In: Pollock NW, Godfrey JM, eds. Diving for Science 2007.
Proceedings of the American Academy of Underwater Sciences 26th Symposium.Dauphin Island, AL: AAUS; 2007.

Using SCUBA and Snorkeling Methods to Obtain Model Parameters for an Ecopath Network Model for Calabash Caye, Belize, Central America

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Abstract

We have been collecting biological data for the construction of a food web model of Calabash Caye, Belize using Ecopath with Ecosim software. Characterization of the mangrove, seagrass and coral reef environments surrounding Calabash Caye will provide baseline data for a network model of the trophic relationships in this area, which is currently being considered as a marine protected area. Our Ecopath model follows a previously published Puerto Rico – Virgin Islands 50-compartment model; 27 of the compartments represent fishes. The collection of fish biomass and abundance data was done using visual surveys with both SCUBA and snorkel. Important dietary information was gathered from fish collected by spearfishing, beach seine, gill nets and hook and line. Smaller benthic invertebrates were collected using a small suction dredge and larger invertebrates were counted along visual transects using SCUBA and snorkeling. Additional data for various compartments that were not sampled, including birds, phytoplankton, benthic autotrophs and detritus, come from other Belizean or Caribbean studies and literature values. Abundance and biomass of all compartments were determined and converted to g wet weight·m-2. Selected Ecopath outputs, such as effective trophic levels and mixed trophic impacts, allow us to gain insight into trophic structure and how changes in biomass travel through the food web to affect other species. The model will enable Belizean scientists and managers to monitor and formulate predictions about potential ecosystem changes that are associated with the marine reserve.

Introduction

The Mesoamerican Barrier Reef system is the second largest barrier reef in the world and provides a 220 km off-shore boundary that runs the length of Belize. As is common throughout the Caribbean, mangroves and seagrass beds are intimately connected to the reef system (Bossi and Cintron, 1990; Kitheka, 1997; Moberg and Rönnbäck, 2003; Mumby *et al.*, 2004; Harborne *et al.*, 2006; Mumby, 2006) and line Belize's eastern shoreline, supporting a variety of organisms that may eventually inhabit the reefs. Each of these ecosystems provides valuable functions and services to the natural environment as well as to humans (Costanza *et al.*, 1997).

The Belize reef system is home to many commercially and recreationally important species, such as groupers, snappers, tarpon, conch and lobster (Gardiner and Harborne, 2000). Marine target species are sought after by artisanal, recreational and commercial fishermen. In many cases, the fisheries are self-regulated; there are 13 registered cooperatives owned, operated and managed by the fishers themselves (Gillet, 2003). Behind tourism and agriculture, fisheries represent Belize's third most important industry (McField *et al.*, 1996). In 1995, Belize exported $20 million BZ alone, with lobster and conch contributing greater than 90% of the total value of exported seafood (McField *et al.*, 1996). Shrimp and finfish are also important, but to a much lesser extent.

Belize has been pro-active in protecting its coastal marine resources. Since 1982, Belize has created thirteen marine protected areas (MPAs) (CZMAI, 2003). These MPAs exist along the coastline, but several areas remain unprotected. The Turneffe Islands atoll has been identified as an area necessary for the completion of a national protected area system (Meerman and Wilson, 2005). It has also been nominated as a United Nations Educational, Scientific, and Cultural Organization (UNESCO) Man and the Biosphere (MAB) Reserve (CZMAI, 2003). It is expected that the formation of an MPA or MAB reserve at the Turneffe Islands will cause significant shifts in the trophic structure of the ecosystem (Polunin and Roberts, 1993; Roberts, 1995). Without baseline data, it will be difficult to track changes in trophic flows and food web structure. The collection of such data and construction of a network model of trophic flows are the objectives of this study.

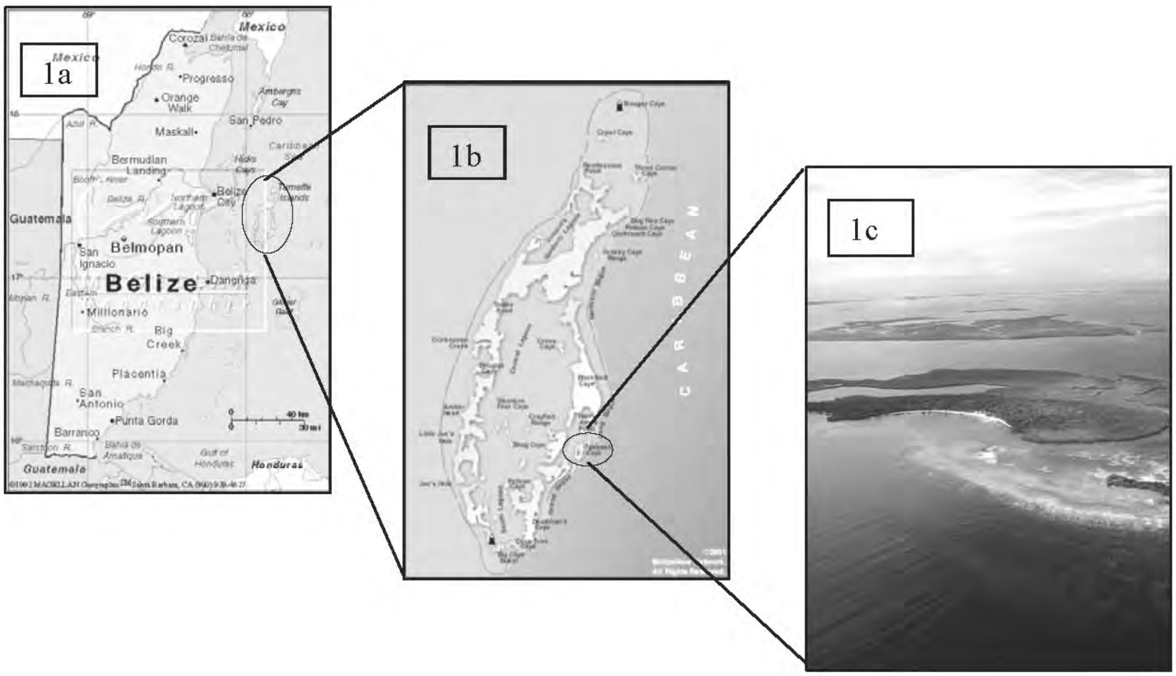
A network analysis model can be useful to predict multi-species interactions that may occur due to changes in fishery harvests should the MPA be established. Ecopath is a network modeling software package that was first developed by Polovina (1984a, 1984b) to mathematically estimate the standing stock and production budget of the French Frigate Shoals ecosystem in the northwest Hawaiian Islands. Ecopath has since been developed to its present form of Ecopath with Ecosim 5.1, which combines the biomass budget approach of Polovina with network analysis theory (Ulanowicz, 1986) for analyzing flows between compartments. It also includes time (Ecosim) and space (Ecospace) dynamic simulation modules to investigate how the system will change over time in response to policies on fishing and MPAs (Christensen and Pauly, 1992; Christensen and Walters, 2004; Libralato *et al.*, 2006).

Previously, a network model was developed for a Caribbean coral reef ecosystem, and we used this as a base model. Opitz (1993, 1996) created a 30-year comprehensive network model of the Puerto Rico – Virgin Islands (PRVI) coral reef ecosystem using Ecopath II software. The Opitz model served as a starting point for the construction of our Calabash Caye food web model. We wanted to collect site-specific data for Calabash Caye coral reefs, seagrass beds and mangroves to measure the abundance and biomass of benthic invertebrates and fishes and to collect dietary data on some of the fishes. Our goal was to provide managers with the data necessary to help make informed policy decisions regarding Calabash Caye marine resources. The construction of this Ecopath network model will represent a baseline condition of the ecosystem prior to establishment as a protected area, describe trophic interactions among members of the Calabash Caye ecosystem, and identify any major gaps in knowledge that should be addressed with further research.

Methods

Site Description

The Turneffe Islands are located on the second submarine ridge on the Belize continental shelf (Figure 1a). The Turneffe Islands atoll is about 48 km long and 16 km wide at its widest point. This formation of mangrove islands is 10–16 km east of the Mesoamerican Barrier Reef, with a nearly 300 m deep channel between barrier reef and the Turneffe Islands (Garcia and Holtermann, 1998). The University of Belize research station, the Institute for Marine Studies (IMS), is located on Calabash Caye, a small mangrove caye located on the southeastern side of the atoll, nearly 51 km off the coast of Belize (Figures 1b and 1c). Researchers from East Carolina University (ECU) have been utilizing the facilities at IMS since 1999 for a tropical marine ecology course, where several student research projects have been conducted. Specific data from these projects (especially Rueter, 2004) have been combined with new data collected in this study to create an Ecopath network model of the Calabash Caye system.



Figures 1a, b and c. Maps of study areas: 1a) Map of Belize, Central America (from Magellan Geographix); 1b) Turneffe Islands Atoll (from BelizeNow Network); 1c) Calabash Caye examined from the northeast (photo from Coral Caye Conservation).

A shallow central lagoon, filled with *Thalassia* and *Halimeda spp.*, dark organic muds and some small patch reefs, is about 500 m long and up to 8 m deep (Garcia and Holtermann, 1998). There is very little flushing or circulation that occurs within the lagoon (Gischler, 2003). Mangroves cover most of the caye, especially red mangrove *Rhizophora mangle,* black mangrove *Avicennia germinans,* and white mangrove *Laguncularia racemosa*. Seagrass beds are dominated by *Thalassia testudinum* with lesser amounts of *Syringodium filiforme, Halodule wrightii* and a variety of algal species, and can be found between the mangrove-lined coast and the coral reefs. The coral reefs show typical West Indian windward coral reef zonation patterns (Garcia and Holtermann, 1998).

Ecopath Model Parameters

Ecopath models are composed of compartments, or biomass pools, that can be represented by a single species, life stage of a single species, or group of similar species. The basic input requirements for each compartment are biomass, consumption, production, diet and unassimilated diet to consumption ratio. The 50 compartment PRVI model created by Opitz (1996) using Ecopath II served as the template for the Calabash Caye Ecopath model. Compartments were identified by group number accompanied by the common names of representative members of that group. For a more complete listing, see Table 1 for the representative members of each compartment. Specific information about the compartments can be found below in the section on Biological Data Collections and in Opitz (1996), Barry (2006) and Chagaris (2006). Site-specific measurements for fish and invertebrate biomasses and fish dietary data were collected in mangrove, seagrass and coral reef habitats, and all data were combined for the construction of one model of Calabash Caye. This model, constructed using Ecopath with Ecosim 5.0, emphasizes an inclusive ecosystem rather than three independent systems. Compartments not sampled at Calabash Caye (such as seabirds, turtles, phytoplankton) were filled with data from the Opitz (1996) model or the diet study conducted by Randall (1967).

Table 1. Selected characteristics of the 50-compartment Calabash Caye ecosystem model, arranged by effective trophic level.

Group Number	Model Compartment Name	Representative Members	Effective Trophic Level	Biomass (gWW/m2)
28	Sea birds	birds	4.5	0.003
2	Sharks/scombrids, carnivorous	sharpnose shark, bonnethead, mackerel, tunny	4.2	2E-09
4	Intermediate jacks, carnivorous	palometa, bar/yellow/horse-eye jack, blue runner	3.9	1.233
18	Large groupers, carnivorous	black grouper, itajara	3.9	2E-09
29	Squids	squids	3.9	0.8
12	Large reef fish, carnivorous	hogfish, barracuda, cubera snapper, moray eel	3.8	3.072
1	Large sharks/rays, carnivorous	southern stingray, eagle ray, blacktip shark, nurse shark	3.7	0.247
5	Small jacks, carnivorous	scad, ladyfish	3.6	0.015
13	Intermediate reef fish, carnivorous 3	trumpetfish, flounder, creole wrasse, tilefish, coney, graysby, rock/red hind	3.6	4.894
15	Small schooling fish, pelagic	silversides	3.6	3.529
16	Engraulidae, herbivorous	anchovies	3.6	4.33
17	Small reef fish, carnivorous 2	fairy basslet, clown wrasse, harlequin bass	3.6	1.257
7	Large-intermediate schooling fish, pelagic	needlefish, herrings	3.5	7.15
14	Small reef fish, carnivorous 1	yellowhead wrasse, chromis, hamlet, razorfish	3.5	4.886
27	Small Gobiidae, carnivorous	yellowline goby, sharknose goby	3.5	0.0000072
3	Large jacks, carnivorous	jacks, permit	3.4	0.027
6	Intermediate reef fish, carnivorous 1	bonefish, mutton snapper, schoolmaster, black margate, angelfish	3.4	2.394
8	Intermediate reef fish, carnivorous 2	butterflyfish, mojarra, grunts, squirrelfish, porgy, goatfish, sergeant major, lane/gray/mahogany snapper	3.4	6.75
31	Octopuses	octopi	3.3	3.025
34	Shrimps/hermit crabs/ stomatopods	all shrimps, hermit crabs and stomatopods	3.1	5.199
19	Intermediate reef fish, carnivorous 4	filefish, angelfish, rock beauty	3	1.967
21	Small reef fish, omnivorous 2	beaugregory, yellowdamselfish, puffer	2.9	0.0664
32	Lobsters	spiny lobsters	2.8	1.986
30	Sea turtles	sea turtles	2.7	0.00614
36	Asteroids	sea stars	2.7	5.4
45	Corals/sea anemones	all corals and anemones	2.7	109.51
39	Chitins/scaphopods	chitons and tusk shells	2.6	32.997
46	Zooplankton	zooplankton	2.6	31.2
35	Small benthic arthropods	small crustaceans	2.5	5.949
40	Polychaetes/priapuloids/ophiuroids	segmented worms, penis worms, brittle stars	2.5	23.509
43	Ascidians/barnacles/ bryozoans	tunicates, barnacles, moss animals	2.5	45
20	Small reef fish, omnivorous 1	damselfish, orange spotted filefish	2.4	1
22	Small reef fish, omnivorous 3	goldspot goby	2.4	1.152
33	Crabs	all crabs	2.4	26.6
38	Gastropods	conch, snails and slugs	2.4	26.789
37	Echinoids	sea urchins	2.2	17.1
41	Holothuroids/sipunculids/ echiuroids/hemichordates	sea cucumber, peanut worms, echiuroid worms	2.2	30.978
9	Hemiramphidae, herbivorous	halfbeaks	2.1	2E-09
11	Intermediate reef fish, herbivorous	surgeonfish, doctorfish, tang, durgeon	2.1	7.003
42	Bivalves	bivalved mollusks	2.1	43.345
10	Kyphosidae, herbivorous	sea chubs	2	0.00000001
23	Large Scaridae, herbivorous	rainbow/midnight/queen parrotfish	2	0.00000001
24	Intermediate Scaridae, herbivorous	princess/redfin/stoplight parrotfish	2	28.135
25	Small Scaridae, herbivorous	striped/redband parrotfish	2	7.026
26	Blenniidae, herbivorous	redlip blenny	2	1.067
44	Sponges	all sponges	2	95
47	Decomposers/microfauna	decomposing bacteria	2	15
48	Phytoplankton	photosynthetic plankton	1	42
49	Benthic autotrophs	seagrasses and algae	1	2000
50	Detritus, POM, DOM	nonliving organic material	1	2000

Biological Data Collection

Field surveys of mangrove, seagrass and coral reef sites were completed in June 2005 using snorkel and SCUBA gear. This sampling time frame was based on previous studies in Belize that found little or no seasonal variation in fish abundance and biomass (Sedberry and Carter 1992) and the Mesoamerican Barrier Reef System (MBRS) recommendation that fish, coral, algae and mangrove surveys be completed between June 1 and July 31 to account for variations in environmental conditions (Almada-Villela *et al.*, 2003).

Three habitat types were sampled – mangroves, seagrasses and coral reefs. Seventy random x and y (UTM) points were created in Excel and locations were transformed into a sampling map using ArcView. Survey site information was mapped over a base map using a Landsat 7 satellite image from May 23, 2000. Eight sites within each habitat (24 sites total) were selected for estimating biomass of fish and benthic invertebrates, while fishes collected for the diet matrix were sampled at different locations where various gear could be more efficiently deployed (Figure 2). Areas in water deeper than 11 m were not sampled due to light absorption problems associated with visual surveys, gear limitations and difficulties associated with repetitive diving.

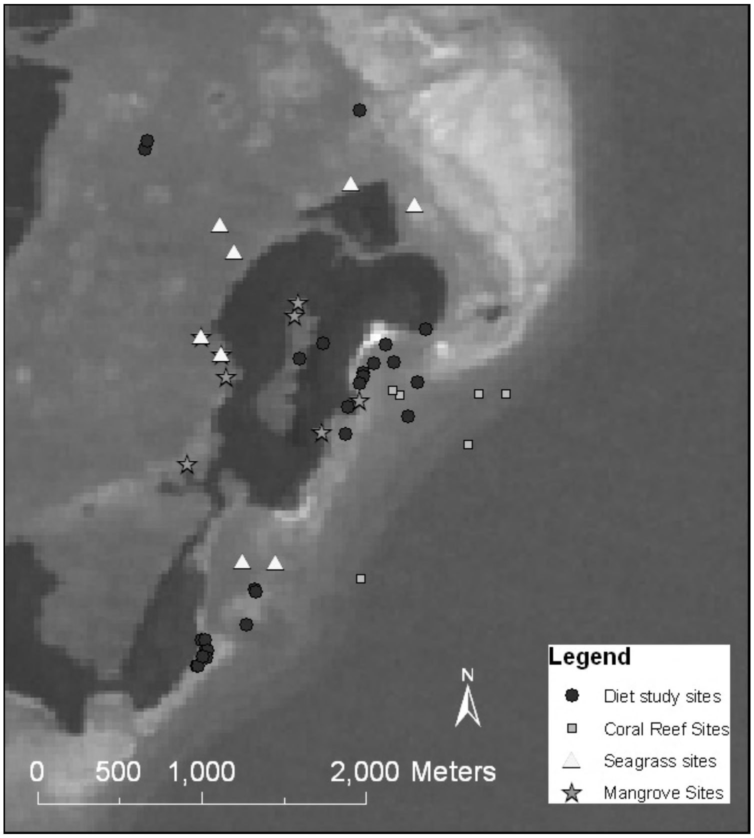


Figure 2. Calabash Caye study sites identified by habitat type and method of sampling. Landsat 7 satellite image from May 23, 2000.

Fish Biomass Measurement

Transect lines and radial point counts were used to visually survey the fish populations. These methods are similar to techniques used by the MBRS (Almada-Villela *et al.*, 2003) and Reef Check (www.reefcheck.org), groups that also collect data about Belizean reefs. The radial point count requires a stationary diver and was designed so that non-mobile, cryptic species could be observed

(Bohnsack and Bannerot, 1982; Buxton and Smale, 1989; Polunin and Roberts, 1993; Roberts, 1995). Because the transect line and radial point systems may select for fish with different behaviors, the two methods were combined to reduce bias from each method.

Surveys were made within one hour of sunrise and sunset, periods of maximal crepuscular activity. Fish sightings were recorded on a dive slate with prepared data sheet and attached T-bar unit (a 1.27 cm diameter PVC pipe of 60 cm length). At each site, fish were counted along a 30 m x 2.0 m transect line followed by a 7.5 m radial point count at the end, and returned along the same 30 m transect performing another census. A second transect/radial point survey was conducted at least 15 m away from and parallel to the first (Figure 3). The total area surveyed was 593 m^2. Only fish observed along the transects and within the radial point surveys were counted. At mangrove sites, only one transect/radial survey was performed (area sampled = 297 m^2).

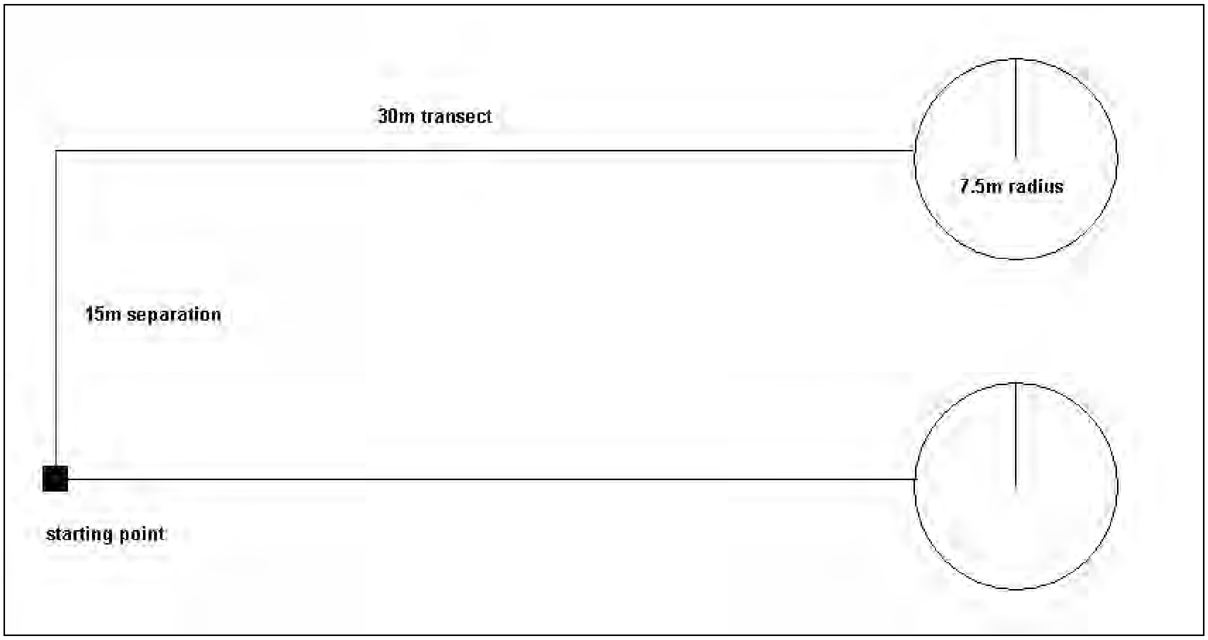


Figure 3. Diagram of fish abundance and biomass sampling survey. A 7.5 m radial point count was conducted at the end of each 30 m transect.

To estimate individual fish total length, we modified procedures used by Bell *et al.* (1984), Bohnsack and Bannerot (1986) and MBRS (Almada-Villela *et al.*, 2003). Length-weight relationships published by Bohnsack and Harper (1988), Opitz (1996), Cleveland and Montgomery (2003) and Fishbase (Froese and Pauly, 2006; www.fishbase.org) were used to calculate biomass of each species identified. We calculated fish weight based on the midpoint of its size class (*e.g.*, for size class 6-10 cm, biomass was calculated using 8.0 cm). Mean biomasses were used for all reporting and statistical analyses.

Benthic Invertebrate Biomass Measurement

Benthic samples are often difficult to collect using only one method because substrates can vary substantially from organic-rich, soft-bottomed mangrove sites to rhizome- and root-dense seagrass beds to carbonate rock and coral rubble. To eliminate sampling bias associated with using different sampling techniques, a modification of Brook's (1979) suction dredge was used for this study. A gasoline-powered irrigation pump was used, providing 3.5 hp and 145 gal/min to pump water through hoses with an inside diameter of 7.5 cm. At the suction head, the opening was reduced to 3.75 cm, creating the Venturi vacuum effect necessary to cause sufficient suction. Collection bags, attached at the outlet of the suction head, had a mesh width of 2 mm (or 3 mm stretch) and easily contained the 7,065 cm^3 samples. Triplicate samples were taken at sites corresponding to the fish biomass surveys (eight locations each in mangrove, seagrass and coral reef areas).

Most samples were collected using SCUBA. A bottomless 20 L bucket with 30 cm inside diameter was placed on the substrate to delineate sample surface area and to contain mobile species. Samples were dredged to a depth of 10 cm. Any seagrasses or algae present in the sample were manually removed from the substrate inside the bucket and sucked into the sample bag. All samples were collected mid-day, usually between 1500 and 1800 hours local time, and fixed with 10% formalin-seawater mixture. Despite the 2.0 mm mesh collection bag, large shells and benthic autotrophs prevented particles smaller than 2.0 mm from passing through the mesh bag. Thus, samples were passed through a 500 µm sieve to remove all benthic invertebrates that were alive at the time of collection. A microscope was used to identify benthic invertebrates and classify them into the corresponding Opitz (1996) non-fish groups. Specimens were weighed to the nearest 0.00001 g wet weight using a Mettler H51 precision balance.

Additional visual surveys of macroinvertebrates were conducted by a snorkeler along thirty-meter transects at five mangrove, six seagrass and eight coral reef locations. All macroinvertebrates encountered within a meter along either side of the transects were counted and sizes estimated. A size-weight relationship for each species was determined from the published literature (Cary, 1916; Doran, 1958; Horn, 1982; Hunte *et al.*, 1989; Pauly, 1993; Pomory, 1998; SEAMAP-SA, 2002; Muthiga and Jaccarini, 2004). Biomasses (g wet weight·m^{-2}) of each group observed during the visual surveys were then added to the biomass values from the microinvertebrate (suction dredge) sampling.

Fish Diet Study

Fish were collected using experimental gill nets that were 38.10 m long, 1.83 m deep, and composed of five 7.62 m sections with increasing mesh size from 2.5-12.7 cm stretch mesh monofilament. A 15 m bag seine with 0.64 cm ace mesh netting was used to sample the fish community present in the seagrass areas along the shoreline. A 1.8 m pole spear and hook and line were used to sample the fishes within the reef. All spear fishing was done while snorkeling.

A sieve fractionation technique was used as described by Carr and Adams (1972), Luczkovich and Stellwag (1993), Christian and Luczkovich (1999), and Luczkovich *et al.* (2002) to examine the stomach contents of each individual. Weight was measured to 0.00001 gram using a Mettler H51 precision balance. Fish with empty stomachs were not analyzed.

A 137 by 137 square diet matrix consisting of 96 fish species and 41 non-fish groups was constructed using dietary data from this study (Chagaris, 2006), Randall (1967), Fishbase (Froese and Pauly, 2006; www.fishbase.org), and Opitz (1996). Within each cell of the matrix, the proportion of each prey to the overall diet of its predator was entered so that the diet for each consumer summed to one. The taxonomic level of organisms identified from stomach contents in this study and Randall (1967) varied from species to broader categories, with most invertebrates grouped under broader taxonomic categories. The non-fish prey aggregations used by Opitz (1996) allowed for representation of all prey items in the diet matrix. Dietary data for non-fish taxa were taken directly from the diet composition matrix in PRVI Ecopath model (Opitz, 1996). 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).

Model Balancing and Analysis

In order for Ecopath to formulate outputs, the model must first be mass-balanced, accounting for all mortality within the system and providing enough prey biomass to support their associated predators. The model was mass-balanced by first manually adjusting parameters with least confidence in its source data followed by running the auto-mass balancing routine, a feature of Ecopath with Ecosim 5.0.

Ecopath generates up to 37 different outputs ranging from basic analysis of each compartment to ecosystem-level indicators to network analysis of pathways (Christensen *et al.*, 2005). For simplicity, we have chosen only to examine those outputs that reflect system-wide trophic information (effective trophic levels, trophic level diagram and mixed trophic impacts). The Ecopath approach to determining effective trophic levels uses a routine that assigns primary producers and detritus a trophic level of 1. Consumers' trophic levels (TLs) are calculated as 1 + 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 $TL = 1 + [0.4(1) + 0.6(2)] = 2.6$. Effective trophic levels (ETLs) are calculated using diet matrix information and visualized in the trophic level diagram. The mixed trophic impacts matrix and diagram show how small increases in the biomass of one compartment can impact all other compartments. This is done by computing the material flow into and out of each compartment, and scaling these flows by the total flows from all compartments. Thus, if one compartment comprises the bulk of the material flow into another compartment, it will have a large impact on that compartment if it is removed or increased. This is summed over all possible pathways to estimate the total mixed trophic impact of any compartment on another.

Results and Discussion

Interpretation of Model Outputs

Biomass in Balanced Compartments

The greatest biomass was associated with benthic producers (seagrasses and algae) and organic matter (detritus, particulate organic matter or POM, dissolved organic matter or DOM), as would be expected at the base of a food web (Table 1). The next largest standing stocks were associated with large invertebrate groups that provide structure on the reef (corals/anemones = 109.5 g wet wt·m^{-2}; sponges = 95 g wet wt·m^{-2}). Other invertebrate groups associated with the benthos were next most important in biomass (ascidians/barnacles/bryozoans = 45 g wet weight·m^{-2}; bivalves = 43.3 g wet wt·m^{-2}; chitins/scaphopods = 33.0 g wet wt·m^{-2}; holothuroids and related taxa = 31.0 g wet wt·m^{-2}). Phytoplankton (42 g wet wt·m^{-2}) and zooplankton (31.2 g wet wt·m^{-2}) were next most dominant in biomass. Among fishes, herbivorous parrotfishes (Intermediate Scaridae = 28.1 g wet wt·m^{-2}) had the largest biomass, while carnivorous fishes (large groupers, jacks, scombrids, rays and sharks) were less than 1 g wet wt·m^{-2} each.

Effective trophic levels

In the Calabash Caye model, seabirds (Group 28; ETL = 4.5) represented the apex predators in this system because they consumed only fishes and had no predators; the biomass of this group was relatively small (Table 1 and Figure 4). Sharks and scombrids (Group 2) were representative of the second highest trophic group with an ETL of 4.2 (also with relatively low biomass). There were 19 compartments with ETLs from 3.0 to 3.9, the largest of which were three carnivorous reef fish groups dominated by different species of jacks (Groups 6, 8 and 13). There were 26 compartments with

ETLs from 2.0 to 2.9, the largest of which represented parrotfish, and three compartments [detritus (Group 50), benthic autotrophs (Group 49) and phytoplankton (Group 48)] were classified at ETL 1.0.

Mixed trophic impacts

Direct and indirect tropic impacts are shown as a matrix of impacting groups (rows) and impacted groups (columns) (Figure 5). The mixed trophic impacts were largely positive (black upward bars) when lower trophic levels (detritus, benthic producers, decomposers/microfauna, zooplankton) were the impacting groups. These are the 'bottom-up' effects that would be expected if production increased at lower trophic levels. One exception is that Group 19 (dominated by angelfishes) would undergo a negative trophic impact. In contrast, mixed trophic impacts were largely negative (gray downward bars) when top-level groups [intermediate jacks (Group 3), schoolmasters and yellowtail snappers (Group 6) and hogfishes/barracudas/snappers (Group 12)] were the impacting groups. These are the 'top-down' effects. If these top predators were to increase, decreases would be expected in most other groups.

If targeted species such as large sharks/rays (Group 1), sharks/scombrids (Group 2), intermediate jacks (Group 4) and hogfishes/barracudas/snappers (Group 12), were to experience an increase in biomass (possibly due to reduction of fishing pressure after the establishment of an MPA), then there would be negative impacts on 18 fish compartments due to increased predation and/or competition and positive impacts on 12 fish compartments as a result of reduction of their predators and/or competitors (Figure 5). A closer look at the large sharks/rays (Group 1), present only in very low biomass in the Calabash model, revealed important trophic information. Only two species within this compartment (compared to 13 species in the PRVI model) were observed or collected at Calabash indicating that the species may be overfished, not selected by the sampling gear, avoided divers, or existed in deeper water outside of our sampling boundaries. The absence of these large sharks and scombrids may allow a greater abundance of herbivorous reef fish around Calabash Caye (Table 1 and Figure 4).

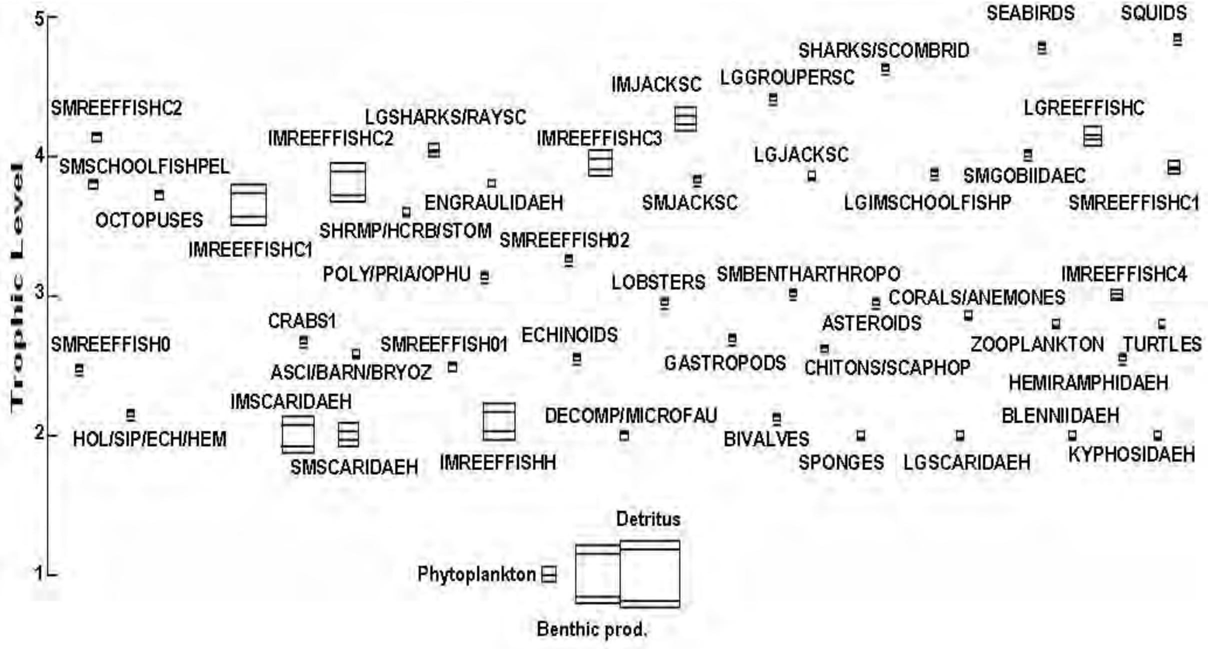
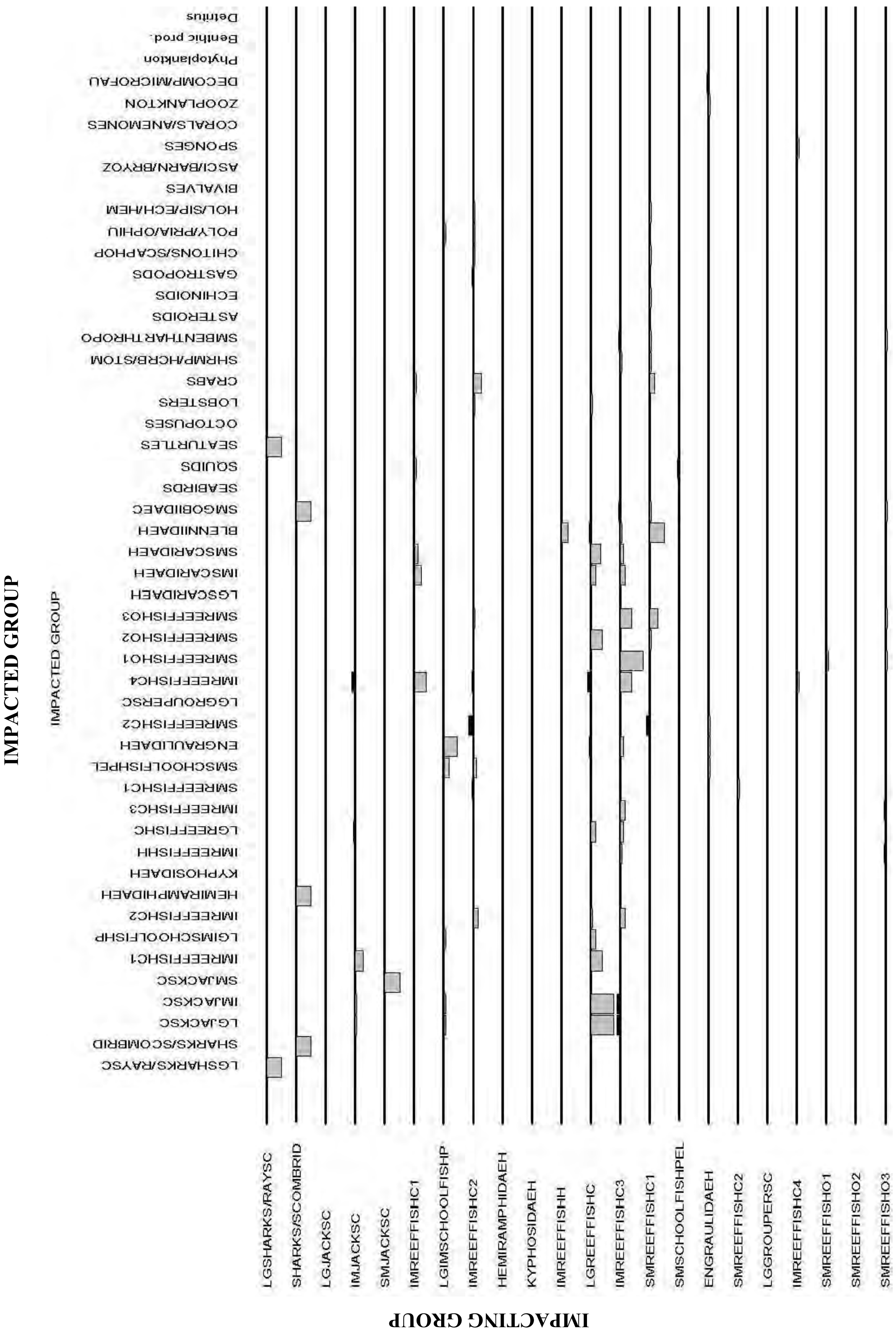


Figure 4. Trophic level diagram for the 50-compartment Calabash Caye ecosystem model. The vertical axis represents the trophic level of the compartment and the horizontal axis is dimensionless.


IMPACTED GROUP
IMPACTED GROUP
Detritus
Benthic prod.
Phytoplankton
DECOMP/MICROFAU
ZOOPLANKTON
CORALS/ANEMONES
SPONGES
ASCI/BARN/BRYOZ
BIVALVES
HOL/SIP/ECH/HEM
POLY/PRIA/OPHIU
CHITONS/SCAPHOP
GASTROPODS
ECHINOIDS
ASTEROIDS
SMBENTHARTHROPO
SHRMP/HCRB/STOM
CRABS
LOBSTERS
OCTOPUSES
SEATURTLES
SQUIDS
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LGREEFFISHC
IMREEFFISHC3
SMREEFFISHC1
SMSCHOOLFISHPEL
ENGRAULIDAEH
SMREEFFISHC2
LGGROUPERSC
IMREEFFISHC4
SMREEFFISHO1
SMREEFFISHO2
SMREEFFISHO3
IMPACTING GROUP

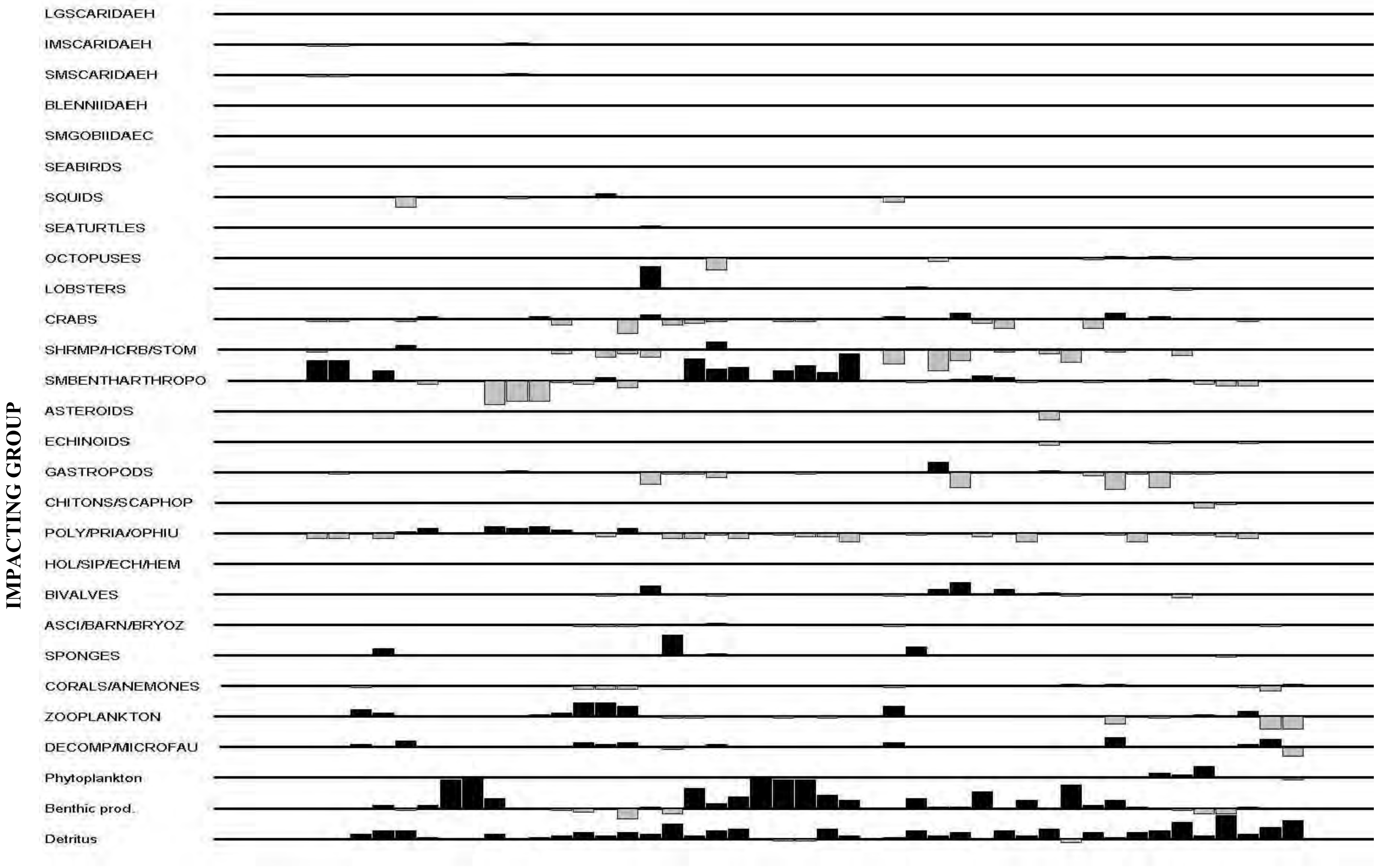

Figure 5. Mixed trophic impact diagram for the Calabash Caye ecosystem. Black bars represent positive impacts and gray bars represent negative impacts.

Some commonly targeted species, especially snappers, can play a significant role in the Calabash Caye ecosystem (Figure 6). Of the three snapper compartments (solid box, Figure 6), a small increase in the biomass of only one compartment (hogfishes/barracudas/snappers, Group 12), would have large negative impacts on several other fish compartments in the system. In terms of the abundant herbivorous fishes (dashed box, Figure 6), particularly the parrotfishes (Groups 24 and 25), small changes in their biomasses would not yield significant changes in most fish groups, although hogfishes/barracudas/snappers (Group 12) would be positively impacted by such a change.

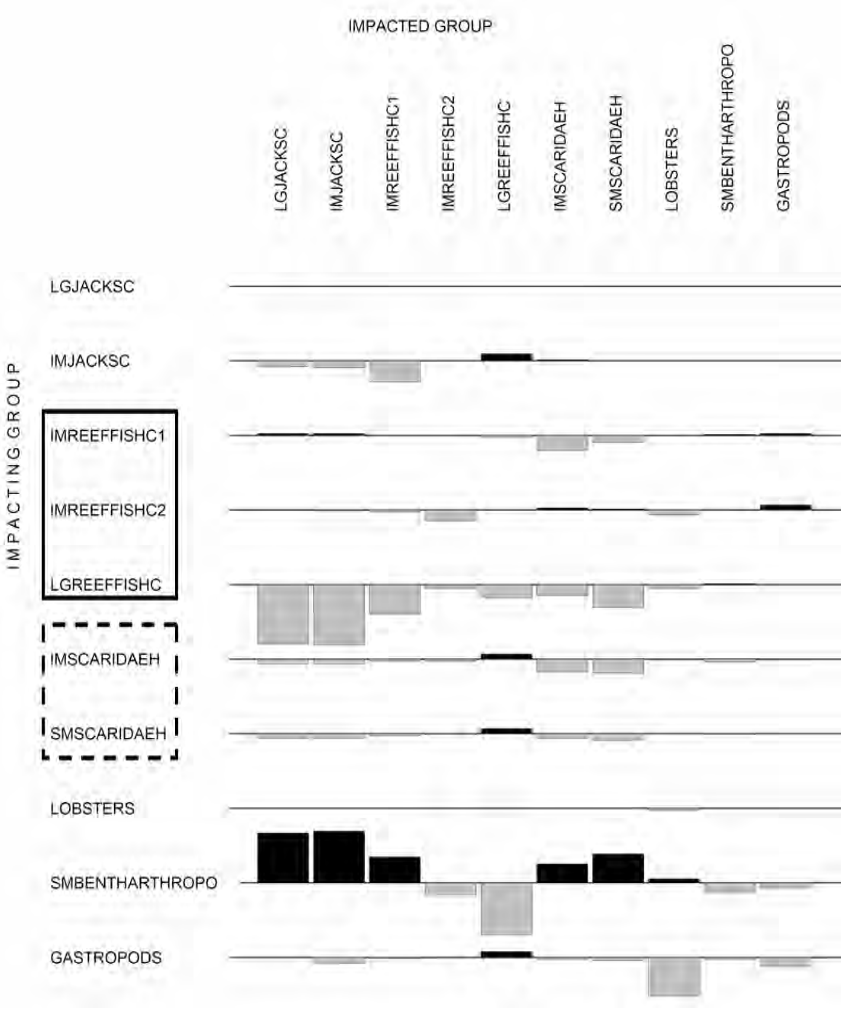

Figure 6. Mixed trophic impacts for Calabash Caye ecosystem with emphasis on snappers (solid box) and parrotfishes (dashed box).

The mixed trophic impact output showed the importance of small benthic arthropods (ETL = 2.51) in this system (Figure 6). The small benthic arthropods compartment had a biomass of only 6.0 g wet weight per square meter (Table 1). A small increase in the biomass of this compartment produced small positive or negative impacts on nearly every compartment in the Calabash model. This may indicate that these organisms are keystone group of species (Libralato *et al.*, 2006) within the Calabash Caye ecosystem. These organisms were found only at mangrove and seagrass sites using the suction dredging method. This suggests the critical importance of coral reef-associated habitats and the necessity to manage coastal development to conserve these habitats (Mumby *et al.*, 2004).

Examination of Model Construction

Our fish hbiomass data suggest that three separate models could be constructed to show the differences between mangrove, seagrass and coral reef habitats. Separate models might be beneficial to managers who can focus on 'smaller' networks, providing specific fish and non-fish compartmental data for each habitat. Ecopath with Ecosim 5.0 can be used to partition habitats within the ecosystem. However, due to the interconnectedness of the three sub-systems, it may be difficult to demarcate strict boundaries between the habitats.

The diets of the fish examined during this study were found to be similar to Randall (1967). Any differences in the diets between the two studies are likely attributable to the small sample sizes of some fishes from Calabash. Small differences in the diets of fish aggregated in our model may be masked by having multiple species in each compartment. For example, a fish at Calabash Caye may prey upon one species of xanthid crab while the same species of fish examined by Randall (1967) may eat a different species of xanthid crab, but in the model they are both feeding from the 'crabs' compartment. Because organisms are grouped into functionally or taxonomically similar compartments, dietary data reported in the literature from nearby or similar systems may prove to be sufficient for most ecosystem models. Refer to Chagaris (2006) for additional information regarding the diet matrix.

Ecopath uses a top-down approach to mass-balancing models. However, our data revealed large imbalances at the lowest trophic levels largely because many of those compartments were not sampled directly at Calabash Caye (especially detritus, benthic autotrophs, phytoplankton and zooplankton). As such, our manual mass-balancing method involved adjusting compartments and their parameters from the bottom-up. Higher trophic level compartments were deemed more reliable than the lower trophic level compartments. Care was taken to keep our values within reasonable ranges by frequently referring to the Opitz (1996) PRVI model. See Barry (2006) and Chagaris (2006) for additional information regarding the construction and balancing of the Calabash Caye model.

Applications for Use in Management

Our Ecopath model represents the most complete model to date of the Calabash Caye ecosystem. However, many assumptions were made to provide complete parameterization of the model. Dame and Christian (2006) call into question four major sources of uncertainty in ecological network analysis models: natural variability of input parameters, data collection methods, model construction, and algorithm assumptions. Should we have used the same 50 compartments as Opitz (1996), or should we have grouped our species according to our own assumptions? By using the same species aggregations, we can easily compare the Puerto Rico-Virgin Islands and Calabash Caye models (see Barry [2006] and Chagaris [2006] for comparisons). However, there were some differences in species groups between the two models. Fortunately, the data still exist, and new Calabash models can be created. Are the model outputs valid, and can they be trusted for making management decisions? To test validity, it may be helpful to create a similar Ecopath model for a current Belize MPA, such as the Hol Chan Marine Reserve, and compare outputs. Christensen and Walters (2004) warn against making management decisions based solely on the outputs of these models, but it is a starting point.

Perhaps this preliminary Calabash Caye model is most useful in making qualitative predictions about the effects that species removals or additions will have on the community structure. Important data that can improve the model include fisheries harvest data and life history data. These two sets of information can allow for model simulations using Ecopath with Ecosim, which may provide another method to predict ecosystem-wide changes. It may also be important to conduct lobster and conch surveys at Calabash Caye (not done in this study) to provide accurate biomass data, since these fisheries are so important to the Belize economy. With or without the creation of a new marine protected area at Calabash Caye, our model provides managers with an important tool that may allow them to prevent devastating changes in the ecosystem that may be caused by human interactions.

Acknowledgments

The authors thank the staff members at the IMS field station at Calabash Caye for logistical assistance, Molly Kilpatrick for conducting visual benthic surveys, the students of the Belize Marine Ecology class and our dive master/dive safety officer Mark Keusenkothen.

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