, rock beauty
20	small reef fish, omnivorous 1	damselfish, orangespotted filefish
21	small reef fish, omnivorous 2	beau gregory, yellow damselfish, puffer
22	small reef fish, omnivorous 3	goldspot goby
23	large scaridae, herbivorous	rainbow parrotfish, midnight parrotfish, queen parrotfish
24	intermediate scaridae, herbivorous	princess parrotfish, redfin parrotfish, stoplight parrotfish

Table 2 continued

Compartment Number	Compartment Name	Representative Members
25	small scaridae, herbivorous	striped parrotfish, redband parrotfish
26	blennidae, herbivorous	redlip blenny
27	small gobiidae, carnivorous	yellowline goby, sharknose goby
28	sea birds	birds
29	squids	squids
30	sea turtles	sea turtles
31	octopus	octopi
32	lobsters	spiny lobster
33	crabs	all crabs
34	shrimps/hermit crabs/stomatopods	all shrimps, hermit crabs, and stomatopods
35	amphipods/isopods/tanaids/pycnogonids	small crustaceans
36	asteroids	sea stars
37	echinoids	sea urchins
38	gastropods	conch, snails and slugs
39	chitons/scaphopods	chitons and tusk shells
40	polychaetes/priapuloids/ophiuroids	segmented worms, penis worms, brittle stars
41	holothuroids/sipunculids/echiuroids/hemichordates	sea cucumber, peanut worms, echiuroid worms,
42	bivalves	bivalved mollusks
43	ascidians/barnacles/bryozoans	tunicates, barnacles, moss animals (hydra)
44	sponges	all sponges
45	sea anemones/corals	all corals and anemones
46	zooplankton	see Table 1
47	microfauna	decomposing bacteria
48	phytoplankton	photosynthetic plankton
49	benthic autotrophs	seagrass and algae
50	detritus	nonliving organic material

1979) (Deehr unpublished). Molly Kilpatrick also collected data on the density of macroinvertebrates such as echinoderms, tunicates, sponges, and large mollusks via visual census surveys of 60 m² areas (Kilpatrick unpublished). Kristine Lindsey collected zooplankton in 2001 using a 90 µm net towed for 5 minutes in mangrove and coral reef areas (Lindsay unpublished). These undergraduate and graduate student project reports are available as unpublished studies from Dr. Joseph Luczkovich (personal communication). For both benthic invertebrates and zooplankton, densities were converted to biomass values using published values (Kilpatrick, unpublished and Heidelberg et al. 2004).

Production/Biomass ratio (P/B) is equivalent to the instantaneous rate of total mortality (Z), it is optional in Ecopath and is estimated from other input data when literature values are not available. Production includes fishery yields plus predation plus net migration plus biomass change plus other mortality, or $P/B = Z = F + M2 + NM + BA + M0$. The production values for this model were obtained from the Opitz (1996) 50 compartment model. Consumption/Biomass ratio (Q/B) is the intake of food by a group over a time per unit of biomass. Q/B ratios carry the same units as P/B. Entry of consumption/biomass ratio is optional and is calculated by Ecopath when literature data is not available provided other input values are entered. Q/B was entered into Ecopath and values were again obtained from the USVI-PR model (Opitz 1996).

Ecotrophic efficiency (EE) is the part of production that is not considered other mortality. Other mortality consists of organisms dying due to diseases, starvation, etc. (not predation) and ending up as detritus. Therefore, ecotrophic efficiency is a proportion

of production that is used within the system through biomass accumulation, predation, migration, or export. Ecotrophic Efficiency is expected to be between 0 and 1. Small prey species would have an EE close to one due to high predation pressure while apex predator species would have a lower EE. Ecotrophic efficiency may be entered but is usually calculated by Ecopath. All EE's in this model have been calculated by ECOPATH.

Balancing the Model. In order for Ecopath to function properly and make all possible estimates, the model must be mass balanced. This means that there is enough biomass in each compartment to support consumers of that compartment and that consumer biomass is not too high. A model is balanced when all ecotrophic efficiencies are between 0 and 1 and there are no negative respirations. Two approaches may be implemented when balancing the model, the auto mass balance function provided in the Ecopath with Ecosim 5.0 software (Kavanagh et al. 2004), and manual mass balancing.

The auto mass balance approach has the advantages of reducing the lengthy process and opportunity for errors of the manual approach, standardizing results, and allowing exploration of alternative solutions considering the confidence of the data. Repeated runs of the auto mass balance routine will eventually yield a balanced model. The auto mass balance capability adjusts input parameters based on the level of uncertainty as described by the data pedigree. The data pedigree is a part of Ecopath in which each input parameter is assigned a confidence level based on the data source. Where precise sampling is conducted within the system boundaries, there is a lower level of uncertainty and the data is likely to be unaltered by the auto mass balance approach.

Assumptions and estimates from literature values that have a low confidence level and a high level of uncertainty are altered first by the auto mass balance routine. The auto mass balance routine's main function is to reduce the ecotrophic efficiencies until they are all between 0 and 1. This is achieved through a series of steps, or iterations, of the biomass data. A detailed description of this routine is given by Kavanagh et al. (2004).

Although the auto mass balance routine may be more efficient in reducing the ecotrophic efficiencies, it does not allow one to formulate assumptions leading up to a change in input data and often makes undesired changes to original input values. Therefore, I and the other students working with Dr. Luczkovich on this model (Deirdre Barry, Becky Deehr, and Molly Kilpatrick) elected to balance the model manually by adjusting the diet matrix, biomass, P/B, and Q/B based on what we know about our sampling strategies. To do this we first identified where the major problems were. In our unbalanced model, we noticed that EE values of nearly all invertebrate compartments were very high and assumed that the suction dredge technique did not adequately sample all invertebrates. Thus, we began at the bottom living compartment (49) and worked our way up the trophic positions by modifying the diet matrix and increasing biomass values of the compartments for which we had the least confidence in our data. We regularly consulted the changes which Opitz (1996) made in these compartments to balance her model to determine if and how much each compartment was either under estimated (low biomass) or over consumed (high EE). Doing this one compartment at a time allowed us to monitor changes that took place in the ecotrophic efficiencies when a low biomass was increased to correct for sampling issues.

Another cause of high EE was possible when predators fed outside of the artificial sampling boundaries causing over-consumption of species resident in the sampling area. If so, then an import value of 0.90 was entered into the diet matrix meaning that 90% of the animal's diet comes from outside of the system. Thus, percent diet for each prey item was reduced by 10% and ecotrophic efficiencies were lowered. Next, we would consult the changes that Opitz (1996) made to the diets while balancing her model.

Compartments whose diets were not represented by data from Belize were adjusted according to the changes in Opitz. In cases where adjustments were needed, we matched the value of the most dominant prey compartment in Opitz and subtracted the difference from the compartment that had a high EE. For example in trying to reduce the EE of crabs, if a fish was consuming 40% crabs and 12% gastropods, yet Opitz had a value of 25% for gastropods, then in the Belize model diet matrix, gastropods were increased to 25% and crabs were reduced to 27%.

Upon careful examination of the diet matrix, we then began to increase the biomass and production/biomass of the benthic compartments to bring the EE values to below 1. Production was increased according to the changes made in Opitz (1996). In some cases, biomass values needed to be increased by orders of magnitude for compartments that were assumed to be underrepresented by sampling (as determined by Becky Deehr). For example, polychaetes (40) had an observed biomass of 0.57 g/m^2 from the suction dredge, yet in order for the EE to be below one, the biomass was increased to 23.509. No production values for any fish compartments were changed because we regarded those data to be most reliable due to bio-energetic modeling.

Biomass of fish compartments 6, 7, 8, and 11 were lowered so that there would be less consumption on the benthic prey items. The biomass of these fish compartments were perhaps overestimated because the visual census potentially allows fish to be counted twice.

To balance the fish compartments, we started with the ones that had the highest EE values. The fish compartments with high EE values, such as gobies (27) and blennies (26) were usually deemed underrepresented in the visual census by Deirdre Barry. By analyzing the diet matrix and increasing the biomass, we were able to bring the ecotrophic efficiency to below 10.0 for all compartments. Once this was achieved, we decided to use the auto-mass balance routine described above because small changes in biomass of one compartment would cause its prey compartments to become slightly unbalanced. The auto-mass balance feature handles these small problems much more efficiently without making drastic changes to input values. After two runs of the auto-mass balance routine the Calabash model was mass-balanced and all EE values were 1.0 or less.

Results

Fish Collection

The gear types used in this study combined to select for a wide variety of fish species, yet each had their own advantages and disadvantages. Table 3 provides a summary of the species collected for the diet study. Experimental gill nets were used most often and proved to be a very time-efficient method of gathering fish. They selected for 20 different species in 10 families ranging in size from 90 mm to 705 mm. These nets were set in three locations in front of the IMS laboratory that were primarily seagrass beds but were closely positioned to the adjacent coral reef.

Seine nets were used in shallow seagrass areas to collect fish of smaller sizes and juvenile stages of larger species. This method selected for 18 species of fish in 14 families ranging in size from 25 mm to 376 mm and was also very efficient. Only 19 of the 117 specimens collected with the seine net were found to have empty stomachs. A 1.8 m pole spear was used to collect 11 species of larger reef fish in 7 families ranging in size from 116 mm to 525 mm. All of the fish collected with the spear at the reef buoy and other locations had a recent meal while those that were speared underneath the dock had empty stomachs. Hook and line was used along the reef slope and lagoons and selected for 5 species of fish in 3 families ranging in size from 205 mm to 766 mm. Most of these specimens had empty stomachs or only the bait in the stomachs.

Stomach Content Analyses

The food-habit data are presented as percent dry mass in alphabetical order by family in Appendix A. Within each family, the individual fish are listed alphabetically

Table 3. Summary of fishes collected during July 2003 and June 2004 at Calabash Caye, Belize.

Family	Genus	species	Common	SP-CODE	n	# Sites	Gear	SL (mm)				# empty
								min	max	Avg.	Med.	
Acanthuridae	<i>Acanthurus</i>	<i>chirurgus</i>	Doctorfish	ACACHI	3	1	SN	25.1	56.0	39.0	36.0	1
Albulidae	<i>Albula</i>	<i>vulpes</i>	Bonefish	ALBVUL	35	4	GN	222.0	492.0	297.5	266.0	15
Atherinidae	<i>Atherinomorus</i>	<i>stipes</i>	Hardhead silverside	ATHSTI	24	1	SN	45.0	66.0	54.7	54.0	4
Aulostomidae	<i>Aulostomus</i>	<i>maculatus</i>	Trumpetfish	AULMAC	1	1	SP	370.0	370.0	370.0	370.0	0
Belontiidae	<i>Strongylura</i>	<i>notata</i>	Redfin needlefish	STRNOT	23	2	SN	122.0	376.0	136.5	184.0	7
Carangidae	<i>Caranx</i>	<i>bartholomaei</i>	Yellow jack	CARBAR	1	1	SN	25.0	25.0	25.0	25.0	0
	<i>Caranx</i>	<i>crysos</i>	Blue runner	CARCRY	1	1	SN	48.0	48.0	48.0	48.0	0
	<i>Caranx</i>	<i>latus</i>	Horse-eyed jack	CARLAT	2	2	GN	226.0	335.0	280.5	280.5	1
	<i>Caranx</i>	<i>ruber</i>	Bar jack	CARRUB	3	3	GN, HL, SP	195.0	345.0	257.7	233.0	2
	<i>Trachinotus</i>	<i>falcatus</i>	Permit	TRAFAL	4	2	GN, SN	58.0	124.0	89.6	88.3	1
	<i>Trachinotus</i>	<i>goodei</i>	Palometa	TRAGOO	1	1	GN	153.0	153.0	153.0	153.0	0
Carcharinidae	<i>Carcharhinus</i>	<i>limbatus</i>	Blacktip shark	CARLIM	1	1	GN	705.0	705.0	705.0	705.0	1
Dasyatidae	<i>Dasyatis</i>	<i>americana</i>	Southern stingray	DASAME	2	2	GN	325.0	479.0	402.0	402.0	1
Gerreidae	<i>Gerres</i>	<i>cinereus</i>	Yellowfin mojarra	GERCIN	46	6	GN, SN, SP	31.0	268.0	120.8	116.5	18
Gobiidae	<i>Bathygobius</i>	<i>mystacium</i>	Island frillfin	BATMYS	2	1	SN	55.0	60.0	57.5	57.5	1
Haemulidae	<i>Anisotremus</i>	<i>surinamensis</i>	Black margate	ANISUR	1	1	GN	380.0	380.0	380.0	380.0	0
	<i>Haemulon</i>	<i>aurolineatum</i>	Tomtate	HAEAU	1	1	GN	140.0	140.0	140.0	140.0	0
	<i>Haemulon</i>	<i>sciurus</i>	Bluestriped grunt	HAESCI	16	4	GN	127.0	250.0	169.4	160.5	9
	<i>Haemulon</i>	<i>flavolineatum</i>	French grunt	HAEFLA	10	2	GN	122.0	184.0	140.5	133.5	4
Holocentridae	<i>Holocentrus</i>	<i>adscensionis</i>	Squirrelfish	HOLADS	2	1	GN	173.0	185.0	179.0	179.0	0
	<i>Holocentrus</i>	<i>rufus</i>	Longspine squirrelfish	HOLRUF	3	2	GN	130.0	155.0	140.7	137.0	2
Labridae	<i>Lachnolaimus</i>	<i>maximus</i>	Hogfish	LACMAX	4	2	SP	224.0	338.0	277.0	273.0	0
	<i>Xyrichtys</i>	<i>splendens</i>	Green razorfish	XYRSPL	1	1	SN	36.0	36.0	36.0	36.0	0
Lutjanidae	<i>Lutjanus</i>	<i>analis</i>	Mutton snapper	LUTANA	3	2	GN, HL	212.0	284.0	246.7	244.0	0
	<i>Lutjanus</i>	<i>apodus</i>	Schoolmaster	LUTAPO	13	6	GN, SN, SP	48.0	300.0	173.8	159.0	5
	<i>Lutjanus</i>	<i>cyanopterus</i>	Cubera snapper	LUTCYA	1	1	SP	258.0	258.0	258.0	258.0	1
	<i>Lutjanus</i>	<i>griseus</i>	Gray snapper	LUTGRI	2	2	HL, SP	215.0	244.0	229.5	229.5	2
	<i>Lutjanus</i>	<i>jocu</i>	Dog snapper	LUTJOC	1	1	SP	525.0	525.0	525.0	525.0	1
	<i>Lutjanus</i>	<i>mahogoni</i>	Mahogany snapper	LUTMAH	7	3	GN, SP	163.0	264.0	194.7	181.0	5
	<i>Lutjanus</i>	<i>synagris</i>	Lane snapper	LUTSYN	3	2	GN, SN	32.0	226.0	107.0	63.0	1
	<i>Ocyurus</i>	<i>chrysurus</i>	Yellowtail snapper	OCYCHR	2	1	HL	205.0	220.0	212.5	212.5	2
Monacanthidae	<i>Cantherhines</i>	<i>pullus</i>	Orangespotted filefish	CANPUL	2	1	SN	30.0	36.0	33.0	33.0	0
Mullidae	<i>Pseudupeneus</i>	<i>maculatus</i>	Spotted goatfish	PSEMAC	2	1	SN	44.3	46.1	45.2	45.2	1
Pomacentridae	<i>Abudefduf</i>	<i>saxatilis</i>	Sergeant major	ABUSAX	23	2	SN	38.0	59.0	50.3	51.0	5
	<i>Siegastes</i>	<i>adustus</i>	Dusky damselfish	STEADU	2	1	SN	31.0	48.1	39.6	39.6	0
Scaridae	<i>Sparisoma</i>	<i>viride</i>	Stoplight parrotfish	SPAVIR	2	2	GN, SN	32.0	136.0	84.0	84.0	1
Serranidae	<i>Epinephelus</i>	<i>guttatus</i>	Red hind	EPIGUT	1	1	SP	312.0	312.0	312.0	312.0	1
Sphyraenidae	<i>Sphyraena</i>	<i>barracuda</i>	Great barracuda	SPHBAR	9	6	GN, SN	65.7	766.0	408.4	363.0	4
Syngnathidae	<i>Syngnathus</i>	<i>caribbaeus</i>	Caribbean pipefish	SYNCAR	1	1	SP	107.0	107.0	107.0	107.0	0

GN = gill net, HL = hand line, SN = seine net, SP = spear

by genus and then species. All organic material found in the stomachs of examined fish is reported in their diets even though it may not have been specifically sought as food. It was not uncommon to find sand, stones, or seagrass in the stomachs of known carnivores, or small crustaceans and mollusks in the stomachs of herbivorous fishes. This may represent items that were accidentally ingested with the prey or in an attempt to capture prey. In this study, plant material, which was found in the stomachs of carnivorous fishes, was included in the diet, whereas the study conducted by Randall (1967) omitted such occurrences from the diet analyses. Inorganic material was not included in the diets of the fishes analyzed from Calabash Caye because it presumably has no contribution to the energy of the fish.

Identification of organisms found in fish stomachs are given at the highest possible taxonomic level of species. Often times the condition of the organism only permits identification at the level of genera, family, or phylum. Therefore, the same species may be represented under several classifications. For example, the same species of crab may be labeled as *Portunus floridanus*, *Portunus sp.*, Portunidae, Brachyuran crab, crab, or simply crustacean depending on how much damage was done during mastication and how extensively it was digested.

Algae Feeders. There were five species examined in this study that were feeding predominately on algae, they are Doctorfish (*Acanthurus chirurgus*), Orangespotted filefish (*Cantherhines pullus*), Sergeant major (*Abudefduf saxatilis*), Dusky damselfish (*Stegastes adustus*), and juvenile Stoplight parrotfish (*Sparisoma viride*). The species listed here appear to be grazing very close to the substrate because there were often

pieces of sediment, forams, and associated seagrass found in the stomachs along with the algae. The damselfish and parrotfish selected for the harder, red coralline algae while the other three species were found to feed on the softer green and brown algae. Overall, these herbivorous fishes fed more on green and brown algae than they did red algae.

Plankton feeders. No fish examined were found to consume phytoplankton, but some were found to feed upon organisms that make up the zooplankton (Table 1). The Hardhead silverside (*Atherinomorus stipes*) and tomtate (*Haemulon aurolineatum*) had stomachs containing copepods and eggs or larvae from fish, arthropods and mollusks. The silversides possess relatively long and fine gill rakers for sieving out small crustaceans and other plankters (Hiatt and Strasburg 1960) while the tomtate most likely selected organisms from the plankton by visual means. Two other species were found to feed on the benthonic fauna rather than on mid-water plankton. These are the juvenile Blue runner (*Caranx crysos*) and Green razorfish (*Xyrichtys splendens*), which consumed benthic copepods and amphipods.

Carnivores. The coral reef at Calabash Caye is abound with carnivorous fishes of all sizes that feed upon a variety of prey items. These can be separated into fossorial feeders that burrow and dig to feed on benthic organisms, those that consume larger epibenthic or mid-water fauna, and lastly the larger resident and roving carnivores that forage over the reefs at regular or irregular intervals. Combinations of any of these carnivorous feeding habits are common and evident in the prey items found in these fishes' stomachs.

Fossorial carnivores such as Bonefish (*Albula vulpes*) and Goatfish (*Pseudopenus maculatus*) have a mouth that is positioned sub-terminally and adapted for foraging in the sediment. These species were often found to have pieces of the sediment in their stomachs with a variety of crustaceans, annelids, and other benthic organisms. The diets of juvenile Yellow jack (*Caranx bartholomaei*), Permit (*Trachinotus falcatus*), Palometa (*Trachinotus goodei*), and Yellowfin mojarra (*Gerres cinereus*) reflect some degree of fossorial feeding habits evidenced by the presence of small benthic arthropods and worms in the stomachs.

There were many species found to feed on the epibenthos other than those mentioned above. The Southern stingray (*Dasyatis americana*), Black margate (*Anisotremus surinamensis*), Mutton snapper (*Lutjanus analis*), Schoolmaster (*Lutjanus apodus*), Mahogany snapper (*Lutjanus mahogoni*), and Lane snapper (*Lutjanus synagris*) rove the reefs and adjacent seagrass flats foraging on larger organisms such as crabs, hermit crabs, gastropods, and bivalves. Fishes preying upon similar benthic organisms that are considered to be resident cover smaller areas when searching for food and include Bluestriped grunts (*Haemulon sciurus*), French grunt (*Haemulon flavolineatum*), Squirrelfish (*Holocentrus adscensionis*), Longspine squirrelfish (*Holocentrus rufus*), and Hogfish (*Lachnolaimus maximus*).

Finally, the carnivorous fishes that feed higher up in the water column include resident Trumpet fish (*Aulostomus maculatus*) and the more motile Redfin needlefish (*Strongylura notata*). Species that possibly travel further distances to adjacent reef and seagrass areas to feed on mid-water organisms are Bar jack (*Caranx ruber*), Great

barracuda (*Sphyraena barracuda*), and the snapper mentioned above that are of larger sizes. These predators obtain a large percentage of their diet by eating other fish but are also capable of eating other invertebrates as well.

The Diet Matrix

The complete, 137 by 137 square diet matrix with 96 fish species and 41 non-fish groups is provided in digital format on accompanying CD. Constituents are listed in order of the compartment number to which Opitz (1996) (Table 2) assigned them in the 50-Box ECOPATH model so that the matrix could be easily collapsed to fit the aggregations of that model. Predators are listed in rows and the columns represent prey.

Food Web Visualizations

The 137 taxa in the Calabash Caye food web were analyzed using the REGE algorithm and a matrix of similarity coefficients was generated and is available in digital format. An increase in R^2 values from cluster optimization revealed 10 isotrophic classes ($R^2 = 0.523$) of fishes and 9 isotrophic classes ($R^2 = 0.428$) of non-fish groups (Figures 4 and 5) for a total of 19 separate classes or colors. Clusters 20 (autotrophs) and 21 (detritus) were not included in the cluster optimization but manually added as a separate color. Table 4 provides a list of these clusters and their respective members along with the color assigned to it in the food web diagram presented in Figures 6 and 7. Figure 6 shows the food web diagram created in NetDraw without labels and Figure 7 shows the diagram with labels. These are two-dimensional, multi-dimensional scaling (MDS) plots

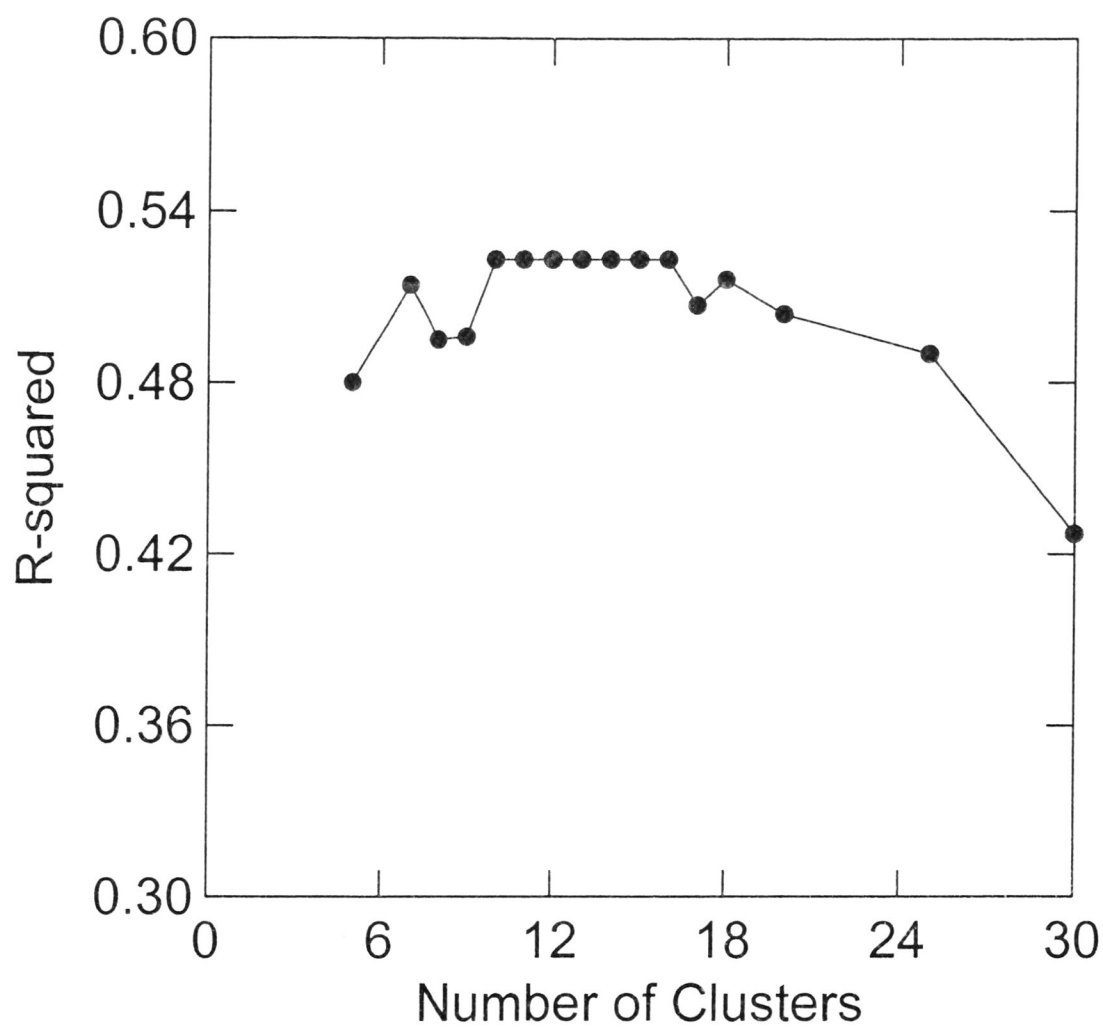


Figure 4. Plot of R^2 as it changes with the number of k-clusters of fish from the cluster optimization analysis using the REGE coefficients as a similarity

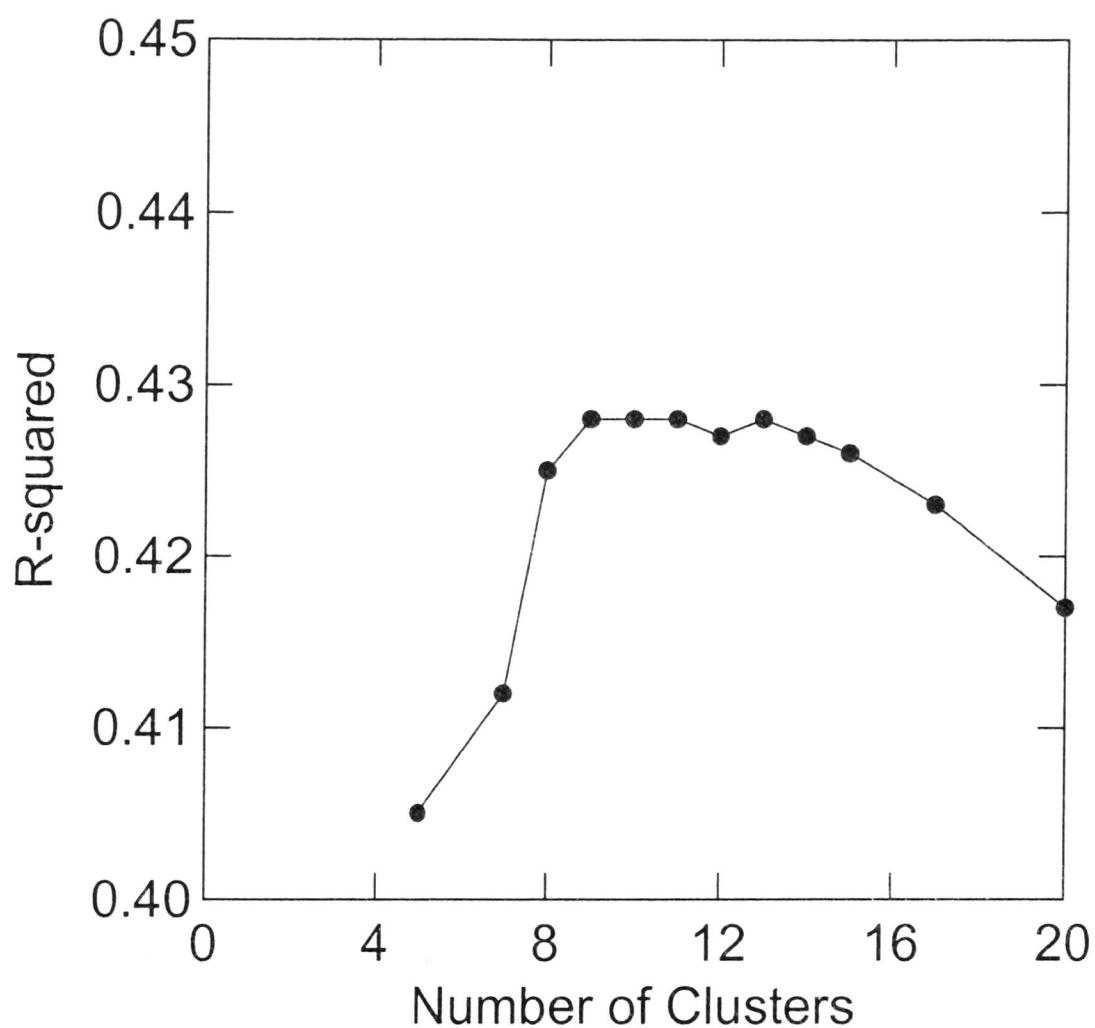


Figure 5. Plot of R^2 as it changes with the number of k-clusters of non-fish groups from the cluster optimization analysis using the REGE coefficients as a similarity.

Table 4. The 21 clusters of fish or non-fish groups from the 137 by 137 diet matrix based on the similarity of their REGE coefficients and used as a color attribute for NetDraw food web diagram.

Cluster	# of members	Members	Color	Shape
1	38	DASAME, AETNAR, TRAFALJUV, CARBARJUV, ALBVUL, LUTANA, LUTAPO, ANISUR, CHAACU, CHASTR, EUCARE, GERCIN, ANIVIR, HAEFLA, HAESCI, HOLASC, HOLRUF, LUTGRI, LUTSYN, MULMAR, PSEMAC, CALCAL, LACMAX, GYMFUN, EPISTR, BODRUF, HALRAD, MALPLU, CEPFUL, EPIADS, EPIGUT, HALBIV, HALGAR, HALPOE, HYPPUE, HALMAC, SERTIG, CANROS	red	circle
2	5	POMACR, CANMAC, HOLCIL, HOLTRI, POMPAR	dk. green	circle
3	6	CARLAT, CARRUB, STRNOT, LUTMOH, LUTCYA, BOTLUN	purple	circle
4	14	TRAGOOJUV, OCYCHR, HARCUL, HARHUM, OPIOGL, HAEAUR, CLEPAR, CHRCYA, ALLHAR, ATHSTI, JENLAM, ANCHPE, ANCLYO, GRALOR	yellow	circle
5	2	CARBAR, AULMAC	orange	circle
6	2	CARLIM, SPHBAR	dk. gray	circle
7	4	CHACAP, STEVAR, STELEU, STEPLA	lt. yellow	circle
8	2	ACAPOL, CAPCRU	aqua	circle
9	4	CARLATJUV, GERCINJUV, BATMYS, SYRSPL	lt. pink	circle
10	19	ABUSAXJUV, KYPINC, KYPSEC, ACABAH, ACACHI, ACACHIJUV, ACACOE, MELNIG, MICCHR, STEFUS, CANPUL, GNATHO, SCATAE, SPARUB, SPAVIR, SPAVIRJUV, SCAISE, SPAAUR, OPHATL	blue	circle
11	1	PYCONGONIDS	dk. Blue	diamond
12	9	BRITTLESTAR, HEMICHORDATE, BRYOZOANS, BARNACLES, ASCIDIANS, FIRECORAL, SEAFANS, SEANEMONES, STONEYCORAL	red/ orange	diamond
13	7	TURTLES, TANAIDS, STARFISH, CHITONS, SIPUNCULIDS, ECHIUROIDS, SEACUCUMBER	burgandy	diamond, thing
14	2	SCAPHOPODS, PRIAPULOIDS	white	diamond
15	6	CRAB, SHRIMPS, AMPHIPODS, GASTROPODS, POLYCHAETES, BIVALVES	lt. gray	diamond
16	5	OCTOPI, SPINYLOBSTER, STOMATOPODS, HERMITCRABS, URCHINS	olive	diamond
17	1	ISOPODS	blue/ green	diamond
18	3	SPONGES, ZOOPLANKTON, MICROFAUNA	lt. purple	diamond
19	2	BIRDS, SQUID	lt. blue	up triangle, diamond
20	3	BENTHICALGAE, SYMBIOALGAE, PHYTOPLANKTON, AND SEAGRASS	bright green	box
21	1	DETRITUS	black	down triangle

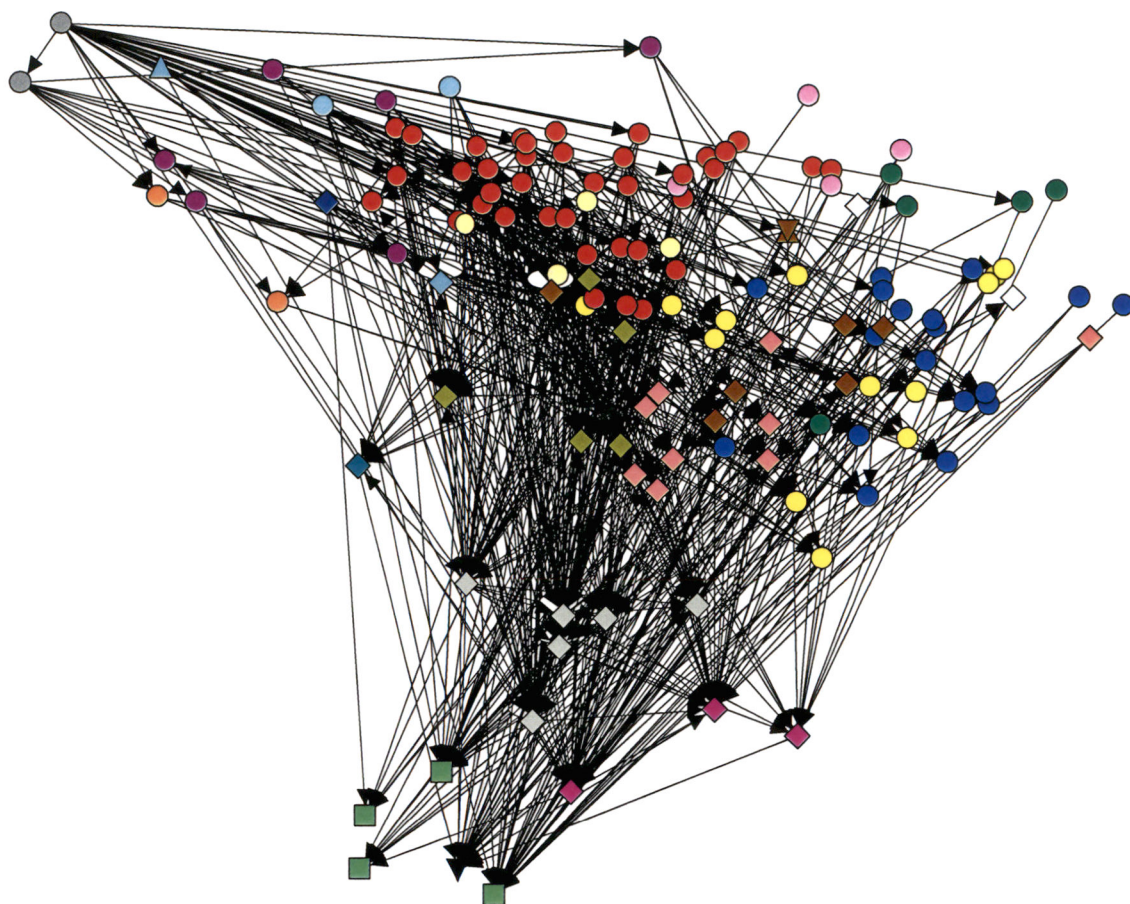


Figure 6. Food web diagram created in NetDraw of 137 fish and non-fish groups of Calabash Caye, Belize with coloration applied based on REGE similarities.

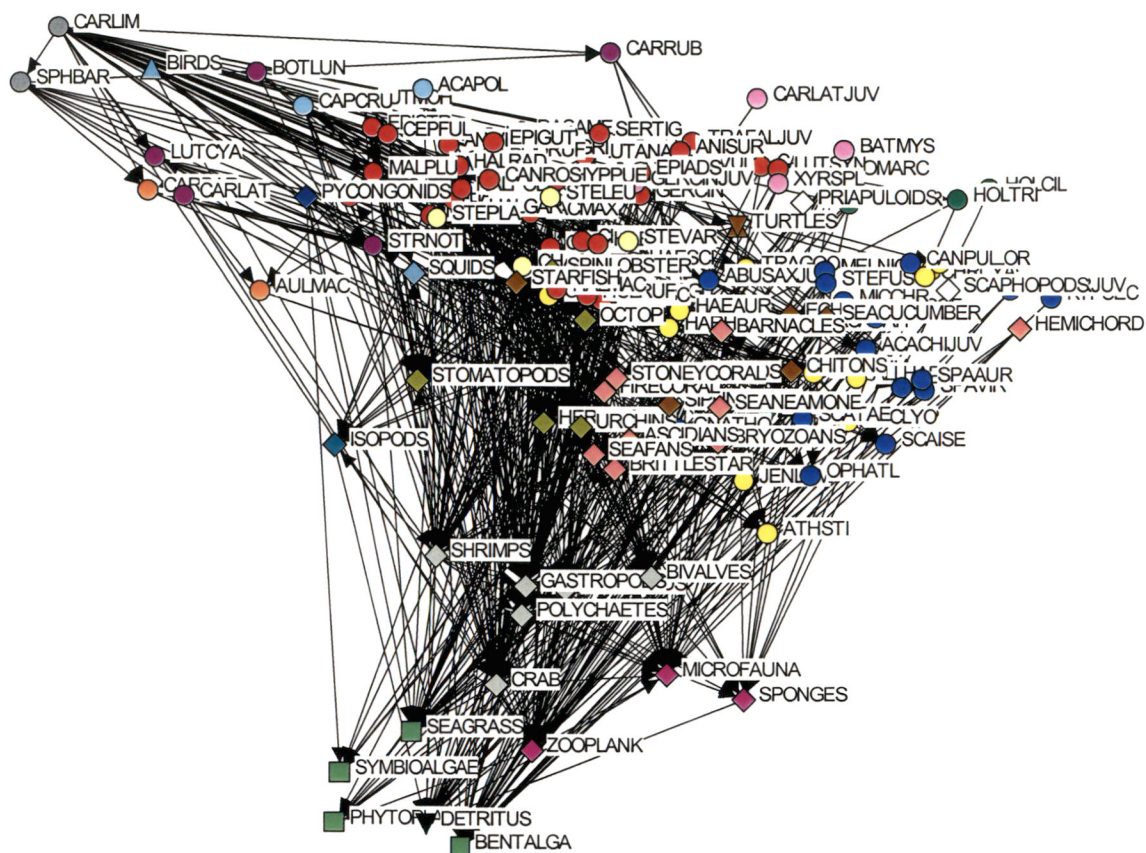


Figure 7. Food web diagram of Calabash Caye, Belize created in NetDraw with labels turned on.

of the REGE coefficients with the color classes from the cluster analysis used to code the “isotrophic” classes. The lines from nodes connect only to prey items that are greater than 2% of the diet so that the food web diagram represents the more important predator-prey interactions. The diagram has been oriented so that primary producers are at the bottom and the predators are at the top. A different shape of node was given to taxa of fish (circle), birds (triangle), reptiles (geometric shape), invertebrates (diamond), autotrophs (square), and detritus (downward triangle).

A more simplified depiction of this food web was generated from the 50 compartment (Table 2) diet matrix obtained from the balanced Ecopath model described below. The color classes are different from those above and are given in Table 5 but the shapes of the nodes are the same. Figure 8 is a multi-dimensional scaling plot of the 50 by 50 diet matrix.

Diet Comparisons

I have compared the diets of 20 species of fish from Calabash Caye with those from 1960’s West Indies using regular equivalence. Both sets of species under comparison had the same assumed set of predators so that any differences in the REGE coefficient is due solely to difference in their prey. Table 6 gives the REGE coefficients of the diets of 20 species eligible for comparison. Species that have a high REGE coefficient are equivalent because they are equally related to equivalent others based on their diets. REGE coefficients ranged from 0.350 (Bar jack) to .956 (Reef squirrelfish). To determine if the fish of the West Indies 1960’s will cluster into the same “isotrophic classes” as those from this study, I repeated the cluster optimization routine used to color

Table 5. 16 classes of the 50 x 50 diet matrix used for coloring members of groups in figure 8.

Cluster	Compartment Members	Color	Shape
1	9, 10, 11, 20, 22, 23, 24, 25, 26	blue	circle
2	6, 8, 12, 13, 14, 21	red	circle
3	27	light blue	circle
4	18	dark green	circle
5	3	burgundy	circle
6	19	orange	circle
7	2	gray	circle
8	5, 7, 15, 16, 17	yellow	circle
9	1, 4	light pink	circle
10	31, 32	purple	diamond
11	30, 33, 34, 35, 36, 37, 38, 39, 41, 43, 45	light gray	diamond, thing
12	28	light blue	up triangle
13	29	light green	diamond
14	42, 44, 46, 47	teal	diamond
15	48, 49	green	box
16	50	black	down triangle

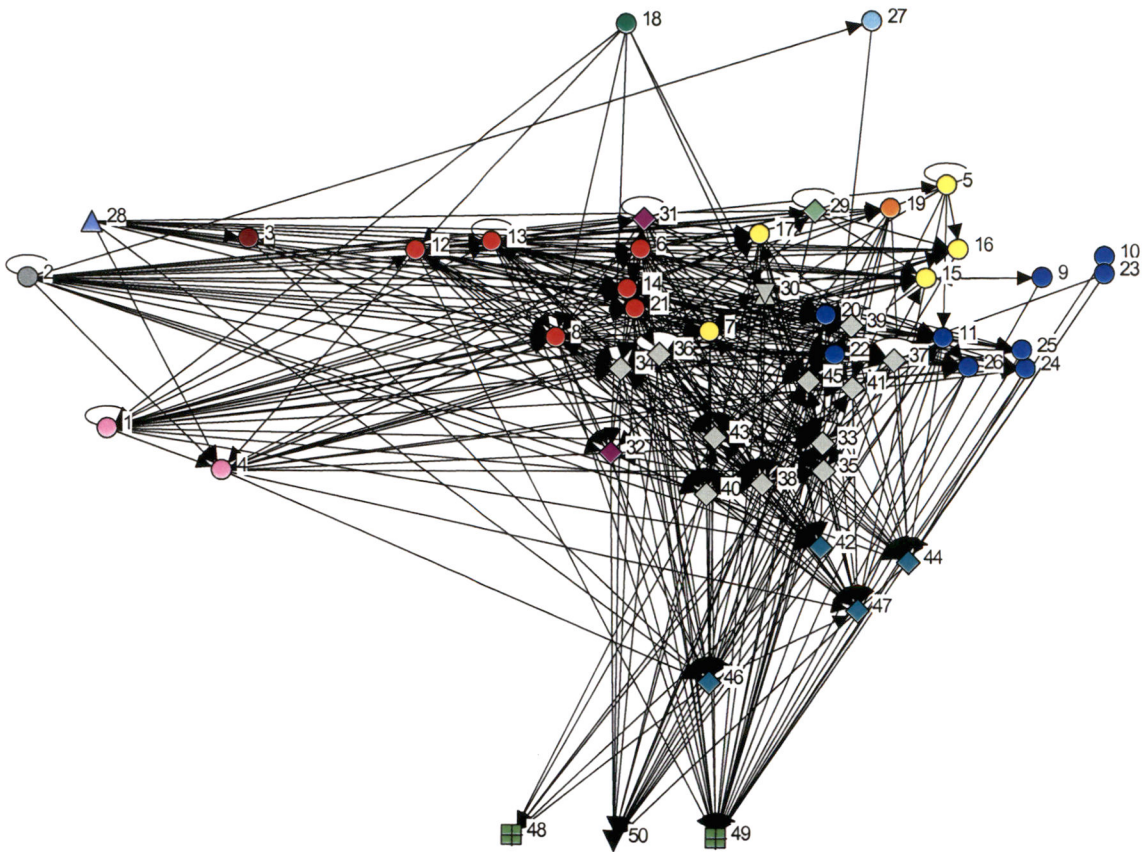


Figure 8. MDS plot of the 50 by 50 compartment food web model of Calabash Caye, Belize.

Table 6. REGE similarity coefficients of the diets of fishes collected at Calabash Caye, Belize 2003 and 2004 and those from the West Indies, 1967.

<i>Genus</i>	<i>Species</i>	Common name	REGE
<i>Holocentrus</i>	<i>ascensionis</i>	Reef squirrelfish	0.956
<i>Holocentrus</i>	<i>rufus</i>	Longspine squirrelfish	0.927
<i>Atherinomorus</i>	<i>stipes</i>	Hardhead silversides	0.872
<i>Lachnolaimus</i>	<i>maximus</i>	Hogfish	0.837
<i>Lutjanus</i>	<i>analis</i>	Mutton snapper	0.822
<i>Lutjanus</i>	<i>mohagoni</i>	Mahogany snapper	0.816
<i>Haemulon</i>	<i>sciurus</i>	Bluestriped grunt	0.752
<i>Gerres</i>	<i>cinereus</i>	Yellowfin mojarra	0.724
<i>Haemulon</i>	<i>flavolineatum</i>	French grunt	0.715
<i>Dasyatis</i>	<i>americana</i>	Southern stingray	0.688
<i>Albula</i>	<i>vulpes</i>	Bonefish (CC - FL Keys)	0.676
<i>Haemulon</i>	<i>aurolineatum</i>	Tomtate	0.672
<i>Lutjanus</i>	<i>synagris</i>	Lane snapper	0.659
<i>Stegastes</i>	<i>fuscus</i>	Dusky damselfish	0.615
<i>Xyrichtys</i>	<i>splendens</i>	Green razorfish	0.592
<i>Lutjanus</i>	<i>apodus</i>	Schoolmaster	0.591
<i>Sphyraena</i>	<i>barracuda</i>	Great barracuda	0.581
<i>Anisotremus</i>	<i>surinamensis</i>	Black margate	0.521
<i>Aulostomus</i>	<i>maculatus</i>	Trumpetfish	0.481
<i>Caranx</i>	<i>ruber</i>	Bar jack	0.350

the food web diagram. As the number of clusters changed, the total similarity within classes changed, and is represented by an R^2 value. Figure 9 shows that a maximum R^2 of 0.481 was obtained for clusters 9 through 14. Thus, the nine clusters presented in Table 7 are the simplest solution to explain the variability in the diets. Each cluster represents an “isotrophic” class in which members of the cluster have similar prey items and similar predators. Of the 20 species under comparison, only Green razorfish (XYRSPL), Tomtate (HAEAUR), Trumpetfish (AULMAC), and Bar jack (CARRUB) from this study and Randall (1967) were placed into separate clusters.

To better visualize any differences in trophic position, I regenerated the 137 node food web diagram above with 20 additional nodes for fish with diets from the West Indies, one each for the species under comparison (Figure 10). The species are arranged by a non-metric multidimensional scaling so that fish with similar prey and similar predators are positioned close to each other. Of the twenty species being compared, 6 were identified by the distances between them, as having some significant dissimilarity in diet.

The ECOPATH Model

Results of Mass Balancing. The basic parameterization of the original input data, unbalanced, is provided in Table 8. Biomass, production/biomass (P/B), and consumption/biomass (Q/B) were all entered while ecotrophic efficiency (EE) and production/consumption (P/Q) values were estimated by ECOPATH. The compartments with the largest EE's are mostly the biomasses of the benthic compartments were greatly increased under the assumption that our sampling methods underrepresented many

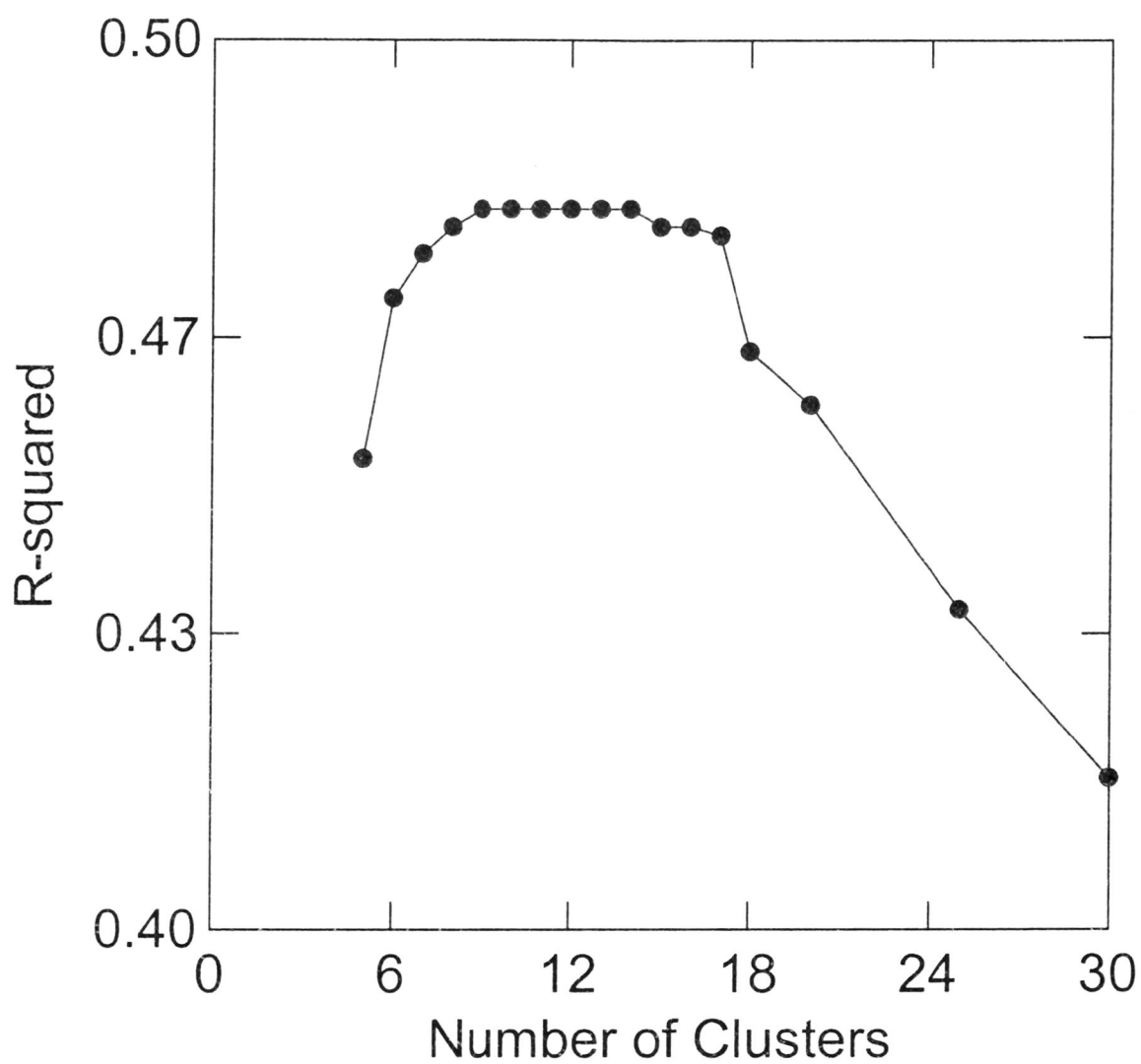


Figure 9. Plot of R^2 as it changes with the number of k-clusters of fish from the cluster optimization routine using REGE coefficients as a similarity measure.

Table 7. 9 k-clusters based on REGE coefficients as determined by the cluster optimization routine. The 40 species in bold are those in which diets were compared.

Cluster	# of members	Members
1	15	TRAGOOJUV, HARCUL, HARHUM, OPIOGL, HAEAUR , CLEPAR, CHRCYA, XYRSPLUSVI , ALLHAR, ATHSTI , ATHSTIUSVI , JENLAM, ANCHP, ANCLYO, GRALOR
2	56	DASAME , DASAMEUSVI , AETNAR, TRAFALJUV, CARBARJUV, ALBVUL , ALBVULFLKEY , LUTANA , LUTANAUSVI , LUTAPO , LUTAPOUSVI , ANISUR, ANISURUSVI, OCYCHR, CHAACU, CHACAP, CHASTR, EUCARE, GERCIN , GERCINUSVI , ANIVIR, HAEAURUSVI , HAEFLA , HAEFLAUSVI , HAESCI , HAESCIUSVI , HOLASC , HOLASCUSVI , HOLRUF , HOLRUFUSVI , LUTGRI, LUTSYN, LUTSYNUSVI, MULMAR, PSEMAC, CALCAL, LACMAX , LACMAXUSVI , GYMFUN, EPISTR, AULMACUSVI , BODRUF, HALRAD, MALPLU, CAPCRU, CEPFUL, EPIADS, EPIGUT, HALBIV, HALGAR, HALPOE, HYPPUE, HALMAC, SERTIG, CANROS, OPSBET
3	6	CARBAR, CARLAT, STRNOT, LUTMOH , LUTMOHUSVI , LUTCYA, BOTLUN
4	2	CARRUB , AULMAC
5	3	ACAPOL, STELEU, STEPLA
6	21	ABUSAXJUV, KYPINC, KYPSEC, ACABAH, ACACHI, ACACHIJUV, ACACOE, MELNIG, MICCHR, STEFUS , STEFUSUSVI , STEVAR, CANPUL, GNATHO, SCATAE, SPARUB, SPAVIR, SPAVIRJUV, SCAISE, SPAAUR, OPHATL
7	4	CARLIM, CARRUBUSVI , SPHBAR , SPHBARUSVI
8	4	CARLATJUV, GERCINJUV, BATMYS, XYRSPL
9	5	POMARC, CANMAC, HOLCIL, HOLTRI, POMPAR

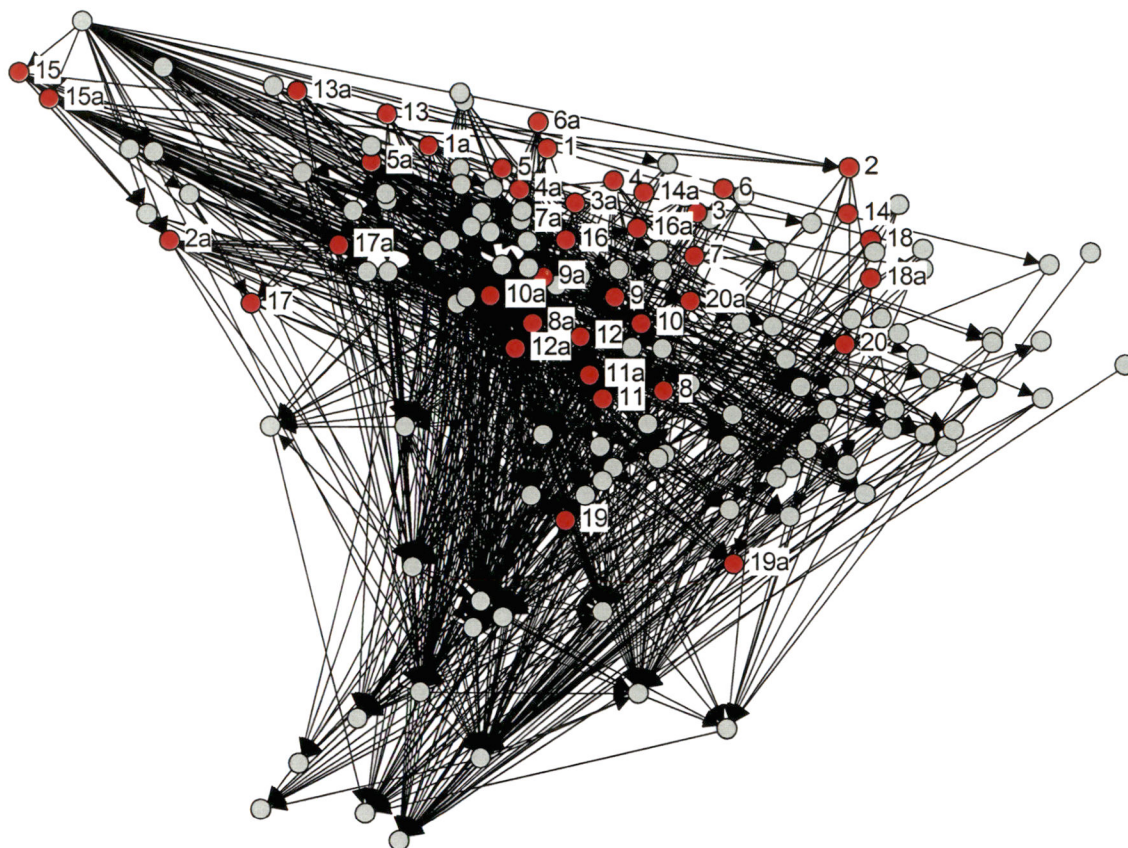


Figure 10. Food web diagram comparing diets from Calabash Caye and the West Indies (Randall 1967). Only the fish 20 fish in discussion are colored red. Fish species are identified as follows with those from the West Indies represented by an "a". (1) Southern stingray, (2) Bar jack, (3) Bonefish, (4) Mutton snapper, (5) Schoolmaster, (6) Black margate, (7) Yellowfin mojarra, (8) Tomtate, (9) French grunt, (10) Bluestriped grunt, (11) Reef squirrelfish, (12) Longspine squirrelfish, (13) Mahogany snapper, (14) Lane snapper, (15) Barracuda, (16) Hogfish, (17) Trumpetfish, (18) Green razorfish, (19) Hardhead silversides, (20) Dusky damselfish.

Table 8. Basic parameterization of unbalanced Ecopath model of Calabash Caye, Belize.

Group Name	Trophic Level	Habitat Area (fraction)	Biomass in hab. area (gC/m ²)	biomass (gC/m ²)	Production/Biomass (year)	Consumption/Biomass (year)	Ecotrophic Efficiency	Production/Consumption
1 LGSHARKS/RAYSC	4.04	1.000	1.236	1.236	0.240	4.900	0.306	0.049
2 SHARKS/SCOMBRID	4.58	1.000	0.00000001	0.00000001	0.340	9.150	0.035	0.037
3 LGJACKSC	3.87	1.000	0.103	0.103	0.525	5.700	0.305	0.092
4 IMJACKSC	4.27	1.000	6.163	6.163	1.170	9.150	0.241	0.128
5 SMJACKSC	3.83	1.000	0.075	0.075	0.830	12.500	0.015	0.066
6 IMREEFFISHC1	3.66	1.000	29.928	29.928	0.580	6.850	0.151	0.085
7 LGIMSCHOOLFISHP	3.89	1.000	31.92	31.92	0.680	12.400	0.349	0.055
8 IMREEFFISHC2	3.81	1.000	35.52	35.52	1.265	10.300	0.497	0.123
9 HEMIRAMPHIDAEH	2.56	1.000	0.00000001	0.00000001	1.230	39.100	0.086	0.031
10 KYPHOSIDAEH	2.00	1.000	0.00000001	0.00000001	0.600	23.600	0.000	0.025
11 IMREEFFISHH	2.11	1.000	27.354	27.354	0.710	25.650	0.093	0.028
12 LGREEFFISHC	4.14	1.000	3.905	3.905	0.380	3.900	2.189	0.097
13 IMREEFFISHC3	3.95	1.000	11.405	11.405	0.640	6.400	0.418	0.100
14 SMREEFFISHC1	3.91	1.000	1.893	1.893	1.665	9.800	1.231	0.170
15 SMSCHOOLFISHPEL	3.79	1.000	2.941	2.941	3.540	18.850	7.247	0.188
16 ENGRAULIDAEH	3.80	1.000	0.019	0.019	2.835	43.400	537.689	0.065
17 SMREEFFISHC2	4.13	1.000	0.898	0.898	3.820	14.650	0.878	0.261
18 LGGROUPERS	4.41	1.000	0.00000001	0.00000001	0.370	2.300	0.000	0.161
19 IMREEFFISHC4	3.00	1.000	1.093	1.093	0.550	6.000	14.257	0.092
20 SMREEFFISHO1	2.50	1.000	1.25	1.25	1.600	16.400	0.101	0.098
21 SMREEFFISHO2	3.25	1.000	0.072	0.072	1.505	16.000	4.801	0.094
22 SMREEFFISHO3	2.48	1.000	0.096	0.096	2.530	39.700	26.029	0.064
23 LGSCARIDAEH	2.00	1.000	0.00000001	0.00000001	0.850	13.500	0.000	0.063
24 IMSCARIDAEH	2.01	1.000	28.135	28.135	1.155	20.750	0.445	0.056
25 SMSCARIDAEH	2.01	1.000	7.026	7.026	0.940	33.900	1.114	0.028
26 BLENNIIDAEH	2.01	1.000	0.012	0.012	2.840	36.100	294.342	0.079
27 SMGOBIIDAEH	4.02	1.000	0.000036	0.000036	3.140	17.450	0.000	0.180
28 SEABIRDS	4.78	1.000	0.015	0.015	5.400	80.000	0.000	0.068
29 SQUIDS	4.84	1.000	1	1	1.250	18.700	5.417	0.067
30 SEATURTLES	2.81	1.000	0.015	0.015	0.150	3.500	18.302	0.043
31 OCTOPUSES	3.72	1.000	28	28	1.900	6.760	0.080	0.281
32 LOBSTERS	2.96	1.000	1.09	1.09	0.450	7.400	1.083	0.061
33 CRABS	2.68	1.000	1.158	1.158	1.170	14.000	190.582	0.084
34 SHRMP/HCRB/STOM	3.60	1.000	0.981	0.981	1.800	26.900	59.305	0.067
35 SMBENTHARTHROPO	3.02	1.000	0.0255	0.0255	2.400	125.500	1300.442	0.019
36 ASTEROIDS	3.00	1.000	0.000911	0.000911	0.490	3.240	744.036	0.151
37 ECHINOIDS	2.56	1.000	3.77	3.77	1.100	3.700	2.170	0.297
38 GASTROPODS	2.70	1.000	1.027	1.027	2.500	14.000	73.546	0.179
39 CHITONS/SCAPHOP	2.62	1.000	0.0204	0.0204	0.340	11.700	895.002	0.029
40 POLY/PRIA/OPHIU	3.14	1.000	0.57	0.57	4.140	61.600	62.139	0.067
41 HOL/SIP/ECH/HEM	2.15	1.000	0.00253	0.00253	0.290	3.360	7159.524	0.086
42 BIVALVES	2.12	1.000	0.365	0.365	2.230	9.500	50.126	0.235
43 ASCI/BARN/BRYOZ	2.59	1.000	2.091	2.091	2.300	24.000	2.265	0.096
44 SPONGES	2.00	1.000	1.167	1.167	1.500	5.000	21.896	0.300
45 CORALS/ANEMONES	2.87	1.000	4.752	4.752	1.090	9.000	3.316	0.121
46 ZOOPLANKTON	2.80	1.000	0.0209	0.0209	40.000	165.000	409.274	0.242
47 DECOMP/MICROFAU	2.00	1.000	5.4	5.4	195.000	2050.000	0.093	0.095
48 Phytoplankton	1.00	1.000	42	42	70.000	-	0.010	-
49 Benthic prod.	1.00	1.000	2230	2230	13.250	-	0.046	-
50 Detritus	1.00	1.000	2000	2000	-	-	0.336	-

benthic species. At this point, the fish compartments remained relatively unchanged with exception to compartments 6, 7, 8, and 11. The biomass of these compartments was lowered to reduce the EE of its prey under the assumption that our sampling methods overestimated these resident reef fish. After manually mass-balancing the benthic compartments and those fish groups with EE's larger than 10.0, we then obtained a model in which all 50 compartments had EE's less than 10.0 (Table 9). From here, we began to use the auto-mass balance feature to obtain EE values of 1 or less. This routine reduces the sum of excess EE of all compartments by adjusting biomass and dietary data. Following one run (1000 iterations) of the auto mass-balance routine, the maximum EE was 1.142. On the 85th iteration of the second run, the maximum EE was 1.0. Table 10 gives the basic estimates of this balanced model with the final input values. Tables 11 and 12 are the balanced and unbalanced diet matrices from the Ecopath model.

The respiration/biomass (R/B) ratio reflects the activity level of an organism. R/B should be between 1-10/yr for fish and as high as 50-100/yr for copepods. This value can be raised or lowered by adjusting the proportion of food that is not assimilated on the basic input form. Increasing the proportion of consumption that is unassimilated will leave less energy to respiration, thereby reducing the R/B ratio. By default, Ecopath assigns all compartments a value of 0.200. To obtain reasonable R/B ratios, we adjusted the Unassimil. /Consumption value for 13 groups (9, 10, 11, 16, 18, 22, 24, 25, 26, 28, 31, 32, 33) (Table 13).

Table 9. Basic parameterization following manual mass-balancing of the Ecopath model of Calabash Caye, Belize.

Group Name	Trophic Level	Habitat Area (fraction)	Biomass in hab. area (gC/m ²)	Biomass (gC/m ²)	Production/Biomass (year)	Consumption/Biomass (year)	Ecotrophic Efficiency	Production/Consumption
1 LGSHARKS/RAYSC	3.80	1.000	1.236	1.236	0.240	4.900	0.031	0.049
2 SHARKS/SCOMBRID	4.36	1.000	0.00000001	0.00000001	0.340	9.150	0.035	0.037
3 LGJACKSC	3.57	1.000	0.103	0.103	0.525	5.700	0.456	0.092
4 IMJACKSC	4.05	1.000	6.163	6.163	1.170	9.150	0.342	0.128
5 SMJACKSC	3.63	1.000	0.075	0.075	0.830	12.500	0.015	0.066
6 IMREEFFISHC1	3.50	1.000	14.964	14.964	0.580	6.850	0.067	0.085
7 LGIMSCHOOLFISHP	3.67	1.000	11.172	11.172	0.680	12.400	3.480	0.055
8 IMREEFFISHC2	3.59	1.000	17.711	17.711	1.265	10.300	4.786	0.123
9 HEMIRAMPHIDAEH	2.52	1.000	0.00000001	0.00000001	1.230	39.100	0.086	0.031
10 KYPHOSIDAEH	2.00	1.000	0.00000001	0.00000001	0.600	23.600	0.000	0.025
11 IMREEFFISHH	2.10	1.000	13.677	13.677	0.710	25.650	2.690	0.028
12 LGREEFFISHC	3.97	1.000	6	6	0.380	3.900	8.945	0.097
13 IMREEFFISHC3	3.77	1.000	11.405	11.405	0.640	6.400	7.810	0.100
14 SMREEFFISHC1	3.66	1.000	3.786	3.786	1.665	9.800	5.508	0.170
15 SMSCHOOLFISHPEL	3.60	1.000	2.941	2.941	3.540	18.850	4.415	0.188
16 ENGRAULIDAEH	3.60	1.000	3.325	3.325	2.835	43.400	1.781	0.065
17 SMREEFFISHC2	3.76	1.000	0.898	0.898	3.820	14.650	5.642	0.261
18 LGGROUPEH	4.29	1.000	0.00000001	0.00000001	0.370	2.300	0.000	0.161
19 IMREEFFISHC4	3.00	1.000	1.093	1.093	0.550	6.000	8.142	0.092
20 SMREEFFISHO1	2.43	1.000	1.25	1.25	1.600	16.400	1.529	0.098
21 SMREEFFISHO2	3.02	1.000	0.072	0.072	1.505	16.000	2.231	0.094
22 SMREEFFISHO3	2.43	1.000	0.96	0.96	2.530	39.700	2.254	0.064
23 LGSCARIDAEH	2.00	1.000	0.00000001	0.00000001	0.850	13.500	0.000	0.063
24 IMSCARIDAEH	2.01	1.000	28.135	28.135	1.155	20.750	0.262	0.056
25 SMSCARIDAEH	2.01	1.000	7.026	7.026	0.940	33.900	0.874	0.028
26 BLENNIIDAEH	2.01	1.000	0.6	0.6	2.840	36.100	1.905	0.079
27 SMGOBIIDAEH	3.83	1.000	0.000036	0.000036	3.140	17.450	0.000	0.180
28 SEABIRDS	4.58	1.000	0.015	0.015	5.400	80.000	0.000	0.068
29 SQUIDS	4.01	1.000	1	1	1.250	18.700	2.132	0.067
30 SEATURTLES	2.76	1.000	0.015	0.015	0.150	3.500	1.884	0.043
31 OCTOPUSES	3.36	1.000	8.4	8.4	1.900	6.760	0.831	0.281
32 LOBSTERS	2.90	1.000	1.09	1.09	0.450	7.400	7.887	0.061
33 CRABS	2.60	1.000	19	19	1.600	14.000	3.957	0.114
34 SHRMP/HCRB/STOM	3.16	1.000	15	15	2.800	26.900	1.820	0.104
35 SMBENTHARTHROPO	2.83	1.000	22	22	5.000	62.750	1.143	0.080
36 ASTEROIDS	2.75	1.000	3	3	0.490	3.240	3.526	0.151
37 ECHINOIDS	2.25	1.000	9.5	9.5	1.100	3.700	5.055	0.297
38 GASTROPODS	2.43	1.000	29	29	2.800	14.000	1.638	0.200
39 CHITONS/SCAPHOP	2.62	1.000	31.5	31.5	0.340	11.700	1.363	0.029
40 POLY/PRIA/OPHIU	2.56	1.000	25.5	25.5	5.200	61.600	1.150	0.084
41 HOL/SIP/ECH/HEM	2.15	1.000	30	30	0.310	3.360	1.224	0.092
42 BIVALVES	2.12	1.000	35	35	2.230	9.500	2.085	0.235
43 ASCI/BARN/BRYOZ	2.54	1.000	45	45	2.300	20.000	0.923	0.115
44 SPONGES	2.00	1.000	95	95	1.500	5.000	1.083	0.300
45 CORALS/ANEMONES	2.78	1.000	97	97	1.090	9.000	1.038	0.121
46 ZOOPLANKTON	2.60	1.000	26	26	40.000	165.000	1.222	0.242
47 DECOMP/MICROFAU	2.00	1.000	15	15	280.000	2050.000	0.830	0.137
48 Phytoplankton	1.00	1.000	42	42	70.000	-	0.532	-
49 Benthic prod.	1.00	1.000	2000	2000	13.250	-	0.102	-
50 Detritus	1.00	1.000	2000	2000	-	-	0.992	-

Table 10. Basic parameterization of balanced Ecopath model of Calabash Caye, Belize.

Group Name	Trophic Level	Habitat Area (fraction)	Biomass in hab. area (gC/m2)	Biomass (gC/m2)	Production/Biomass (year)	Consumption/Biomass (year)	Ecotrophic Efficiency	Production/Consumption
1 LGSHARKS/RAYSC	3.66	1.000	0.247	0.247	0.240	4.900	0.032	0.049
2 SHARKS/SCOMBRID	4.17	1.000	0.000000002	0.000000002	0.340	9.150	0.052	0.037
3 LGJACKSC	3.41	1.000	0.027	0.027	0.525	5.700	0.924	0.092
4 IMJACKSC	3.91	1.000	1.233	1.233	1.170	9.150	0.930	0.128
5 SMJACKSC	3.63	1.000	0.015	0.015	0.830	12.500	0.016	0.066
6 IMREEFFISHC1	3.37	1.000	2.394	2.394	0.580	6.850	0.178	0.085
7 LGIMSCHOOLFISHP	3.54	1.000	7.15	7.15	0.680	12.400	0.840	0.055
8 IMREEFFISHC2	3.35	1.000	6.75	6.75	1.265	10.300	1.000	0.123
9 HEMIRAMPHIDAEH	2.10	1.000	0.000000002	0.000000002	1.230	39.100	0.127	0.031
10 KYPHOSIDAEH	2.00	1.000	0.000000001	0.000000001	0.600	23.600	0.000	0.025
11 IMREEFFISHH	2.07	1.000	7.003	7.003	0.710	25.650	0.948	0.028
12 LGREEFFISHC	3.83	1.000	3.072	3.072	0.380	3.900	0.973	0.097
13 IMREEFFISHC3	3.63	1.000	4.894	4.894	0.640	6.400	1.000	0.100
14 SMREEFFISHC1	3.49	1.000	4.886	4.886	1.665	9.800	0.996	0.170
15 SMSCHOOLFISHPEL	3.59	1.000	3.529	3.529	3.540	18.850	0.918	0.188
16 ENGRAULIDAEH	3.60	1.000	4.33	4.33	2.835	43.400	0.778	0.065
17 SMREEFFISHC2	3.63	1.000	1.257	1.257	3.820	14.650	0.979	0.261
18 LGROUPERS	3.90	1.000	0.000000002	0.000000002	0.370	2.300	0.000	0.161
19 IMREEFFISHC4	2.99	1.000	1.967	1.967	0.550	6.000	0.900	0.092
20 SMREEFFISHO1	2.40	1.000	1	1	1.600	16.400	0.927	0.098
21 SMREEFFISHO2	2.93	1.000	0.0664	0.0664	1.505	16.000	0.983	0.094
22 SMREEFFISHO3	2.41	1.000	1.152	1.152	2.530	39.700	0.996	0.064
23 LGSCARIDAEH	2.00	1.000	0.000000001	0.000000001	0.850	13.500	0.000	0.063
24 IMSCARIDAEH	2.01	1.000	28.135	28.135	1.155	20.750	0.087	0.056
25 SMSCARIDAEH	2.01	1.000	7.026	7.026	0.940	33.900	0.340	0.028
26 BLENNIIDAEH	2.01	1.000	1.067	1.067	2.840	36.100	0.574	0.079
27 SMGOBIIDAEH	3.51	1.000	0.00000072	0.00000072	3.140	17.450	0.000	0.180
28 SEABIRDS	4.50	1.000	0.003	0.003	5.400	80.000	0.000	0.068
29 SQUIDS	3.89	1.000	0.8	0.8	1.250	18.700	0.969	0.067
30 SEATURTLES	2.73	1.000	0.00614	0.00614	0.150	3.500	0.974	0.043
31 OCTOPUSES	3.31	1.000	3.025	3.025	1.900	6.760	0.957	0.281
32 LOBSTERS	2.75	1.000	1.986	1.986	0.450	7.400	1.000	0.061
33 CRABS	2.43	1.000	26.6	26.6	1.600	14.000	1.000	0.114
34 SHRMP/HCRB/STOM	3.09	1.000	5.199	5.199	2.800	26.900	1.000	0.104
35 SMBENTHARTHROPO	2.51	1.000	5.949	5.949	5.000	62.750	1.000	0.080
36 ASTEROIDS	2.71	1.000	5.4	5.4	0.490	3.240	0.992	0.151
37 ECHINIDS	2.24	1.000	17.1	17.1	1.100	3.700	0.792	0.297
38 GASTROPODS	2.37	1.000	26.789	26.789	2.800	14.000	1.000	0.200
39 CHITONS/SCAPHOP	2.62	1.000	32.997	32.997	0.340	11.700	1.000	0.029
40 POLY/PRIA/OPHIU	2.50	1.000	23.509	23.509	5.200	61.600	1.000	0.084
41 HOL/SIP/ECH/HEM	2.15	1.000	30.978	30.978	0.310	3.360	0.999	0.092
42 BIVALVES	2.12	1.000	43.345	43.345	2.230	9.500	1.000	0.235
43 ASCI/BARN/BRYOZ	2.54	1.000	45	45	2.300	20.000	0.664	0.115
44 SPONGES	2.00	1.000	95	95	1.500	5.000	0.763	0.300
45 CORALS/ANEMONES	2.66	1.000	109.51	109.51	1.090	9.000	0.618	0.121
46 ZOOPLANKTON	2.60	1.000	31.2	31.2	40.000	165.000	0.919	0.242
47 DECOMP/MICROFAU	2.00	1.000	15	15	280.000	1000.000	0.940	0.280
48 Phytoplankton	1.00	1.000	42	42	70.000	-	0.594	-
49 Benthic prod.	1.00	1.000	2000	2000	13.250	-	0.091	-
50 Detritus	1.00	1.000	2000	2000	-	-	0.569	-

Table 11 continued

	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1							0.041								
2															
3	0.001														
4	0.104														
5															
6	0.014														
7	0.139														
8	0.080	0.057					0.191								
9															
10															
11	0.017														
12	0.006	0.005					0.232								
13	0.006	0.012													
14	0.012	0.007				0.032									
15	0.044	0.026													
16	0.006	0.052													
17		0.002													
18															
19	0.003	0.016													
20															
21	0.005														
22		0.052	0.014							0.015					
23															
24	0.091	0.021													
25	0.095	0.016													
26		0.046	0.014							0.014					
27															
28															
29	0.005														
30							0.035								
31	0.036	0.009				0.014									
32	0.007						0.426								
33	0.158	0.187	0.142			0.039	0.075			0.056					
34	0.046	0.145	0.133			0.296			0.005	0.038					
35	0.001	0.002	0.263	0.009		0.030			0.073	0.027	0.050				
36										0.013					
37	0.008	0.034	0.041							0.034					
38	0.082	0.042	0.073			0.018			0.004	0.039					
39		0.008	0.014			0.006									
40		0.055	0.088			0.158			0.066	0.106					
41		0.011	0.010			0.003		0.002		0.010					
42	0.019	0.030	0.021			0.008			0.002	0.017					
43		0.031		0.017				0.030	0.025	0.084					
44		0.015						0.888	0.024	0.057		0.002	0.007		
45		0.026						0.033	0.003	0.087		0.001	0.000	0.004	
46		0.092	0.184	0.967	1.000	0.391		0.000	0.027	0.073	0.210				
47	0.001		0.000	0.007		0.005			0.070	0.081					0.005
48															
48	0.012		0.003				0.046	0.616	0.167	0.370	0.997	0.993	0.996	0.498	
50								0.086	0.082	0.370					0.498

Table 11 continued

	42	43	44	45	46	47
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34						
35						
36						
37						
38						
39						
40		0.003				
41						
42						
43						
44						
45						
46		0.230		0.425		
47	0.120	0.167		0.100	0.800	
48	0.160	0.433			0.200	
48				0.325		
50	0.720	0.167	1.000	0.150		1.000

Table 12. Diet matrix of balanced 50-compartment Ecopath model of Calabash Caye, Belize.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11
1 LGSHARKS/RAYSC	0.002										
2 SHARKS/SCOMBRID		0.002									
3 LGJACKSC											
4 IMJACKSC	0.002	0.005			0.002						
5 SMJACKSC		0.005			0.001						
6 IMREEFFISHC1	0.001	0.002		0.006							
7 LGIMTSCHOOLFISHP	0.002	0.026		0.006	0.015						
8 IMREEFFISHC2	0.006	0.001		0.001		0.008		0.013			
9 HEMIRAMPHIDAEH		0.017									
10 KYPHOSIDAEH											
11 IMREEFFISHH	0.001	0.002			0.017	0.006					
12 LGREEFFISHC	0.000	0.000									
13 IMREEFFISHC3	0.001	0.002				0.001					
14 SMREEFFISHC1	0.002	0.008				0.005					
15 SMSCHOOLFISHPEL	0.002	0.004		0.024	0.001	0.024	0.031	0.025	0.040		
16 ENGRAULIDAEH	0.002	0.006		0.001	0.020		0.061				
17 SMREEFFISHC2	0.002	0.001		0.006							
18 LGGROUPEPSC											
19 IMREEFFISHC4	0.002					0.027					
20 SMREEFFISHO1	0.002	0.000									
21 SMREEFFISHO2	0.001	0.000									
22 SMREEFFISHO3						0.007		0.004			
23 LGSCARIDAEH											
24 IMSCARIDAEH				0.006		0.049		0.001			
25 SMSCARIDAEH		0.000				0.025		0.001			
26 BLENNIIDAEH		0.000		0.006		0.001		0.001			0.003
27 SMGOBIIDAEH		0.001									
28 SEABIRDS											
29 SQUIDS		0.005				0.004					
30 SEATURTLES	0.001										
31 OCTOPUSES		0.007				0.004					
32 LOBSTERS		0.001						0.001			
33 CRABS	0.014	0.001		0.019		0.209	0.010	0.231			0.001
34 SHRMP/HCRB/STOM	0.016	0.001	0.004	0.004		0.016	0.007	0.031			0.002
35 SMBENTHARTHROPO	0.000			0.002		0.003	0.022	0.029			0.000
36 ASTEROIDS											
37 ECHINIDS						0.002		0.019			
38 GASTROPODS	0.019	0.000	0.093			0.029		0.049			0.000
39 CHITONS/SCAPHOP		0.000						0.009			
40 POLY/PRIA/OPHIU		0.001				0.006	0.175	0.252			0.003
41 HOL/SIP/ECH/HEM	0.006					0.001		0.013			0.000
42 BIVALVES	0.017	0.001				0.002		0.050			
43 ASCI/BARN/BRYOZ						0.023		0.008			
44 SPONGES						0.222					0.001
45 CORALS/ANEMONES						0.005		0.033			0.006
46 ZOOPLANKTON			0.003	0.019	0.943	0.278	0.476	0.109			0.032
47 DECOMP/MICROFAU				0.003		0.010	0.208	0.016			0.001
48 Phytoplankton											
49 Benthic prod.	0.000					0.036	0.008	0.106	0.960	1.000	0.641
50 Detritus	0.000										0.312
Import	0.900	0.900	0.900	0.900							

Table 12 continued

	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1							0.072								
2															
3	0.001														
4	0.112														
5															
6	0.015														
7	0.090														
8	0.086	0.056					0.049								
9															
10															
11	0.019														
12							0.050								
13	0.002	0.003													
14	0.013	0.007				0.038									
15	0.048	0.025													
16	0.007	0.060													
17		0.003													
18															
19	0.003	0.016													
20		0.046													
21	0.004														
22		0.050	0.019							0.016					
23															
24	0.098	0.024													
25	0.101	0.019													
26		0.007	0.019							0.016					
27															
28															
29	0.006														
30							0.062								
31	0.038	0.010				0.019									
32	0.008						0.752								
33	0.169	0.215	0.187			0.037	0.015			0.011					
34	0.049	0.063	0.038			0.045			0.001	0.008					
35	0.001	0.002	0.070	0.009		0.040			0.073	0.029	0.050				
36										0.014					
37	0.009	0.039	0.049							0.031					
38	0.087	0.048	0.096			0.023			0.001	0.042					
39		0.009	0.018			0.008									
40		0.064	0.116			0.143			0.066	0.115					
41		0.013	0.014			0.004	0.002			0.011					
42	0.021	0.035	0.027			0.011			0.002	0.019					
43		0.035		0.017			0.030	0.025	0.092						
44		0.018					0.888	0.025	0.062		0.002	0.007			
45		0.030					0.033	0.003	0.039		0.001	0.000	0.004		
46		0.105	0.343	0.967	1.000	0.627	0.000	0.028	0.080	0.210					
47	0.001		0.000	0.007		0.007			0.071	0.088					0.005
48															
49	0.012		0.004				0.046	0.621	0.218	0.370	0.997	0.993	0.996	0.498	
50								0.087	0.109	0.370					0.498

Table 12 continued

	42	43	44	45	46	47
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33						
34						
35						
36						
37						
38						
39						
40		0.003				
41						
42						
43						
44						
45						
46		0.230		0.340		
47	0.120	0.167		0.115	0.600	
48	0.160	0.433			0.200	
49				0.373		
50	0.720	0.167	1.000	0.172	0.200	1.000

Table 13. Respiration to Biomass ratios of unbalanced and balanced models.

Group Name	Unbalanced		Balanced	
	unassimil./ consumption	respiration/ biomass	unassimil./ consumption	respiration/b iomass
1 LGSHARKS/RAYSC	0.200	2.460	0.200	2.460
2 SHARKS/SCOMBRID	0.200	4.810	0.200	4.810
3 LGJACKSC	0.200	2.370	0.200	2.370
4 IMJACKSC	0.200	3.150	0.200	3.150
5 SMJACKSC	0.200	5.840	0.200	5.840
6 IMREEFFISHC1	0.200	2.950	0.200	2.950
7 LGIMSCHOOLFISHP	0.200	6.080	0.200	6.080
8 IMREEFFISHC2	0.200	3.650	0.200	3.650
9 HEMIRAMPHIDAEH	0.200	21.000	0.350	9.270
10 KYPHOSIDAEH	0.200	12.960	0.300	8.240
11 IMREEFFISHH	0.200	13.970	0.300	8.840
12 LGREEFFISHC	0.200	1.580	0.200	1.580
13 IMREEFFISHC3	0.200	2.560	0.200	2.560
14 SMREEFFISHC1	0.200	2.550	0.200	2.550
15 SMSCHOOLFISHPEL	0.200	4.230	0.200	4.230
16 ENGRAULIDAEH	0.200	20.370	0.350	7.350
17 SMREEFFISHC2	0.200	1.150	0.200	1.150
18 LGGROUPERSC	0.200	0.640	0.100	1.100
19 IMREEFFISHC4	0.200	2.500	0.200	2.500
20 SMREEFFISHO1	0.200	6.640	0.200	6.640
21 SMREEFFISHO2	0.200	6.590	0.200	6.590
22 SMREEFFISHO3	0.200	18.760	0.350	6.850
23 LGSCARIDAEH	0.200	6.400	0.200	6.400
24 IMSCARIDAEH	0.200	10.140	0.300	5.990
25 SMSCARIDAEH	0.200	18.460	0.350	8.290
26 BLENNIIDAEH	0.200	15.980	0.300	8.760
27 SMGOBIIDAEH	0.200	4.190	0.200	4.190
28 SEABIRDS	0.200	37.200	0.300	21.200
29 SQUIDS	0.200	8.720	0.200	8.720
30 SEATURTLES	0.200	1.800	0.200	1.800
31 OCTOPUSES	0.200	0.256	0.100	1.608
32 LOBSTERS	0.200	3.540	0.100	5.020
33 CRABS	0.200	5.200	0.100	8.000
34 SHRMP/HCRB/STOM	0.200	10.540	0.200	10.540
35 SMBENTHARTHROPO	0.200	27.650	0.200	27.650
36 ASTEROIDS	0.200	0.964	0.200	0.964
37 ECHINIDS	0.200	0.020	0.200	0.020
38 GASTROPODS	0.200	2.800	0.200	2.800
39 CHITONS/SCAPHOP	0.200	6.340	0.200	6.340
40 POLY/PRIA/OPHIU	0.200	26.560	0.200	26.560
41 HOL/SIP/ECH/HEM	0.200	1.396	0.200	1.396
42 BIVALVES	0.200	1.240	0.200	1.240
43 ASCI/BARN/BRYOZ	0.200	7.400	0.200	7.400
44 SPONGES	0.200	2.500	0.200	2.500
45 CORALS/ANEMONES	0.200	3.220	0.200	3.220
46 ZOOPLANKTON	0.200	19.000	0.200	19.000
47 DECOMP/MICROFAU	0.200	670.000	0.200	40.000
48 Phytoplankton	0.200	-	-	-
49 Benthic prod.	0.200	-	-	-
50 Detritus	0.200	-	-	-

Basic Analysis. In Ecopath, the trophic levels are fractional and represent the percent of diet that comes from each trophic level. Seabirds (28) have the highest trophic level at 4.50, followed by sharks and scombrids (2) with a trophic level of 4.17, and then Intermediate Jacks and Scombrids (4) with a TL of 3.91 (Table 14). Figure 11 compares the differences in trophic levels of compartments from the Calabash Caye, Belize Ecopath 5.0 model and that of the USVI-PR Ecopath II model (Opitz 1996). The patterns of the lines closely match one another meaning that the trophic levels of both systems appear to be very similar. There is expected to be very little, if any, variation in TL for the invertebrate and non-fish groups because the diets of these organisms are nearly the same in both models. The most notable differences in TL are in the engraulids (16), large jacks (3), and hemiramphids (9). The average TL for Calabash Caye is 2.797 and for the U.S. Virgin Island - Puerto Rico system is 2.754, again indicating similar trophic structure among the systems.

The omnivory index (OI) as calculated by Ecopath is the variance of the trophic level of a consumer's prey groups. A consumer with an omnivory index value of zero is specialized, and feeds on only one trophic level. A large omnivory index indicates that the consumer feeds on many trophic levels. Table 14 provides the omnivory indices for Calabash Caye, Belize and USVI-PR Ecopath models. In the Calabash Caye model, there are three fish groups with an $OI = 0$, they are the kyphosids (10), engraulids (16), and small gobies (27). The most generalized feeders in the Belize model are the sea birds (28) ($OI = 1.001$), sharks and scombrids (2) ($OI = 0.896$), and intermediate jacks (4) ($OI = 0.728$). Figure 12 gives an illustration of the differences in the OI values between

Table 14. Trophic Levels and omnivory indices of Calabash Caye and USVI-PR ecosystems as calculated by Ecopath.

Group Number	Group Name	Trophic Level		Omnivory Index	
		Calabash Caye	U.S.V.I. - Puerto Rico	Calabash Caye	U.S.V.I. - Puerto Rico
1	LGSHARKS/RAYSC	3.660	3.920	0.629	0.595
2	SHARKS/SCOMBRID	4.170	4.155	0.896	0.303
3	LGJACKSC	3.410	4.050	0.471	0.368
4	IMJACKSC	3.910	3.630	0.728	0.399
5	SMJACKSC	3.630	3.600	0.043	0.028
6	IMREEFFISHC1	3.370	3.480	0.209	0.308
7	LGIMSCHOOLFISHP	3.540	3.470	0.189	0.270
8	IMREEFFISHC2	3.350	3.440	0.285	0.251
9	HEMIRAMPHIDAEH	2.100	2.520	0.258	1.077
10	KYPHOSIDAEH	2.000	2.000	0.000	0.000
11	IMREEFFISHH	2.070	2.020	0.111	0.026
12	LGREEFFISHC	3.830	3.660	0.507	0.318
13	IMREEFFISHC3	3.630	3.440	0.202	0.283
14	SMREEFFISHC1	3.490	3.355	0.042	0.170
15	SMSCHOOLFISHPEL	3.590	3.595	0.003	0.009
16	ENGRAULIDAEH	3.600	2.320	0.000	0.410
17	SMREEFFISHC2	3.630	3.570	0.059	0.152
18	LGGROUPERS	3.900	3.890	0.117	0.460
19	IMREEFFISHC4	2.990	2.990	0.070	0.036
20	SMREEFFISHO1	2.400	2.580	0.397	0.549
21	SMREEFFISHO2	2.930	2.980	0.459	0.469
22	SMREEFFISHO3	2.410	2.480	0.482	0.476
23	LGSCARIDAEH	2.000	2.000	0.005	0.004
24	IMSCARIDAEH	2.010	2.000	0.007	0.001
25	SMSCARIDAEH	2.010	2.000	0.011	0.000
26	BLENNIIDAEH	2.010	2.010	0.005	0.015
27	SMGOBIIDAEH	3.510	3.285	0.000	0.000
28	SEABIRDS	4.500	4.240	1.001	0.271
29	SQUIDS	3.890	3.910	0.196	0.189
30	SEATURTLES	2.730	2.730	0.459	0.453
31	OCTOPUSES	3.310	3.310	0.055	0.071
32	LOBSTERS	2.750	2.820	0.326	0.301
33	CRABS	2.430	2.430	0.481	0.419
34	SHRMP/HCRB/STOM	3.090	3.085	0.462	0.403
35	SMBENTHARTHROPO	2.510	2.285	0.567	0.283
36	ASTERIODS	2.710	2.710	0.461	0.439
37	ECHINOIDS	2.240	2.170	0.295	0.176
38	GASTROPODS	2.370	2.370	0.375	0.334
39	CHITONS/SCAPHOP	2.620	2.380	0.280	0.259
40	POLY/PRIA/OPHIU	2.500	2.350	0.421	0.328
41	HOL/SIP/ECH/HEM	2.150	2.100	0.128	0.090
42	BIVALVES	2.120	2.100	0.106	0.090
43	ASCI/BARN/BRYOZ	2.540	2.340	0.472	0.368
44	SPONGES	2.000	2.000	0.000	0.001
45	CORALS/ANEMONES	2.660	2.340	0.551	0.368
46	ZOOPLANKTON	2.600	2.600	0.240	0.240
47	DECOMP/MICROFAU	2.000	2.000	0.000	0.000
48	Phytoplankton	1.000	1.000	0.000	0.000
49	Benthic prod.	1.000	1.000	0.000	0.000
50	Detritus	1.000	1.000	0.270	0.367

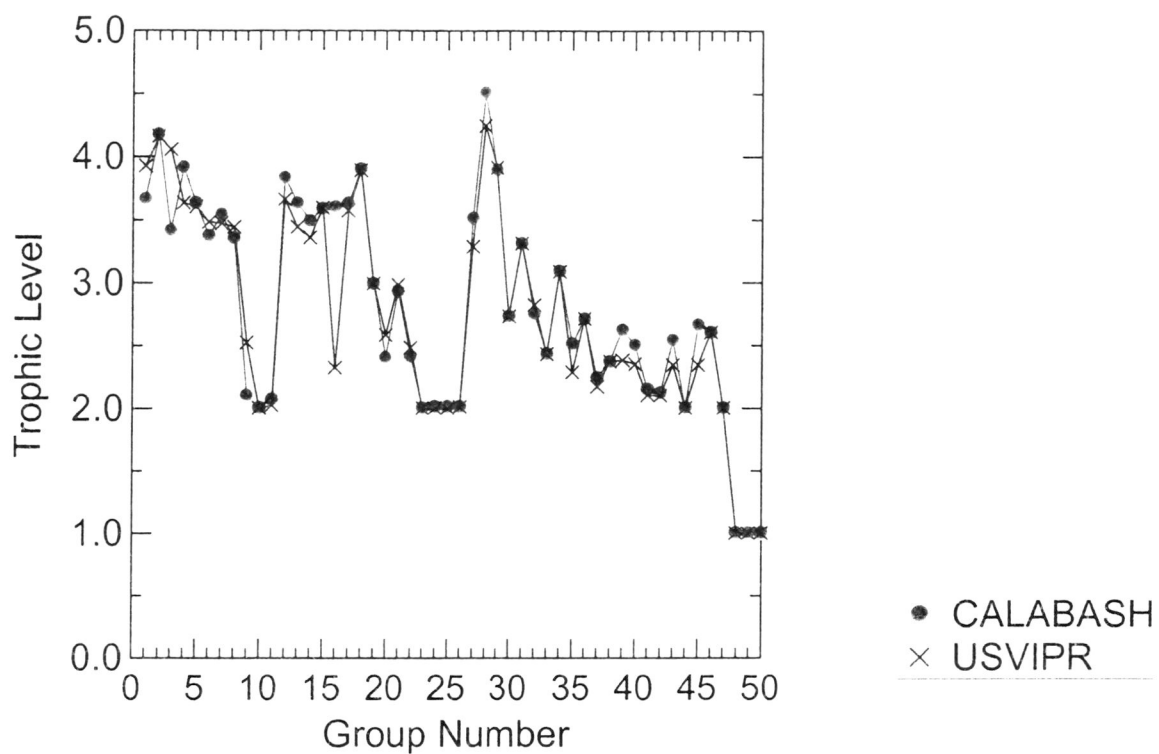


Figure 11. Comparison of trophic levels from Calabash Caye, Belize and the USVI-PR ecosystem as calculated by Ecopath.

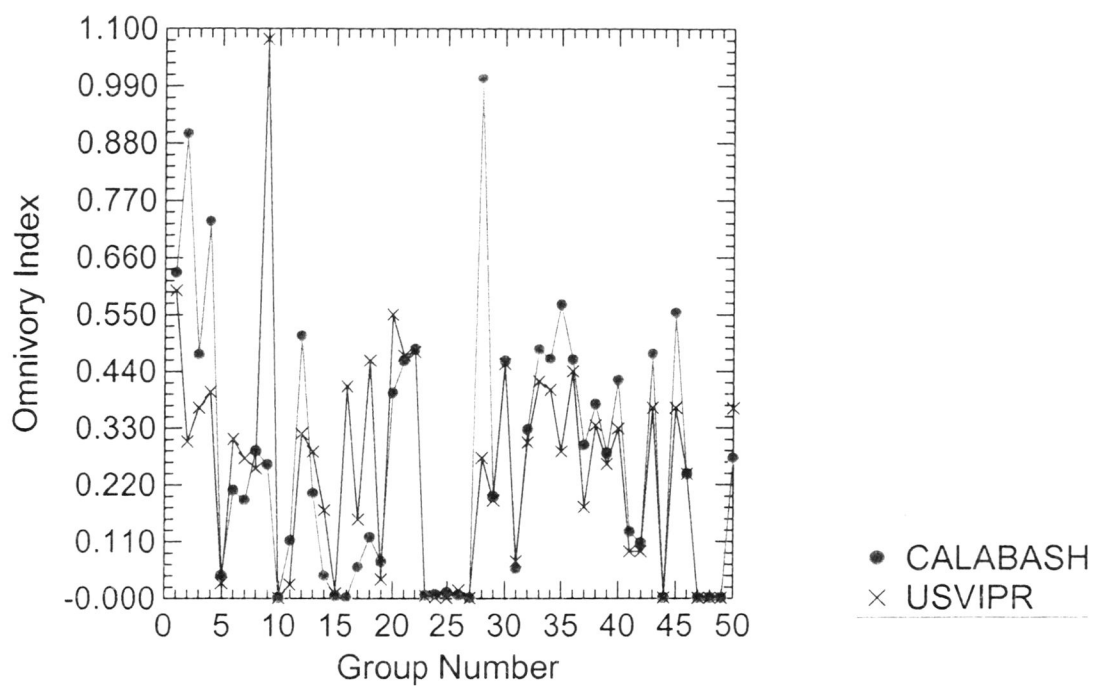


Figure 12. Comparison of the omnivory index for the compartments in the Calabash Caye, Belize and USVI-PR system.

Calabash Caye and the USVI-PR system for each compartment. There is more variance among OIs of the two systems than there is for TL. The OIs for the fish groups differ more than those of non-fish groups. Those groups with the greatest difference in OI values from the two models are the hemiramphids (9), seabirds (28), and sharks and scombrids (2).

Summary Statistics. Summary statistics for both Calabash Caye and the USVI-PR systems are presented in table 15. Total system throughput (TST) is the sum of all flows in a system ($TST = \text{total consumption} + \text{total export} + \text{total respiration} + \text{total flows to detritus}$) and gives an indication to the size of the system in terms of flow. According to TST, the USVI-PR system is larger with a value of 107,473 gWW/m²/year while the TST at Calabash Caye is 77,058 gWW/m²/year. There is less primary production (Pp) in the USVI-PR ($Pp = 20,025 \text{ gWW/m}^2/\text{year}$) coral reef system than there is at Calabash Caye ($Pp = 29,440 \text{ gWW/m}^2/\text{year}$). The Pp/R ratio is greater at Calabash Caye ($Pp/R = 7.257$) than at the USVI-PR reef area ($Pp/R = 0.616$). The Pp/B ratio is also higher at Calabash Caye ($Pp/B = 11.115 \text{ per year}$) than at the USVI-PR system ($Pp/B = 6.570 \text{ per year}$). Net system production is the difference between total Pp and total respiration. Net system production at Calabash Caye ($= 25,383.188 \text{ gWW/m}^2/\text{year}$) is larger than at the USVI-PR reef area ($= -12,498 \text{ gWW/m}^2/\text{year}$). A negative net system production is possible in systems with large amounts of import. Finally, the total respiration to total biomass ratio (system R/B) is lower at Calabash Caye with an $R/B = 1.532$, while the USVI-PR system R/B is estimated to be 10.670.

Table 15. Summary statistics for Calabash Caye and the U.S. Virgin Island - Puerto Rico reef area.

Estimate	Calabash	USVI - PR	Units
Total system throughput	77058.000	107473.000	gWW/m ² /year
Calaculated total net primary production	29440.000	20025.000	gWW/m ² /year
Total respiration	4056.812	32523.000	gWW/m ² /year
Total system biomass (excluding detritus)	2648.598	3047.984	gWW/m ²
System primary production/respiration	7.257	0.616	
System primary production/biomass	11.115	6.570	
System biomass/throughput	0.034	0.028	
Net system production	25383.188	-12498.000	gWW/m ² /year
System respiration/biomass	1.532	10.670	
Connectance index	0.196	0.237	
System omnivory index	0.274	na	

Two system-level indices that give insight into the structure of food webs are the connectance index (CI) and the system omnivory index (OI). The connectance index is the ratio of the number of actual links to the number of possible links. A high CI implies that the food web is more web-like while a low CI implies that the food web is more linear in structure. The CI at Calabash Caye is 0.196, which is less than that at the USVI-PR system (CI = 0.237). The value of the CI is largely dependent on the level of taxonomic detail used to represent prey groups. Because the prey groups are aggregated at the same level of identification in both models, the CI is a valid index for comparing food web structure between these two systems. An alternative index is the system omnivory index (OI), which is the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The system OI is a measure of how feeding interactions are distributed among trophic levels and also characterizes the extent to which a system displays web-like features. The system OI was not available for the USVI-PR model (Opitz 1996), but in the Calabash Caye model it is equal to 0.274.

Niche Overlap. Niche overlap is an index for quantifying how species overlap using the diet matrix. A value of zero suggests that the two species do not share resources and a value of one would suggest that species completely overlap, intermediate values show partial overlap in resource utilization. Figure 13 is a plot of the compartments that exhibit an overlap of 0.5 or greater. If two compartments have a high predator overlap index (x-coordinate) then they have similar predators, if they have a high prey overlap index (y coordinate) then they have similar prey. If two compartments have a high overlap of both predators and prey, they may be candidates for aggregation

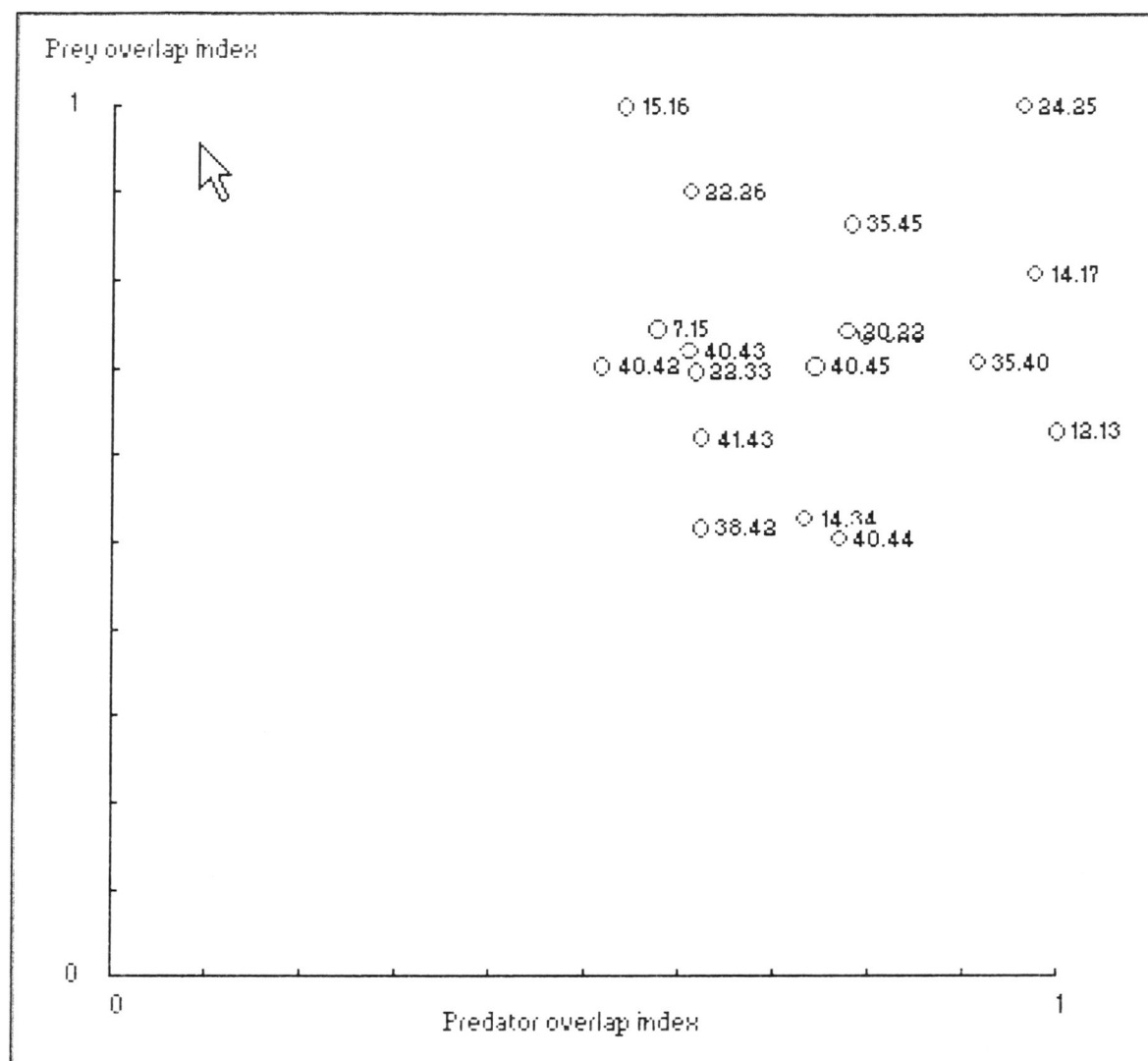


Figure 13. Niche overlap plot from the Calabash Caye model.

into a single group. Seventeen groups from the Calabash Caye model have niche overlaps in predators and prey of 0.50 or higher, meaning that these groups have at least 50% of their prey in common and at least 50% of their predators in common. The largest overlap of any fish groups is between the intermediate scarids (24) and small scarids (25), they have a prey overlap index of 1.00 and a predator overlap index of 0.963. The second largest overlap of two fish groups is between small schooling reef fish 1 (14) and small schooling reef fish 2 (17), they have a prey overlap index of 0.809 and a predator overlap index of 0.975. The third greatest overlap in fish groups is between the small schooling pelagic fish (15) and the engraulids (16), they have a prey overlap index of 0.999 and a predator overlap index of 0.543.

Network Analyses. Ascendency (A) is a measure of average mutual information (AMI) scaled by total system throughput (TST) where AMI is the average amount of constraint on a unit of currency in passing from one compartment to the next. Ascendency represents how organized a system is, and increases as the number of flows are reduced while at the same time strengthening the remaining flows. In other words, as the number of flows decreases and strengthens, more is known about what paths a unit of energy will take when it enters the system. When comparing ascendency across ecosystems, it is best to express it as a percentage of the system capacity (C). Values for A/C are nearly the same for both Calabash Caye ($A/C = 32.5$) and USVI ($A/C = 33.7$) (Table 16). Ascendency may increase due to more TST or AMI and tends to rise as the system matures and becomes more specialized and coherent. The capacity is also higher in the USVI-PR system ($C = 438,213$ flowbits) than Calabash Caye, which has a $C =$

Table 16. Ascendency, overhead, and capacity estimates for Calabash Caye, Belize and the USVI-PR reef system.

Source	Calabash Caye, Belize					
	Ascendency (flowbits)	Ascendency (%)	Overhead (flowbits)	Overhead (%)	Capacity (flowbits)	Capacity (%)
Import	152.0	0.1	3.1	0.0	155.0	0.1
Internal flow	66,537.1	23.3	152,202.5	53.3	218,739.6	76.6
Export	17,530.1	6.1	16,484.3	5.8	34,014.4	11.9
Respiration	8,720.3	3.1	24,083.5	8.4	32,803.9	11.5
Totals	92,939.5	32.5	192,773.4	67.5	285,712.9	100.0
US Virgin Islands - Puerto Rico						
Import	952.0	0.2	2,678.0	0.6	3,630.0	0.8
Internal flow	94,210.0	21.5	226,071.0	51.6	320,281.0	73.1
Dissipations (export + respiration)	52,362.0	12.0	61,940.0	14.1	114,302.0	26.1
Totals	147,524.0	33.7	290,689.0	66.3	438,213.0	100.0

285,712.9 flowbits.

Table 17 provides a list of cycling indices and path length. The Finn cycling index (FCI) (Finn 1976) is the percentage of total systems throughput that cycles through the system. The FCI at Calabash Caye (FCI = 19.03) and the USVI-PR model (FCI = 18.30) are nearly the same. Finn's mean path length represents the average number of groups that an incoming unit of energy travels through before leaving the system. The Finn mean path length for Calabash Caye is 4.368 and for USVI-PR is 3.118.

Tables 18, 19, and 20 give the import (on trophic level I only), consumption by predators, export, flow to the detritus, respiration, and throughput by each trophic level. The trophic levels in this analysis are discrete and calculated based on diet composition to follow the traditional Lindeman spine trophic structure. In each of these tables, detritus and primary producers are represented in trophic level I. Table 18 presents flows originating from primary producers, table 19 summarizes the flows originating from detritus, and table 20 presents the summed flows through trophic levels for the system.

Transfer efficiencies are given in table 21 and represent the ratio between the sum of exports from a given trophic level plus the flow that is transferred from one trophic level to the next and the throughput on the trophic level. This ratio expresses how efficiently energy transfers from one trophic level to the next. At Calabash Caye and the USVI-PR, trophic levels II and III are most efficient in transferring energy up the food web. The system transfer efficiency (TE) is given as a percentage calculated as the geometric mean for trophic levels II-IV. Calabash Caye has a system TE of 24.5% while

Table 17. Cycling indices and path lengths of Calabash Caye and USVI-PR.

Parameter	Calabash		Units
	Caye	USVI - PR	
Predatory cycling index	0.420	1.090	% of throughput w/o detritus
Throughput cycled (including detritus)	14664.340	19686.000	gWW/m2/year
Throughput cycled (excluding detritus)	59.040	158.830	gWW/m2/year
Finn's cycling index	19.030	18.300	% of total throughput
Finn's mean path length	4.368	3.118	

Table 18. Flows through trophic levels from primary producers at Calabash Caye.

Trophic level (TL) \ Flow	Import	Cons by Pred	Export	Flow to Det	Respiration	Throughput
X		0	0	0	0	0
IX		0	0	0	0	0
VIII		0	0	0.001	0.001	0.002
VII		0.006	0	0.011	0.023	0.04
VI		0.064	0	0.107	0.233	0.405
V		0.58	0	0.954	2.048	3.582
IV		5.104	0	8.696	18.702	32.502
III		45.161	0	99.767	162.835	307.764
II		449.101	0	1003.476	1240.25	2692.827
I	-0.103	4145.298	0	25294.68	-0.012	29439.96
Sum	-0.103	4645.315	0	26407.69	1424.082	32477.08

Table 19. Flows through trophic levels from detritus at Calabash Caye.

Trophic level (TL) \ Flow	Import	Cons by Pred	Export	Flow to Det	Respiration	Throughput
X		0.000	0.000	0.000	0.000	0.000
IX		0.001	0.000	0.001	0.003	0.005
VIII		0.010	0.000	0.016	0.036	0.062
VII		0.095	0.000	0.157	0.341	0.594
VI		0.850	0.000	1.396	2.986	5.232
V		7.540	0.000	14.057	29.418	51.015
IV		70.226	0.000	194.786	279.693	544.705
III		806.703	0.000	970.812	903.427	2680.941
II		4456.941	0.000	3912.252	1416.825	9786.018
I	0.000	17917.680	13583.490	0.000	0.000	31501.160
Sum	0.000	23260.040	13583.490	5093.477	2632.729	44569.730

Table 20. Flows through trophic levels from all combined sources at Calabash Caye.

Trophic level (TL) \ Flow	Import	Cons by Pred	Export	Flow to Det	Respiration	Throughput
X		0.000	0.000	0.000	0.000	0.000
IX		0.001	0.000	0.001	0.003	0.005
VIII		0.010	0.000	0.017	0.037	0.063
VII		0.101	0.000	0.168	0.365	0.634
VI		0.915	0.000	1.503	3.219	5.637
V		8.119	0.000	15.011	31.467	54.597
IV		75.330	0.000	203.481	298.395	577.206
III		851.864	0.000	1070.579	1066.262	2988.706
II		4906.042	0.000	4915.728	2657.076	12478.840
I	-0.103	22062.970	13583.490	25294.680	-0.012	60941.130
Sum	-0.103	27905.360	13583.490	31501.160	4056.812	77046.820
Extracted to break cycles						0.002
Input TL II+ (not in throughput)						11.698
Total throughput						77058.510

USVI has a system TE of 13.2%. Also in table 21 is the proportion of total flow originating from detritus, which is a ratio of the total flows originating from detritus to the total flow originating from both Pp and detritus. These values are similar in both systems (Calabash = 0.58, USVI-PR = 0.52) and may be viewed as an index of the importance of detritus in a system (Odum 1969).

Discussion

Sampling Methods

It has been reported in the literature that fish move from the reef to the surrounding seagrass areas at dusk to feed and return at dawn (Gerking 1994). Thus, gill nets were set to capture fish during this movement. Many fish were still active when the nets were retrieved indicating that these nets selected highly for those species believed to move during crepuscular periods and were effective at capturing specimens with prey items that had been recently ingested. A problem associated with the gill nets are that, in some instances, the amount of time between capture and stomach preservation may have been too long to stop the digestion process and adequately preserve the stomach contents. It is also possible that the stress of being captured in a gill net may cause some fish to regurgitate their last meal.

Active sampling gear such as seine nets and spears do not pose the same problems for stomach content preservation as do passive gear types such as gill nets or traps. Seine nets were efficient when capturing small fishes in seagrass beds. Although spear fishing is a physically demanding and time consuming method of catching fish, it is free from problems associated with other gear and methods that snare or trap fish or use bait. Fish that are caught in traps are often reported to have empty stomachs while the gut contents of a larger fish in a trap may consist of the smaller individuals who were once caught in the same trap. It can be assumed that the stomach contents of a fish taken with a spear or were normally ingested (Randall 1967).

Fish taken on hook and line are feeding because they are hungry and often have empty stomachs or contain only the bait. In this study, careful precaution was taken not to include bait in the stomach content analyses of fish caught on hook and line. Problems associated with using hook and line in diet studies are that some fishes tend to regurgitate during the struggle on the line while others have their stomach everted by the expanding gas bladder when being reeled in rapidly from depths of 15 m or more. The fish in this study were captured in depths shallower than 10 m near the forereef or in mangrove lagoons.

Diet Comparisons

Regular equivalence and multidimensional scaling proved to be useful in comparing the diets of species from Calabash Caye with those from the USVI-PR reef area both statistically and graphically. This measure of similarity gives insight into the trophic roles species play in their own ecosystems rather than just comparing the relative amounts of prey items found in the stomachs. By looking at the REGE coefficients in Table 6 and then viewing their arrangement in the MDS plot (Figure 10) one can quickly draw conclusions about where any differences in diets of fish may lie and easily understand what other fish they share a similar role. Other similarity coefficients used in diet studies are limited in their ability to describe each fish's function in the context of the entire ecosystem because they only examine similarity in prey relationships.

There were dietary differences between species observed by Randall (1967) and those in this study as computed by clustering of REGE similarity coefficients. Green razorfish from the West Indies (Randall 1967) clustered with other zooplanktivores

(cluster 1) from Calabash Caye such as silversides, anchovies, and herrings. The Green razorfish from Calabash Caye were put into the same class as fish that prey on small benthic crustaceans (cluster 8) such as juvenile jacks and juvenile mojarra. Tomtate from West Indies grouped with other grunts (cluster 2) while those from Belize were more similar to zooplanktivorous fish (cluster 1). The trumpetfish from Belize was observed eating only fish and was clustered together only with Bar jack from Belize (cluster 4). In the West Indies diet study, trumpetfish were observed eating fish and shrimp and were thus clustered with other generalized carnivores (cluster 2). Bar jack from the West Indies appear to be feeding on a higher trophic level because they are grouped with barracuda and shark (cluster 7). At Calabash Caye, Bar jack are piscivorous but are eating smaller fish and thus were grouped with the Trumpetfish in cluster 4.

By viewing the regular equivalence MDS plot showing the same species from Calabash Caye and USVI-PR one can observe the differences in trophic niche of the same species at different locations and times. The bar jacks (2) are positioned furthest apart because those in Belize were only observed consuming a few species, all of which were small fish, whereas those reported by Randall from the West Indies consumed a wider variety of prey items (but not all fish) and were thus placed closer to other large, generalized carnivores such as other jacks and large snappers. Trumpetfish (17) were also placed relatively far apart because those analyzed from Calabash Caye were strictly piscivorous while the data from Randall (1967) reported them as eating fish and shrimps. Hardhead silversides (19) are arranged some distance apart from one another because those analyzed in this study consumed amphipods and zooplankton while those from

Randall's study consumed mainly zooplankton and some benthic microfauna, placing them further away from other benthic feeders. Black margate (6) are positioned far apart because those from the West Indies have strong ties to sea urchins and gastropods while those from Belize have ties to crabs and hermit crabs. Lane snapper (14) are not closely positioned to one another because those analyzed from Belize did not prey upon any stomatopods. Finally, the dusky damselfish (20) from Calabash Caye gain more energy from autotrophic organisms than those from the West Indies, which eat more from the detritus compartment.

Differences in the diets of the species described above are most likely due to the small number of samples of these fish taken from Belize. I suspect that the diets of these species would be found to be more similar should additional stomachs be collected from Belize and analyzed. Species of fish that were sufficiently sampled in both studies appear to be functionally similar according to the regular equivalence algorithm. Therefore, unless obvious drastic changes in community structure have occurred at a specific location, it may not be necessary to conduct further diet analyses of an entire community of Caribbean coral reef fish. Slight differences in diets of fishes in the Caribbean Sea will not show up in aggregated compartments of network flow models.

Food Web Visualizations

To reduce the complexity of the coral reef food web at Calabash Caye, Belize "isotrophic" classes of species that occupy similar trophic positions were identified using regular equivalence in UCINET (Borgatti et al. 2002). A comprehensive model of the roles played by each species or groups of species has been generated from the multi-

dimensional scaling of species based on their REGE coefficients. It is clear from viewing the food web display that there are classes of analogous species that perform similar ecological roles and that these classes do in fact overlap. For example, herbivores and zooplanktivores are not easily distinguishable from their placement on the graph (though their colors do separate them from one another). Trophic structure and trophic position have also been revealed in the analysis. Top predators are at one end of the graph, positioned close to other piscivores, and primary producers and detritus are at the other end, intermediate consumers are positioned in between. Anomalies in this graph are not due to the model technique described above, but rather to insufficient dietary data of species with small sample sizes such as Bar jack, juvenile Yellow jack, and Trumpetfish. Lack of percent diet data at the species level for prey fish and the quantifying of qualitative dietary data available for coral reef invertebrates may also lead to some inaccuracies. Nonetheless, this visualization technique is effective in describing the trophic interactions of the coral reef area at Calabash Caye, Belize and useful when making comparisons of food webs at different locations.

The regular equivalence MDS plot (Figures 6 and 7) displays some food web structure and relative position of detritus, primary producers, benthic fauna, intermediate consumers, and top predators in the system. Basal groups such as detritus and the primary producers do not have any incoming ties (no lines with arrows pointing to other nodes) because they function as energy sources. Top predators such as barracuda and sharks (dark gray), carangids, snappers, and needlefish (purple) along with Bar jack and trumpet fish (orange) have no or relatively fewer arrows pointing to them indicating that

they are not often preyed upon by other species in the system. These are also located near the upper left portion of the MDS with other piscivorous fishes, birds (light blue triangle) and squid (light blue diamond).

Carnivorous fish that feed primarily on the benthic macrofauna are considered intermediate feeders and are located below and to the right of piscivorous species and are colored red. This is the largest “isotrophic” class as determined by the k-cluster optimization procedure with 38 members. Fishes such as herrings, sardines, silversides, and anchovies, which consume smaller microfauna and algae, are colored yellow and positioned below the intermediate consumers and to the right. Parrotfish, damselfish, surgeonfish, and chub (blue) are strictly herbivorous and grouped together on the far right side of the diagram slightly below those that feed on small microfauna. Angelfish (dark green), which may be feeding at the same level as those that are colored yellow or blue, are clustered out of such groups and are positioned above them because they are preyed upon less in the system.

Invertebrates such as coral, anemones, and brittle stars (pink diamond) that feed on algae, zooplankton, phytoplankton, and detritus are positioned closely to starfish, chitons, sea cucumbers and turtles (burgundy diamond) because they consume similar prey items. Isopods (blue/green diamond) were not placed with any other taxa because they are small invertebrates that actually consume some fish species as a form of parasitism. Benthic macrofauna such as crabs, shrimp, gastropods, bivalves, amphipods and polychaetes (light gray diamonds) consume mostly plankton, algae, and microfaunal

organisms and are positioned above the autotrophs (green) and zooplankton, sponges, and microfauna (purple). Thus, this MDS plot shows the approximate trophic positions of all 137 components of the system at Calabash Caye, Belize with low trophic positions at the bottom moving towards higher trophic position at the upper left side.

The regular equivalence algorithm is more likely to accurately place species into “isotrophic” classes than structural equivalence because nodes do not need to have the exact same ties to other nodes in order for them to be regularly equivalent. In other words, structural equivalence does not capture the relationship of functionally similar species that share no predators or prey, and are thus seen as very dissimilar.

The applicability of regular equivalence to determining overlap of trophic niche among species was compared to the niche overlap index from Ecopath. This was done first by looking at Figures 8 and 13 to see if those compartments with a high niche overlap in Ecopath are arranged near to one another on the REGE MDS plot of the 50 by 50 diet matrix. Not all groups from the niche overlap plot in Ecopath were placed close together because the predator overlap index in Ecopath is weighted by the rate of consumption for each predator. However, the “isotrophic” classes (and coloring) of compartments determined by using regular equivalence and the cluster optimization routine is in agreement with those that had high overlap indices in Ecopath.

A second way I confirmed this was by comparing the 50 compartment REGE similarity matrix against the prey and predator overlap index matrices from Ecopath. This was computed using a QAP correlation in UCInet. The QAP correlation algorithm proceeds in two steps. In the first step, it computed correlation coefficients between

corresponding cells of the two square data matrices with the same rows and columns. In the second step, it randomly permuted rows and columns (synchronously) of one matrix and recomputed the correlation. The second step was repeated hundreds of times in order to compute the proportion of times that a random measure is larger than or equal to the observed measure calculated in step 1. A low probability ($P < 0.05$) that randomly permuted rows and columns is higher than observed measure suggests a strong relationship between the matrices that is unlikely to have occurred by chance (Borgatti et al. 2002). The correlation between the REGE matrix and the prey overlap index table was .767 (Pearson correlation, $P = 0.000$) and .661 (Jaccard coefficient, $P = 0.004$). The correlation between the REGE matrix and the predator overlap index table was 0.236 (Pearson correlation, $P = 0.000$) and 0.553 (Jaccard coefficient, $P = 0.031$). Both the prey and predator overlap indices significantly correlate with the single REGE measure of similarity, keeping in mind that REGE is based on both predators and prey relations. Therefore, the REGE similarity measure is consistent with the measure of trophic-niche overlap as computed by Ecopath.

Network Analysis

The Ecopath model and Calabash Caye. Herbivorous fishes are known to dominate tropical reef fish fauna (Opitz 1996). The model of Calabash Caye is in agreement with this statement by having three of the largest fish biomass values belonging to compartments of herbivorous fishes such as the Scarids and Acanthurids (compartment 11, 24 and 25). The herbivorous fishes of these compartments make up about 48% of the total fish biomass. While snorkeling this reef area, one can clearly see

that this is true. Many large parrotfish reside on the reef at Calabash Caye and Doctorfish and Surgeonfish graze along the reef in large schools. A large amount of production of these herbivorous fishes that make up such a large portion of the total fish biomass is not transferred to higher trophic levels, rather it is recycled directly to detritus. Sixty percent of the flow of carbon to detritus from fish groups comes from compartments 11, 24 and 25. The natural mortalities of parrotfish (compartment 24 and 25) are also large indicating that they often die and contribute to the detrital pool because natural predators on these species are in low abundance at Calabash Caye. The nutrients from the decomposed fish are then absorbed and assimilated by reef autotrophs such as algae and seagrass. These autotrophs are then consumed by herbivorous fishes in the community representing a very short loop for recycling carbon in the system.

Three general statements about coral reefs are that they have high species diversity, complex trophic relationships, and high rates of production (Ehrlich 1975) despite being surrounded by oceanic waters that provide little to no nutrients. Primary production on coral reefs has been studied extensively for nearly sixty years and is estimated to be approximately 511-6307 gC/m²/year net production (1460-8497 gC/m²/year gross production) (Table 22). Hatcher (1990) described the patterns and processes of coral reef primary productivity and found spatial variability within reef components and variations across oceanic spatial scales. The calculated net primary production at Calabash Caye is 29,440 gWW/m²/year. This was converted to 3,709 gC/m²/year, which falls in the range of the measured values from the literature. The grams of carbon value is an approximation that was obtained by multiplying grams WW

by 0.12 because dry weight of reef fish is approximately 28% of wet weight (Meyer and Schultz 1985) and about 45% of that is carbon (Christian and Luczkovich 1999). The net primary productivity of Calabash Caye is higher than nearly all other estimates given in Table 22 with exception to the high measurements on Eniwetok Atoll by Smith (1973) and Smith and Marsh (1973) and that in the Arabian Sea (Quasim and Sankaranarayanan 1970). Reef margins in the Caribbean appear to be more productive because the reefs are still in an active, upward growth phase as compared to Pacific reefs as they catch up or keep up with sea level (Hatcher 1990). In addition, the reef at Calabash Caye is surrounded by both seagrass and mangrove habitats, which support the reef by providing primary production. Therefore, the primary production for the Calabash Caye system as calculated by Ecopath incorporates all habitats and not just the reef itself. This is a possible explanation to the high estimate of calculated net primary productivity. Nevertheless, Ecopath calculated a net primary productivity value that falls within the range of measured values on coral reefs.

To overcome the lack of nutrients in surrounding waters of coral reefs, there is an existence of shortcuts for the effective recycling of matter. The largest percentage of the total throughput occurs on trophic level II for all flows combined and 86% of total flow from primary producers flows directly to detritus without ever being transferred to higher trophic levels. Thus, the direct recycling of energy at lower trophic levels may be the most effective way for the reef to conserve energy and build biomass. As matter is passed from one trophic level to the next, a large percentage of energy is lost. To summarize this, coral reefs have not evolved to achieve high transfer efficiencies between

Table 22. Primary production of coral reefs.

Location	Gross Primary Production gC/m ² /year	Net Primary Production gC/m ² /year	Source
Production of whole reef communities			
Calabash Caye, Turneffe Atoll, Belize, western Caribbean Sea	na	3709	this study
Puerto Rico, Virgin Islands reef area, eastern Caribbean Sea	na	2033	Opitz (1996)
Rongelap Atoll, N. Marshall Islands, central Pacific Ocean	1460	na	Sargent and Austin (1949)
Rongelap Atoll, N. Marshall Islands, central Pacific Ocean	1500	190	Sargent and Austin (1954)
Eniwetok Atoll, Marshall Islands, central Pacific Ocean	3504	2044	Odum and Odum (1955)
North Kapaa Reef, Kauai, Hawaii, Pacific Ocean	3000, 2900, 7300	1400 511	Kohn and Helfrich (1957)
Kavaratti Atoll, Arab Sea	4494	3618	Quasim and Sankaranarayanan (1970)
Eniwetok Atoll, Marshall Islands, central Pacific Ocean	3241 7358	2190 6307	Smith (1973)
Eniwetok Atoll, Marshall Islands, central Pacific Ocean	4380 8497	2190 6307	Smith and Marsh (1973)
Curacao, Netherlands Antilles, southern Caribbean Sea	5650	2330	Wanders (1976)
Measurements with respirometer			
Plantation Key, Florida, USA	2303	528	Kanwisher and Wainwright (1967)
Eniwetok Atoll, Marshall Islands, central Pacific Ocean (only algae)	1261	946	Marsh (1970)
Kaneohe Bay, Hawaii, Pacific Ocean (only algae)	2495	2080	Litter (1973)

trophic levels but rather to maintain short cycles for effective recycling back to the base of the food web, the detrital pool, via algal production and herbivory. Perhaps algae possess certain levels of toxicity that accumulates in herbivores thereby deterring predator fish from eating them.

Comparison of Caribbean Coral Reef Models. E. P. Odum (1969) presented 24 indices and the trends that are to be expected in the development of ecosystems. Ten of the 24 indices are available in the Ecopath outputs for both Calabash Caye and USVI-PR and have been summarized in Table 23. Seven of the ten indices indicate that the USVI-PR reef area is at a more mature stage of development. Of the most notable comparisons supporting this claim are the ratios involving production. In an immature system, production is expected to be high and biomass is accumulated over time. Mature systems generally have more energy respired as it functions to maintain, rather than build up, biomass levels.

The ratio between primary production (Pp) and respiration (R) is considered to be important in describing the maturity of an ecosystem (Odum 1971). In developing systems, production exceeds respiration and $Pp/R > 1$, while in mature systems, Pp/R approaches one. The ratio between total primary production and total biomass (Pp/B) is also a function of a systems' maturity. In an immature system, production exceeds respiration resulting in a large Pp/B ratio. As a system matures, biomass is accumulated and the Pp/B ratio becomes smaller. Net system production also gives an indication as to the maturity level of an ecosystem. In an immature system, production will be large and respiration small, resulting in a large net system production.

Table 23. Summary of comparisons of ecosystem attributes of Calabash Caye and USVI-PR from Odum (1969).

Ecosystem Attribute	Ecopath output	Developmental stages	Mature stages	Calabash Caye	USVI-PR
Production/respiration	P/R ratio	>1	approaches 1	7.257	0.616
Production/biomass	P/B ratio	high	low	11.115	6.570
Biomass/energy flow	B/TST	low	high	0.034	0.028
Net community production	Net system production	high	low	25,383.188	-12,498.000
Food chains	Connectance index	linear	weblike	0.196	0.237
Total organic matter	System biomass	small	large	2,648.598	3,047.984
Nutrient/energy conservation	Finn cycling index	poor	good	19.030	18.300
Role of detritus	Detrital Flow	unimportant	important	0.580	0.520
Stability (resistance to perturbations)	Overhead	poor	good	192,773.400	290,689.000
Information	Ascendency	low	high	92,939.000	147,524.000

The model outputs indicate differences in the two systems, yet we do not know the cause of these differences. Disturbances such as commercial and recreational fishing, global warming, and coral reef bleaching may be allowing excess production of algae on the reef at Calabash Caye thereby keeping it at a highly productive stage. Should this be the case, it would not be accurate to say that the system at Calabash Caye is less mature.

Other important indices in comparing ecosystems using network analysis are the ascendancy and overhead. Ascendancy is a measure of the average mutual information (AMI) in a system in terms of the possible paths a unit of energy may take when it enters the system scaled by TST. Because the diets of species of fish and invertebrates in the models of Calabash Caye and USVI-PR are quite similar, the number and strength of ties from one compartment to the next do not vary much. Therefore, the difference in ascendancy is most likely a result of a higher TST rather than AMI.

Further Development of the Model. One advantage to building ecosystem models is the ability to identify areas that require more studying. In this model of Calabash Caye, there are deficiencies in the planktonic biomass, benthic biomass, and small fish biomass estimates. First, I suggest that further sampling of the plankton be conducted that can more accurately quantify not only the biomass but also the production rates. Secondly, the sampling method used to gather benthic biomass data did not select for small amphipods, copepods, and nematodes nor did it include large invertebrates such as sponges, conch, lobster, large crabs, and large bivalves (Deehr, unpublished). Although visual censuses were taken on the larger benthos, weight per individual had to be

estimated from literature values (Kilpatrick unpublished). This is a crucial part to accurately representing the biomass of such groups and site specific data is needed.

Thirdly, the visual censuses used to obtain the biomass values for fish species was biased towards those fish that are visible on the reef during daylight. This not only underestimates species that are more active at night and those that are small and hide in reef crevices but can overestimate those species which are highly visible, do not avoid divers, and stand the chance of being counted two or three times. I recommend that some form of sampling be conducted to extract species from reef crevices. The use of rotenone on coral reefs has been effective in accomplishing this (Randall 1963b). Nighttime visual censuses may help to better characterize the biomass of species of squirrelfish as well as invertebrates such as echinoids and octopi that are more active at night.

Finally, in order to optimize the Ecopath model to its fullest potential, a human component should be included and simulations should be run to address the impacts of marine protected areas, overharvesting, and community structure changes caused by tourism activities. This is the most promising application made available by Ecopath models.

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Appendix A: Diets

Acanthuridae (Surgeon fishes, tangs)

Acanthurus chirurgus (Bloch)

Doctorfish

1 location; 3 specimens: 25 to 56 mm SL; 1 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Algae	
Chlorophyta	28.65
Corallinacea	23.83
Phaeophyta	21.37
Udotacea	0.56
Rodomenciacea	8.91
Seagrass	
<i>Halodule wrightii</i>	12.66
<i>Syringodium filiforme</i>	3.57
Copepods	
Harpacticoid	0.43
Unidentifiable eggs	0.04

Albulidae (Bonefishes)

Albula vulpes (Linnaeus)

Bonefish

4 locations; 35 specimens: 222 to 492 mm SL; 15 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Crabs	
<i>Pitho lherminieri</i>	20.77
<i>Panopeus herbstii</i>	4.09
hermit crab	4.07
<i>Mithrax sculptus</i>	3.28
<i>Portunus anceps</i>	3.16
Majidae	1.71
<i>Portunus sp.</i>	1.40
<i>Mithrax forceps</i>	1.26
<i>Cronius ruber</i>	0.97
<i>Mithrax pleurocanthus</i>	0.57
<i>Portunus floridanus</i>	0.31
<i>Hexapanopeus angustifrons</i>	0.22
<i>Batrachonotus sp.</i>	0.04
Mollusks	
Gastropods	10.00
Bivalves	0.85

Unidentifiable small fish	9.36
Stomatopod	3.86
Seagrass	
<i>Thalassia testudinum</i>	2.25
<i>Halodule wrightii</i>	0.17
Annelids	0.02
polychaetes	2.13
siphunculid	0.07
Nematodes	1.23
Amphipods	0.26
Shrimp	
Caridea	0.15
<i>Penaeus sp.</i>	0.14
Penaeidae	0.08
mysids	0.05
Foraminifera	0.10
Unidentifiable crustacean remains	26.21
Unidentifiable eggs	0.02
Unidentifiable animal material	1.20

Atherinidae (Silversides)

Atherinomorus stipes

Hardhead silverside

1 location; 24 specimens: 45 to 66 mm SL; 4 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Amphipods	56.00
Copepods	30.31
Algae	4.97
UI eggs	3.85
Gastropod larvae	2.90
Brachyuran crab larvae	1.49
Platyhelminthes	0.34
nematode	0.14

Aulostomidae (Trumpetfishes)*Aulostomus maculatus*

Trumpetfish

1 location; 1 specimen: 400 mm SL

Food
Unidentifiable small fish

Dry Mass (%)
100.00

Belonidae (Needlefishes)*Strongylura notata* (Poey)

Redfin needlefish

2 locations; 23 specimens: 122 to 376 mm SL; 7 empty

Food
Fish
 Atherinomorus stipes
 Unidentifiable fish remains
Amphipods
Crab
 Portunus sp.
 Crab megalops
 Unidentifiable crab remains
Stomatopods
Syringodium filiforme
isopod eggs and larvae

Dry Mass (%)

25.00
26.05
21.33

8.60
0.80
11.18
1.14
0.26
0.14

Carangidae (Jacks)*Caranx bartholomaei* (Cuvier)

Yellow jack

1 location, 1 specimen: 35 mm SL

Food
Xanthid crabs
Nematode

Dry Mass (%)
88.03
11.97

Caranx crysos

Blue runner

1 location; 1 specimen: 48 mm SL

Food
Amphipods

Dry Mass (%)
100.00

<i>Craranx latus</i> (Agassiz)	Horse-eyed jack
2 locations; 2 specimens: 226 to 335 mm SL; 1 empty	
<u>Food</u>	<u>Dry Mass (%)</u>
Penaeid shrimp	100.00

<i>Caranx ruber</i>	Bar jack
3 locations; 3 specimens: 195 to 345 mm SL; 2 empty	
<u>Food</u>	<u>Dry Mass (%)</u>
Fish	
<i>Atherinomorus stipes</i>	100.00

<i>Trachinotus falcatus</i>	Permit
2 locations; 4 specimens: 58 to 124 mm SL; 1 empty	
<u>Food</u>	<u>Dry Mass (%)</u>
Gastropods	50.13
Hermit crabs	12.26
<i>Thalassia testudinum</i>	9.74
Platyhelminthes	3.42
Bivalves	2.93
Brachyuran megalops stage	1.34

<i>Trachinotus goodei</i>	Palometa
1 location; 1 specimen: 153 mm SL	
<u>Food</u>	<u>Dry Mass (%)</u>
Mysids	80.58
Hermit crabs	19.42

Dasyatidae (Stingrays)

<i>Dasyatis americana</i>	Southern stingray
2 locations; 2 specimens: 325 to 479 mm wide	
<u>Food</u>	<u>Dry Mass (%)</u>
UI crab parts	24.81
Penaeid shrimp	9.93
Stomatopod	6.62
Annelid worm	4.96

UI animal remains

53.68

Gerreidae (Mojarras)*Gerres cinereus*

Yellowfin mojarra

6 locations; 46 specimens: 31 to 268 mm SL; 18 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Amphipods	24.03
Crabs	
<i>Pitho lherminieri</i>	9.85
Portunid crab	8.09
<i>Mithrax sculptus</i>	6.73
Unidentifiable crab remains	0.04
Isopods	8.96
Annelida	5.22
Polychaetes	2.82
Copepods	
Harpacticoid	4.95
Calanoid	2.10
Limpets	4.62
Gastropods	2.17
Nematodes	1.84
Seagrass	
<i>Thalassia testudinum</i>	1.66
<i>Halodule wrightii</i>	1.06
Mysids	1.02
Bivalves	0.45
Penaeid shrimp	0.43
Tanaids	0.12
Hermit crabs	0.11
Unidentifiable crustacean remains	8.20
Unidentifiable fish bones	1.08
Unidentifiable animal remains	4.45

Gobiidae (Gobies)*Bathygobius mystacium*

Island frillfin

1 location; 2 specimens: 55 to 60 mm SL; 1 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Amphipods	97.95

Algae	
Phaeophytes	2.05

Haemulidae (Grunts)

Anisotremus surinamensis Black margate

1 location; 1 specimen: 380 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Crab	
<i>Pitho lherminieri</i>	17.35
<i>Mithrax sp.</i>	10.26
<i>Portunus sp.</i>	5.40
Hermit crab	0.57
Unidentifiable crab remains	52.91
Fish	3.29
<i>Penaeus sp.</i>	2.82
<i>Thalassia testudinum</i>	2.68
Limpets	1.37
Nematodes	1.16
Echinoderm	0.95
coral rubble	0.69
Stomatopod	0.24
Unidentifiable animal remains	0.31

Haemulon aurolineatum Tomtate

1 location; 1 specimen: 140 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Thalassinid shrimp larvae	33.31
Crab	
Brachyuran crab zoea	28.65
Pagurid crab glaucothoe	6.04
Isopods	17.65
Stomatopods	4.57
Amphipods	2.92
Fish	
<i>Atherinomorus stipes</i>	0.61
Unidentifiable animal remains	6.25

Haemulon sciurus

4 locations; 18 specimens: 127 to 250 mm SL; 9 empty

Bluestriped grunt

<u>Food</u>	<u>Dry Mass (%)</u>
Crabs	
<i>Portunus sp.</i>	42.89
Xanthidae	19.58
Portunidae	12.31
<i>Mithrax sculptus</i>	6.77
Unidentifiable juvenile crab	0.47
Limpets	4.33
Amphipods	3.70
Shrimps	
Penaeidae shrimp	2.98
<i>Penaeus sp.</i>	1.47
<i>Thalassia testudinum</i>	2.21
Stomatopods	1.32
Isopods	1.10
Polychaetes	0.58
UI eggs	0.22
Nematodes	0.08

Haemulon flavolineatum

2 locations; 8 specimens: 122 to 184 mm SL; 4 empty

French grunt

<u>Food</u>	<u>Dry Mass (%)</u>
Crab	
Portunidae	7.10
<i>Pitho lherminieri</i>	6.66
<i>Portunus sp.</i>	4.48
Unidentifiable crab remains	22.49
Bivalves	22.35
Limpets	11.73
Seagrass	10.08
Mysids	5.65
Amphipods	0.37
Nematode	0.34
Isopods	0.16
Gastropods	0.03
Unidentifiable crustacean remains	2.86
Unidentifiable animal remains	5.72

Holocentridae (Squirrelfishes)*Holocentrus adscensionis*

Squirrelfish

1 location; 2 specimens: 173 to 185 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Crabs	
<i>Portunus anceps</i>	25.15
<i>Mithrax forceps</i>	16.73
<i>Pitho lherminieri</i>	15.53
<i>Hexapanopeus angustifrons</i>	7.17
<i>Panopeus sp.</i>	2.39
Unidentifiable crab remains	0.79
<i>Podochela sidneyi</i>	0.18
<i>Penaeus sp.</i>	3.61
<i>Thalassia testudinum</i>	1.20
coral rubble	1.20
Unidentifiable fish larvae	1.20
Mysids	0.02

Holocentrus rufus

Longspine squirrelfish

2 locations; 3 specimens: 130 to 155 mm SL; 2 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Crabs	
<i>Cronius ruber</i>	34.47
<i>Pitho lherminieri</i>	26.36
Unidentifiable crab remains	18.37
<i>Penaeus sp.</i>	14.19
Amphipods	2.27
Gastropods	2.03
Nematodes	0.01
Bivalves	0.01
Unidentifiable animal remains	2.29

Labridae (Wrasses)*Lachnolamus maximus*

Hogfish

2 locations; 4 specimens: 224 to 238 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Gastropods	37.26
Crabs	

<i>Portunus sp.</i>	14.86
Hermit crabs	9.70
<i>Mithrax sp.</i>	1.65
Unidentifiable crab remains	13.58
Bivalves	7.18
<i>Thalassia testudinum</i>	5.48
Echinoderm	
<i>Diadema sp.</i> juvenile	4.00
Stomatopods	0.74
Unidentifiable mollusk shells	2.56
Unidentifiable animal remains	3.00

Xyrichtys splendens

Green razorfish

1 location; 1 specimen: 36 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Amphipods	80.44
Copepods - harpacticoid	19.56

Lutjanidae (Snappers)*Lutjanus analis*

Mutton snapper

2 locations; 3 specimens: 221 to 284 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Unidentifiable small fish	33.32
Crab	
<i>Portunus sp.</i>	16.62
<i>Panopeus herbstii</i>	5.54
<i>Mithrax pleurocanthus</i>	4.43
<i>Mithrax forceps</i>	1.11
Unidentifiable crab remains	31.28
Stomatopods	7.21
<i>Thalassia testudinum</i>	0.11
Nematodes	0.10
Unidentifiable animal remains	0.28

Lutjanus apodus

Schoolmaster

6 locations; 13 specimens: 48 to 300 mm SL; 5 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Crabs	
<i>Portunis sp.</i>	14.29
<i>Cronius ruber</i>	9.35
Portunidae	3.68
Unidentifiable crab	15.28
Unidentifiable juvenile crabs	2.10
Fish	
Monocanthidae	14.29
<i>Sparisoma sp.</i>	11.48
Unidentifiable fish	8.01
Shrimp	
Penaidae	4.70
<i>Penaeus sp.</i>	3.28
Seagrass	
<i>Halodule wrightii</i>	0.24
<i>Thalassia testudinum</i>	0.03
Polychaetes	0.01
Unidentifiable animal remains	13.26

Lutjanus mahogoni

Mahogany snapper

3 locations; 7 specimens: 163 to 264 mm SL; 5 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Unidentifiable fish remains	78.84
Unidentifiable crab remains	15.34
Juvenile shrimps	1.69
<i>Thalassia testudinum</i>	0.79
Stomatopods	0.77
Nematodes	0.04
Ctenophoral	0.02
Unidentified crustacean remains	0.79
Unidentifiable animal remains	15.34

Lutjanus synagris

Lane snapper

2 locations; 3 specimens: 32 to 226 mm SL; 1 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Crab	
<i>Macroceloma camptorerum</i>	50.00

Amphipods	36.44
Chlorophytan algae	13.57

Monacanthidae (Filefishes)

Cantherhines pullus

Orangespotted filefish

1 location; 2 specimens: 30 to 33 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Algae	
Ceramium	40.29
Brown alga	21.95
Halimeda	12.48
Ulva	4.86
Unidentifiable eggs	7.47
Sponge (spicules)	5.58
Amphipods	5.43
Bryozoans	1.45
<i>Thalassia testudinum</i>	0.50

Mullidae (Goatfishes)

Pseudupeneus maculatus

Spotted goatfish

1 location; 2 specimens: 44.3 to 46.1 mm SL; 1 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Shrimp	
Penaeidae	29.20
Cumacean	20.29
Unidentifiable crab	28.61
Amphipods	17.33
Nematode	4.57

Pomacentridae (Damsel fishes)

Abudefduf saxatilis

Sergeant major

2 locations; 23 specimens: 38 to 59 mm SL; 5 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Amphipods	30.06
Algae	

Ulvaceae	13.36
Sphacelariaceae	11.03
Phaeophyta	9.24
Cladophoraceae	8.54
Ceramium	8.40
Dasyaceae	3.73
Udotaceae	1.98
Isopods (including larvae)	6.14
Cumacean shrimp	2.86
Seagrass	0.10
<i>Halodule wrightii</i>	2.10
Copepods	
Harpacticoidea	2.25
Polychaete	0.11
Crab megalops	0.10

Stegastes adustus

Dusky damselfish

1 location; 2 specimens: 31 to 48 mm SL

<u>Food</u>	<u>Dry Mass (%)</u>
Algae	
Corallinaceae	54.64
Ceramium	14.58
Udotaceae	0.48
Rodomeniaceae	0.06
Unidentifiable eggs	13.59
Seagrass	
<i>Halodule wrightii</i>	7.66
<i>Syringodium filiforme</i>	0.84
Crab megalops	6.12
Copepod - harpacticoidea	2.07

Scaridae (Parrotfishes)*Sparisoma viride*

Stoplight parrotfish

2 locations; 2 specimens: 32 to 136 mm SL; 1 empty

<u>Food</u>	<u>Dry Mass (%)</u>
Coralline algae	94.63
Forams	5.37

Sphyraenidae (Barracudas)

Sphyraena barracuda

6 locations; 9 specimens: 65.7 to 766.0 mm SL; 3 empty

Great barracuda

Food

Dry Mass (%)

Fish

Selar crumenophthalmus

40.00

Atherinomorus stipes

27.22

Strongylura notata

20.00

Penaeid shrimp larvae

7.69

Copepod - Calanoidea

0.24

Unidentifiable animal remains

4.85

Appendix B: List of Abbreviation Codes

Common name	Genus	Species	CODE
Southern stingray	<i>Dasyatis</i>	<i>americana</i>	DASAME
Spotted eagle ray	<i>Aetobatus</i>	<i>narinari</i>	AETNAR
Blacktip shark	<i>Carcharhinus</i>	<i>limbatus</i>	CARLIM
Permit (juv)	<i>Trachinotus</i>	<i>falcutus</i>	TRAFALJUV
Yellow jack	<i>Caranx</i>	<i>bartholomaei</i>	CARBAR
Horse-eye jack	<i>Caranx</i>	<i>latus</i>	CARLAT
Yellow jack (juv)	<i>Caranx</i>	<i>bartholomaei</i>	CARBARJUV
Horse-eye jack (juv)	<i>Caranx</i>	<i>latus</i>	CARLATJUV
Bar jack	<i>Caranx</i>	<i>ruber</i>	CARRUB
Palometa (juv)	<i>Trachinotus</i>	<i>goodei</i>	TRAGOOJUV
Bonefish	<i>Albula</i>	<i>vulpes</i>	ALBVUL
Mutton snapper	<i>Lutjanus</i>	<i>analis</i>	LUTANA
Schoolmaster	<i>Lutjanus</i>	<i>apodus</i>	LUTAPO
Black margate	<i>Anisotremus</i>	<i>surinamensis</i>	ANISUR
Yellowtail snapper	<i>Ocyurus</i>	<i>chrysurus</i>	OCYCHR
Gray angelfish	<i>Pomacanthus</i>	<i>arcuatus</i>	POMARC
Redfin needlefish	<i>Strongylura</i>	<i>notata</i>	STRNOT
False pilchard	<i>Harengula</i>	<i>culpeola</i>	HARCUL
Red-ear sardine	<i>Harengula</i>	<i>humeralis</i>	HARHUM
Atlantic thread herring	<i>Opisthonema</i>	<i>oglinum</i>	OPIOGL
Longsnout butterflyfish	<i>Chaetodon</i>	<i>aculeatus</i>	CHAACU
Foureye butterflyfish	<i>Chaetodon</i>	<i>capistratus</i>	CHACAP
Banded butterflyfish	<i>Chaetodon</i>	<i>striatus</i>	CHASTR
Silver mojarra	<i>Eucinostomus</i>	<i>aregenteus</i>	EUCARE
Yellowfin mojarra	<i>Gerres</i>	<i>cinereus</i>	GERCIN
Yellowfin mojarra (juv)	<i>Gerres</i>	<i>cinereus</i>	GERCINJUV
Porkfish	<i>Anisotremus</i>	<i>virginicus</i>	ANIVIR
Tomtate	<i>Haemulon</i>	<i>aurolineatum</i>	HAEAUR
French grunt	<i>Haemulon</i>	<i>flavolineatum</i>	HAEFLA
Bluestriped grunt	<i>Haemulon</i>	<i>sciurus</i>	HAESCI
Reef squirrelfish	<i>Holocentrus</i>	<i>ascensionis</i>	HOLASC
Longspine squirrelfish	<i>Holocentrus</i>	<i>rufus</i>	HOLRUF
Gray snapper	<i>Lutjanus</i>	<i>griseus</i>	LUTGRI
Mahogany snapper	<i>Lutjanus</i>	<i>mohagoni</i>	LUTMOH
Lane snapper	<i>Lutjanus</i>	<i>synagris</i>	LUTSYN
Yellow goatfish	<i>Mulloidichthys</i>	<i>martinicus</i>	MULMAR
Spotted goatfish	<i>Pseudupeneus</i>	<i>maculatus</i>	PSEMAC
Sergeant major (juv)	<i>Abudefduf</i>	<i>saxatilis</i>	ABUSAXJUV
Saucereye porgy	<i>Calamus</i>	<i>calamus</i>	CALCAL
Yellow sea chub	<i>Kyphosus</i>	<i>incisor</i>	KYPINC
Bermuda chub	<i>Kyphosus</i>	<i>sectatrix</i>	KYPSEC

Ocean surgeonfish	<i>Acanthurus</i>	<i>bahianus</i>	ACABAH
Doctorfish	<i>Acanthurus</i>	<i>chirurgus</i>	ACACHI
Doctorfish juvenile	<i>Acanthurus</i>	<i>chirurgus</i>	ACACHIUV
Blue tang	<i>Acanthurus</i>	<i>coeruleus</i>	ACACOE
Black durgon	<i>Melichthys</i>	<i>niger</i>	MELNIG
Yellowtail damselfish	<i>Microspathodon</i>	<i>chrysurus</i>	MICCHR
Great barracuda	<i>Sphyræna</i>	<i>barracuda</i>	SPHBAR
Hogfish	<i>Lachnolaimus</i>	<i>maximus</i>	LACMAX
Cubera snapper	<i>Lutjanus</i>	<i>cyanopterus</i>	LUTCYA
Green moray	<i>Gymnothorax</i>	<i>funnebris</i>	GYMFUN
Nassau grouper	<i>Epinephelus</i>	<i>striatus</i>	EPISTR
Trumpetfish	<i>Aulostomus</i>	<i>maculatus</i>	AULMAC
Peacock flounder	<i>Bothus</i>	<i>lunatus</i>	BOTLUN
Spanish hogfish	<i>Bodianus</i>	<i>rufus</i>	BODRUF
Creole wrasse	<i>Clepticus</i>	<i>parrae</i>	CLEPAR
Puddingwife	<i>Halichoeres</i>	<i>radiatus</i>	HALRAD
Sand tilefish	<i>Malacanthus</i>	<i>plumieri</i>	MALPLU
Honeycomb cowfish	<i>Acanthostracion</i>	<i>polygonius</i>	ACAPOL
Grasby	<i>Cephalopholis</i>	<i>cruentata</i>	CAPCRU
Coney	<i>Cephalopholis</i>	<i>fulva</i>	CEPFUL
Rock hind	<i>Epinephelus</i>	<i>adscensionis</i>	EPIADS
Red hind	<i>Epinephelus</i>	<i>guttatus</i>	EPIGUT
Slippery dick	<i>Halichoeres</i>	<i>bivittatus</i>	HALBIV
Yellowhead wrasse	<i>Halichoeres</i>	<i>garnoti</i>	HALGAR
Black-ear wrasse	<i>Halichoeres</i>	<i>poeyi</i>	HALPOE
Blue chromis	<i>Chromis</i>	<i>cyanea</i>	CHRCYA
Barred hamlet	<i>Hypoplectrus</i>	<i>puella</i>	HYPPUE
Island frillfin	<i>Bathygobius</i>	<i>mystacium</i>	BATMYS
Green razorfish	<i>Xyrichtys</i>	<i>splendens</i>	XYRSPL
Reef silversides	<i>Allanetta</i>	<i>harringtonensis</i>	ALLHAR
Hardhead silversides	<i>Atherinomorus</i>	<i>stipes</i>	ATHSTI
Dwarf herring	<i>Jenkinsia</i>	<i>lamprotaenia</i>	JENLAM
Striped anchovy	<i>Anchoa</i>	<i>hepsetus</i>	ANCHEP
Dusky anchovy	<i>Anchoa</i>	<i>lyolepis</i>	ANCLYO
Fairy basslet	<i>Gramma</i>	<i>loreto</i>	GRALOR
Clown wrasse	<i>Halichoeres</i>	<i>maculipinna</i>	HALMAC
Harlequin bass	<i>Serranus</i>	<i>tigrinus</i>	SERTIG
Whitespotted filefish	<i>Cantherines</i>	<i>macroceros</i>	CANMAC
Queen angelfish	<i>Holacanthus</i>	<i>ciliaris</i>	HOLCIL
Rock beauty	<i>Holacanthus</i>	<i>tricolor</i>	HOLTRI
French angelfish	<i>Pomacanthus</i>	<i>paru</i>	POMPAR
Dusky damselfish	<i>Stegastes</i>	<i>fuscus</i>	STEFUS
Cocoa damselfish	<i>Stegastes</i>	<i>variabilis</i>	STEVAR
Orangespotted filefish	<i>Cantherhines</i>	<i>pullus</i>	CANPUL

Beau gregory	<i>Stegastes</i>	<i>leucostictus</i>	STELEU
Yellow damselfish	<i>Stegastes</i>	<i>planifrons</i>	STEPLA
Sharpnose puffer	<i>Canthigaster</i>	<i>rostrata</i>	CANROS
Goldspot goby	<i>Gnatholepis</i>	<i>thompsoni</i>	GNATHO
Princess parrotfish	<i>Scarus</i>	<i>taeniopterus</i>	SCATAE
Redfin parrotfish	<i>Sparisoma</i>	<i>rubripinne</i>	SPARUB
Stoplight parrotfish	<i>Sparisoma</i>	<i>viride</i>	SPAVIR
Stoplight parrotfish (juv)	<i>Sparisoma</i>	<i>viride</i>	SPAVIRJUV
Striped parrotfish	<i>Scarus</i>	<i>iserti</i>	SCAISE
Redband parrotfish	<i>Sparisoma</i>	<i>aurofrenatum</i>	SPAAUR
Redlip blenny	<i>Ophioblennius</i>	<i>atlanticus</i>	OPHATL