

Dataset Paper

Detailed Food Web Networks of Three Greater Antillean Coral Reef Systems: The Cayman Islands, Cuba, and Jamaica

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Food webs represent one of the most complex aspects of community biotic interactions. Complex food webs are represented as networks of interspecific interactions, where nodes represent species or groups of species, and links are predator-prey interactions. This paper presents reconstructions of coral reef food webs in three Greater Antillean regions of the Caribbean: the Cayman Islands, Cuba, and Jamaica. Though not taxonomically comprehensive, each food web nevertheless comprises producers and consumers, single-celled and multicellular organisms, and species foraging on reefs and adjacent seagrass beds. Species are grouped into trophic guilds if their prey and predator links are indistinguishable. The data list guilds, taxonomic composition, prey guilds/species, and predators. Primary producer and invertebrate richness are regionally uniform, but vertebrate richness varies on the basis of more detailed occurrence data. Each region comprises 169 primary producers, 513 protistan and invertebrate consumer species, and 159, 178, and 170 vertebrate species in the Cayman Islands, Cuba, and Jamaica, respectively. Caribbean coral reefs are among the world's most endangered by anthropogenic activities. The datasets presented here will facilitate comparisons of historical and regional variation, the assessment of impacts of species loss and invasion, and the application of food webs to ecosystem analyses.

1. Introduction

Coral reef communities of the Greater Antilles of the Caribbean Sea have a long history of anthropogenic disturbance, driven by the exploitation for food of both vertebrate and invertebrate species [1, 2]. More recently, coral bleaching, storm effects, coral disease, coastal development, pollution, invasive species, and a reduction of herbivorous control of algae in spatial competition with coral [3] have resulted in dramatic declines of diversity and abundance on reefs throughout the region [4–6]. The ongoing and predicted increases of seawater temperature and acidification as consequences of anthropogenic global warming make coral reefs among the most endangered ocean ecosystems, and Greater Antillean reefs may be particularly vulnerable because of their past and recent histories of perturbation [7]. It is therefore increasingly important to integrate species-level data on systematics, ecology, and biogeography into systems-level

data that are informative to regional conservation and management efforts. Here we use food web networks, in close regional proximity, to represent one important aspect of species ecology and present regional variation of detailed ecological networks.

Food web networks seek to capture the complexity of patterns of trophic interaction in biological communities [8]. These networks serve at least two purposes from the perspective of ecosystem protection. First, the basic topology of a food web network is a measure of the robustness or resistance of that community to species removal [9]. Such removals represent local or global extinctions. Network representation of communities can be used to discover interactions that would be lost as a consequence of extinction, and chains or pathways that would be disrupted [10]. They may be used additionally to infer possible secondary extinctions as a result of lost or disrupted paths [11]. The simplest such inference, topological secondary extinction [12], predicts the



FIGURE 1: Map of the northern Caribbean Basin showing regions covered in this paper. Outlines around each region, the Cayman Islands, Cuba, and Jamaica, trace the 100-meter depth contour around each island or group of islands, within which all reef sites used in this study are included. Cyan colour: Cayman Islands; green colour: Cuba; red colour: Jamaica. The region outlined in red, but disconnected from the island of Jamaica, represents Pedro Bank (Map courtesy of The World Marble Globe, version 1.3.3, <http://edu.kde.org/marble/>).

secondary extinction of a species if it loses all its incoming paths, that is, its prey resources, as a consequence of an initial extinction. Topological extinction thus measures the structural robustness of a food web [13], but it is limited to a minimum estimate of secondary extinction because it functions only in the direction of energy flow (bottom-up) [14]. A further limitation is imposed by the typical lack of demographic parameters in complex food web networks (but see [15]), forcing one to ignore demographic changes that could result from the initial extinction(s), such as top-down trophic cascades and Allee effects. Nevertheless, parameter modeling can indicate the potential for demographic instability and tipping points in the community.

A second purpose is the assessment of temporal and geographic variance of interactions within communities. Temporal variation will arise under conditions of varying or changing environments, such as those caused by climate change or biotic invasions, and the possible microevolutionary adaptation to such changes. Geographic variation is expected on the basis of varying composition between communities (β diversity), even those of the same type, whether driven by local environmental differences or stochastic processes, as well as different histories and regimes of anthropogenic disturbance. This measurement of temporal and geographic variation, however, is challenged by the level of ecological detail required to construct a food web network.

The food webs presented in this paper capture, to the greatest extent currently possible, the patterns of trophic interactions in coral reef communities of the Cayman Islands, Cuba, and Jamaica. In constructing the food webs we strove to include as many species as possible, their trophic interactions, and at least for vertebrates whether those species foraged preferentially on coral reefs, or seagrass beds, or both. The results are three highly detailed food webs that should both

serve as useful sources of ecological data within each region and facilitate comparisons across that area of the Greater Antilles and beyond as the number of similar regional datasets increases. The datasets will also be useful tools for assessing the robustness of these ecologically and economically important communities, and the potential outcomes of various types of disturbance and conservation measures.

2. Methodology

This study considers coral reef systems in three national regions: the Cayman Islands, Cuba, and Jamaica. Though the systems are not contiguous within each region, for example, offshore islands and shallows such as Pedro Bank off Jamaica, we consider the reefs within each region to be subject to uniform political administration and subject to similar anthropogenic policies and activities (Figure 1). We therefore refer in the study to three individual regions, namely, the Cayman Islands, Cuba, and Jamaica. Regions are certainly heterogeneous in terms of reef physiography and oceanographic conditions as well as anthropogenic factors. For example, each region has established marine-protected areas (41, 42, and 12 in number for the Cayman Islands, Cuba, and Jamaica, resp.; see World Bank Data Catalog, <http://data.worldbank.org/data-catalog>) where one could expect local species richness and abundance of exploited species to be greater than areas where harvesting is permitted [16–18]. Nevertheless, our data are pooled across localities in each region for two reasons. First, the absence of a species from a locality because of anthropogenic impacts could be intermittent and dependent on the timescales of replenishment by immigration and extirpation. Second, food webs vary in time and space in terms of both species composition as well as the nature (strength and even direction) of trophic interactions [12]. It is therefore useful to present data that are integrated across fine-scale spatial and temporal variation as representative of a region's typical or expected food webs. Those data in turn can serve as starting points for further examination of the effects of finer-scale variation, such as differences between exploited, protected, and pristine areas. In effect, food webs at finer geographic or temporal scales will be subsets of our food webs, with the latter greatly facilitating construction of finer-scale webs.

The compositions of coral reef and associated seagrass communities of the three regions were assessed by extensive review of the available literature and databases [19–124]. Taxa present elsewhere in the Caribbean Sea or Gulf of Mexico, but not recorded explicitly from one of our Greater Antillean locations, were omitted from the dataset. We included only species for which reasonable detail of prey and predator species as well as foraging habitat (see the following) could be obtained; anecdotal records of trophic interactions were not used. This resulted in the underrepresentation of several potentially important taxonomic groups, for example, Asteroidea and Cirripedia. Nevertheless, the dataset includes primary producer species representative of coccolithophores, diatoms (including epiphytic species), filamentous algae, coarsely branched algae, jointed calcareous

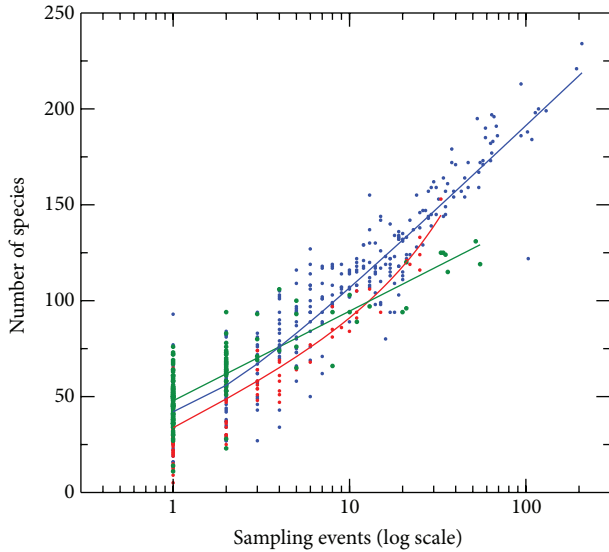


FIGURE 2: Number of sampling events per regional site and number of species discovered, as recorded in the REEF database [125]. Blue: Cayman Islands; green: Cuba; red: Jamaica. Lines are fractional polynomial regressions fit to each dataset. Functions are as follows: Cayman Islands: $24.6x^{-1} + 37.7 \ln x + 17.4$; Cuba: $20.3 \ln x + 47.8$; Jamaica: $1.3x + 19.8 \ln x + 32.5$.

algae, thick leathery algae, coralline encrusting algae, and sea-grasses. Planktonic bacteria are represented as a single entry, or node, in the networks. Consumers are represented by dinoflagellates, planktonic and benthic foraminifera, tintinnids, epibenthic sponges, endolithic sponges, ahermatypic and hermatypic corals, copepods, amphipods, appendicularians, siphonophores, isopods, chaetognaths, scyphozoans, gorgonians, corallimorphs, zoanthids, echinoids, bivalves, gastropods (including pteropods and nudibranchs), polychaetes, holothurians, malacostracan crustaceans, cartilaginous and bony fish, and sea turtles.

Nonvertebrate taxa were treated as occurring uniformly among all three locations because of a general lack of biogeographic specificity at this scale available in published data. More precise data are available for vertebrate species, however, and we took advantage of this to differentiate the three food webs. Vertebrate occurrences were obtained from REEF (<http://www.reef.org/>), GBIF (<http://www.gbif.org/>), and Fishbase (<http://www.fishbase.org/>) databases and utilized to conservatively minimize apparent differences among the locations. We searched the REEF Volunteer Survey database [125] for records of every vertebrate species in our literature dataset. Those species that are not recorded in the survey, but are present in our dataset, were automatically considered to be present. All REEF sites in each region were queried individually, but the results were combined to construct the regional species lists. We included both Expert and Novice observations, again to be conservative in our estimate of the compositional differences among the regions. Our queries covered the period from 1999 to 2010. We considered the presence of a species in at least one site within a region to count for the entire region. This allows for the

possibilities that species were overlooked during surveys and that individuals at one site could relocate to or reproductively seed another site. Furthermore, we ignored demographic data such as estimates of population densities, which are extremely low for some species, and recorded a species as present even if only a single individual was observed, because the REEF data bear a significant sampling effect signal. The impact of sampling effort and number of reports was assessed by comparing the number of reports per site and the number of species recorded for each location. Results indicate clearly that Cuba and Jamaica have been sampled far fewer times than have the Cayman Islands and that lower species richnesses of the former locations in the REEF databases could very well be reversed if sampling was intensified (Figure 2). Moreover, given the much greater area of Cuba's coastal region, important refuges and relatively pristine areas such as Los Jardines de Reina are not captured effectively in the REEF database.

We therefore augmented the data for each location with occurrences recorded in the GBIF and Fishbase databases. While the REEF data were constrained to reports from 1999 to 2010, all GBIF and Fishbase occurrences in the Twentieth century were incorporated into our dataset. This results in a very conservative estimate of present species composition, since the historic databases include species from each location that are not only absent in the REEF surveys but may in fact now be extirpated from a locality. Finally, maximum body length was recorded for all fish species as listed in Fishbase.

Food web assembly was as follows. We included species both restricted to coral reefs and those commonly found in adjacent seagrass beds. All eukaryotic clades resolvable to the species level were considered for inclusion in the food webs, including protistan producers and consumers, but we included only species for which diet could be specified. Most primary producer and invertebrate species were then organized into trophic guilds [11] unless consumer diets are highly specialized and known with specificity; such is the case for cephalopod and stomatopod species. Each guild comprises data on taxonomic composition, trophic ecologies (species prey and predators), and primary habitat. Given uncertainty in the full array of trophic interactions for most of these species, a trophic guild is an aggregation of species where members of a guild potentially share prey drawn from the same guild(s), likewise for predators, and share the same habitat. One hundred and sixty-nine primary producer species were subsequently aggregated into nine guilds while 513 protistan and invertebrate consumers were aggregated into 99 guilds (Figure 3).

Cartilaginous and bony fish diets were obtained from the detailed reports of Randall [39] and Opitz [126]. The Opitz ECOPATH data proved to be particularly valuable, being based on extensive gut analyses, though primarily from the US Virgin Islands. Many fish dietary items, however, are present in very small proportions of total diet diversity and may therefore represent only occasional feeding rather than major dietary components or are possibly ingested incidentally. We thus included only those prey items which comprised 1% or more of a species diet. All vertebrate species were then categorized into three foraging groups: species

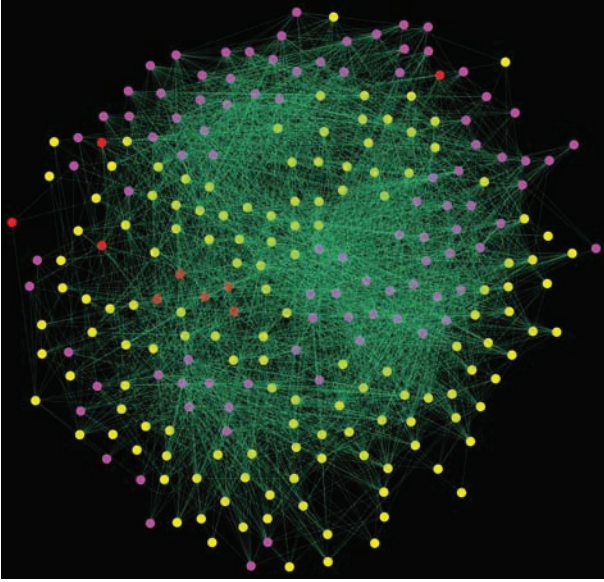


FIGURE 3: Food web illustration of trophic guilds and trophic species, and trophic interactions between them. This web represents the Cuban dataset. All nodes and interactions in the data are illustrated. There are 266 nodes and 3899 interactions (edges) in the network. The obvious complexity of the network emphasizes the improbability of any easy simplification of the data. Node colours are as follows: red: primary producers; magenta: protistan and invertebrate guilds; yellow: vertebrate species and trophic species.

that forage primarily on coral reefs (reef foragers), those that forage primarily in seagrass beds (seagrass foragers), and those that forage frequently in both habitats (reef-seagrass foragers) [126]. Our documentation, however, does not preclude the presence of these species in other coastal habitats not covered in our study, for example, mangrove environments. Vertebrate species were subsequently aggregated if they shared exactly the same prey and predators, thereby representing trophic species [127]. Trophic species are conceptually a subset of trophic guilds [14], and hence the latter term only is used from here on. Ultimately, 184 vertebrate species were aggregated into 162 trophic species (Figure 3).

3. Dataset Description

The dataset associated with this Dataset Paper consists of 7 items which are described as follows.

Dataset Item 1 (Table). Trophic data for the Cayman Islands. Data specify trophic guilds, the number of prey per guild, a list of those prey guilds, and the major foraging habitat of the guild. In the first column is given the Guild Number. Guild numbers are standard among all the datasets; for example, guild number 1 represents planktonic bacteria in the Cayman, Cuban, and Jamaican datasets. In the second column (Guild Description) is given the common language guild descriptions. The descriptions indicate the major trophic niche of the guild in the case of multispecies guilds (e.g.,

Macroplanktonic carnivores I), the major taxon of the guild (e.g., *Eucidaris*), or in the case of vertebrates, a common name of the species (e.g., scorpionfish). In the third column (Foraging Habitat) is given the major foraging habitat of vertebrate guild members. In this column, r means reef; rg, reef and seagrass beds; and g, seagrass beds. In the fourth column (Number of Prey) is given the total number of guilds that contain species that are preyed upon by the guild in question. In the fifth column (Prey) is given a list of prey guilds. Missing data are indicated by a period (.).

Column 1: Guild Number

Column 2: Guild Description

Column 3: Foraging Habitat

Column 4: Number of Prey

Column 5: Prey

Dataset Item 2 (Table). Trophic data for Cuba. Data specify trophic guilds, the number of prey per guild, a list of those prey guilds, and the major foraging habitat of the guild. In the first column is given the Guild Number. Guild numbers are standard among all the datasets; for example, guild number 1 represents planktonic bacteria in the Cayman, Cuban, and Jamaican datasets. In the second column (Guild Description) is given the common language guild descriptions. The descriptions indicate the major trophic niche of the guild in the case of multispecies guilds (e.g., Macroplanktonic carnivores I), the major taxon of the guild (e.g., *Eucidaris*), or in the case of vertebrates, a common name of the species (e.g., scorpionfish). In the third column (Foraging Habitat) is given the major foraging habitat of vertebrate guild members. In this column, r means reef; rg, reef and seagrass beds; and g, seagrass beds. In the fourth column (Number of Prey) is given the total number of guilds that contain species that are preyed upon by the guild in question. In the fifth column (Prey) is given a list of prey guilds. Missing data are indicated by a period (.).

Column 1: Guild Number

Column 2: Guild Description

Column 3: Foraging Habitat

Column 4: Number of Prey

Column 5: Prey

Dataset Item 3 (Table). Trophic data for Jamaica. Data specify trophic guilds, the number of prey per guild, a list of those prey guilds, and the major foraging habitat of the guild. In the first column is given the Guild Number. Guild numbers are standard among all the datasets; for example, guild number 1 represents planktonic bacteria in the Cayman, Cuban, and Jamaican datasets. In the second column (Guild Description) is given the common language guild descriptions. The descriptions indicate the major trophic niche of the guild in the case of multispecies guilds (e.g., Macroplanktonic carnivores I), the major taxon of the guild (e.g., *Eucidaris*),

or in the case of vertebrates, a common name of the species (e.g., scorpionfish). In the third column (Foraging Habitat) is given the major foraging habitat of vertebrate guild members. In this column, r means reef; rg, reef and seagrass beds; and g, seagrass beds. In the fourth column (Number of Prey) is given the total number of guilds that contain species that are preyed upon by the guild in question. In the fifth column (Prey) is given a list of prey guilds. Missing data are indicated by a period (.).

Column 1: Guild Number

Column 2: Guild Description

Column 3: Foraging Habitat

Column 4: Number of Prey

Column 5: Prey

Dataset Item 4 (Table). Guild key. This is a list of all guilds present in Dataset Items 1–3 (Tables) and the taxa assigned to those guilds. There is a total of 265 guilds, though none of the regions described contains all those guilds. There are also several guilds or species that are absent from all the regions, but have nevertheless been recorded in the northern Caribbean region, and are likely to be present in undescribed refuges or occasional members of the regions, for example, the tiger shark *Galeocerdo cuvieri*. In the first column is given the Guild Number; in the second (Taxa), the taxa assigned to guild; in the third (Fish Body Length), the average body size (fork length, cm) of bony and cartilaginous fish species. Maximum body size is recorded if average size is not available. Missing data are indicated by a period (.). In columns 4–6 is shown the presence of vertebrate species in the Cayman Islands, Cuba, or Jamaica indicated by “x” sign.

Column 1: Guild Number

Column 2: Taxa

Column 3: Fish Body Length (cm)

Column 4: Cayman Islands

Column 5: Cuba

Column 6: Jamaica

Dataset Item 5 (Binary Matrix). Binary adjacency matrix of the Cayman Islands food web. Rows are predatory guilds and columns are prey. The ij th element of the matrix is 1 if guild i preys upon species in guild j , and 0 otherwise. Note that the matrices are therefore asymmetric about the diagonal, and that there are 265 rows representing each guild in the dataset. Taxa that are missing from the food web, for example, the tiger shark *Galeocerdo cuvieri*, are included as disconnected nodes, that is, rows and columns comprising zero elements only. This is for consistency with future datasets of related regions in which the species might be present.

Dataset Item 6 (Binary Matrix). Binary adjacency matrix of the Cuban food web. Rows are predatory guilds and columns are prey. The ij th element of the matrix is 1 if guild i preys

upon species in guild j , and 0 otherwise. Note that the matrices are therefore asymmetric about the diagonal and that there are 265 rows representing each guild in the dataset. Taxa that are missing from the food web, for example, the tiger shark *Galeocerdo cuvieri*, are included as disconnected nodes, that is, rows and columns comprising zero elements only. This is for consistency with future datasets of related regions in which the species might be present.

Dataset Item 7 (Binary Matrix). Binary adjacency matrix of the Jamaican food web. Rows are predatory guilds and columns are prey. The ij th element of the matrix is 1 if guild i preys upon species in guild j , and 0 otherwise. Note that the matrices are therefore asymmetric about the diagonal and that there are 265 rows representing each guild in the dataset. Taxa that are missing from the food web, for example, the tiger shark *Galeocerdo cuvieri*, are included as disconnected nodes, that is, rows and columns comprising zero elements only. This is for consistency with future datasets of related regions in which the species might be present.

4. Concluding Remarks

The datasets presented here are syntheses of decades of work by multiple ecologists and systematists; yet they are far from being taxonomically comprehensive. There is a pressing need for additional data of the ecological roles of organisms in important communities such as coral reefs. Nevertheless, the current data should prove to be helpful in both understanding the long-term and large-scale dynamics of these communities and in formulating strategies for the protection of the communities and species within. Ecosystem dynamics play out over multiple scales of time and space [128] and multiple levels of biological organization, from organisms to ecosystems themselves [129]. Organizing data relevant to those scales, such as shifting historical baselines, multiple disturbances that act on different spatial scales, and variance of community composition across those scales, presents significant challenges to the formulation of coherent strategies for the conservation, restoration, and sustainable economic use of coral reef ecosystems in the Caribbean region and elsewhere [6, 130]. At the same time, it is understood that the nature of a species interactions, for example, number or strength, can be important determinants of its probability of extinction (or survival) under different circumstances. It is also understood that the configurations of those interactions for all species in a community are important determinants of the communities resilience to change or robustness against disturbances. Complex network food webs present a basic scaffolding for tying together data on an ecosystem's species richness, biotic interactions, and functional diversity. Much of the work relating food web properties to ecosystem health has dealt so far with model or relatively small communities [131]. The datasets presented here make it possible to extend this work to an ecosystem that is both one of the ocean's richest and most complex and one of its most critically endangered [7].

Finally, these datasets are both starting points and works in progress. They may be used by workers to examine regionwide phenomena such as the trophic impacts of coral bleaching or invasive species, and likewise they can be subsampled to reflect within-region variation of community composition and anthropogenic factors. They are works in progress because they will be revised as data on those already included, as well as omitted species become available, and as the state of Caribbean coral reefs continues to evolve.

Dataset Availability

The dataset associated with this Dataset Paper is dedicated to the public domain using the CC0 waiver and is available at <http://dx.doi.org/10.7167/2013/857470/dataset/>.

Conflict of Interests

The authors declare that they have no competing interests or conflict of interests.

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