A Good Starting Point:
A Promising Trophic Model for Southwest Puerto Rican Coral Reef Ecosystems

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ABSTRACT

Coral reef ecosystems, such as the well-studied La Parguera reef system (SW Puerto Rico), exhibit complex interactions with consequences difficult to predict with conventional fisheries management models. A newly-developed trophic model, based on Ecopath with Ecosim, offers an alternative means to evaluate fishing policies that might achieve desirable ecological and social outcomes, to compare the system to other modeled reef ecosystems, and to explore data and data gaps. The model is based on fisheries and ecological data, primarily centered on species of commercial and ecological importance, grouped by habitat preferences. It has been balanced for current conditions although additional fisheries data (recreational and ornamental) need to be included to improve the representation. The model construction process identified gaps in available data (e.g., diet compositions, metrics of fishing effort, landings, and estimates of primary production) and balancing raised interesting ecological questions. Some groups, such as parrotfish appear to be so underutilized as prey that the accuracy of biomass estimates and our understanding of predator-prey relationships are questioned. Although model structures vary, complicating direct comparisons, a similar Caribbean model built for the 1970 - 1980s estimated total biomass 5.6 times higher than the present model. Changes of this magnitude, if accurate, highlight the need for further study of the roles fishing and environmental changes have played in reshaping this system over the last 30 - 40 years. This modeling effort identified data needs, generated hypotheses for future research, and provides an initial look at ecosystem-based fishery management scenarios for this reef system.

KEY WORDS: Ecosystem model, coral reef ecosystem, Ecopath with Ecosim, fisheries impact, predator-prey

Un Buen Punto de Partida: Un Modelo Trófico Prometedor para los Ecosistemas Puertorriqueños del Arrecife Coralino del Sudoeste

Los ecosistemas de los arrecifes de coral, como el bien estudiado sistema de arrecife La Parguera (SW Puerto Rico), exhiben interacciones complejas con consecuencias difíciles de predecir con modelos convencionales del manejo de las industrias pesqueras. Un modelo trófico desarrollado recientemente, basado en Ecopath con Ecosim, ofrece un medio alternativo para evaluar las polizas pesqueras que podrían lograr resultados ecológicos y sociales deseables, para comparar el sistema a otros ecosistemas de arrecifes modelados, y explorar los datos y huecos de los datos. El modelo se basa en datos ecológicos y de las industrias pesqueras, principalmente centrado en especies de importancia comercial y ecológico, agrupado por preferencias de hábitat. Se ha balanceado para las condiciones actuales aunque los datos adicionales de las industrias pesqueras (recreacionales y ornamentales) necesiten ser incluidos para mejorar la representación. El proceso de construcción del modelo ha identificado huecos en los datos disponibles (por ejemplo, composiciones de dieta, mediciones del esfuerzo pesquero, capturas y estimaciones de la producción primaria) y el balanceo puso a la vista preguntas ecologicas interesantes. Algunos grupos, tales como el pez loro parecen ser utilizados tan poco como presa que la exactitud de las estimaciones de biomasa y nuestra comprensión de relaciones entre presas y depredadores son cuestionados. Aunque las estructuras de los modelos varían, complicando las comparaciones directas, un modelo similar del Caribe construido para los 1970s y 1980s estimo una biomasa total 5.6 veces mayor que el modelo actual. Cambios de esta magnitud, si precisos, subrayan la necesidad de proseguir mas estudios del los papeles que la pesca y cambios ambientales han desempeñado en la remodelación de este sistema en los últimos 30-40 años. Este esfuerzo de modelado ha identificado las necesidades de datos, genero hipótesis para investigaciónes futuras y ofrece una mirada inicial de escenarios a nivel de ecosistemas basados en el manejo de la industria pesquera para este sistema de arrecife.

Un Bon Point de Départ: Un Modèle Trophique Prometteur pour des Écosystèmes Portoricains de Récif Coralien de Sud-ouest

Les écosystèmes de récifs coralliens comme celui de La Parguera (SO Puerto Rico), sont caractérisés par des interactions complexes dont les conséquences sont difficiles à prédire avec des modèles halieutiques conventionnels. Un nouveau modèle trophique, élaboré avec Ecopath with Ecosim, offre un moyen d'évaluer les politiques de gestion qui permettraient d'atteindre les objectifs écologiques et sociaux, de comparer cet écosystème à ceux d'autres récifs, et d'explorer les données et leurs lacunes. Le modèle est basé sur les données écologiques et halieutiques, centré principalement sur les espèces d'intérêt commercial ou écologique, groupées par habitat. Le modèle équilibré représente les conditions actuelles malgré qu'il manque encore les données de pêche récréative et d'espèces ornementales. La construction du modèle a permis d'identifier plusieurs lacunes dans les données disponibles (ex. compositions alimentaire, effort de pêche, débarquements, et estimations de production primaire) et a soulevé d'intéressantes questions d'ordre écologique. Certains groupes comme les poissons perroquets sont sous-utilisés dans le modèle au point de remettre en question l'estimation de leur biomasse, et notre connaissance des relations prédateur-proie dans le système. Bien que la structure varie d'un modèle à l'autre, compliquant les comparaisons directes, la biomasse totale estimée par le modèle des Caraïbes des années 1970-1980 est 5.6 fois plus élevé que celle du présent modèle. S'ils s'avéraient réels, ces changements soulignent la nécessité de se pencher sur l'influence de la pêche et des changements environnementaux sur la structure de ces écosystèmes au cours des 30-40 dernières années.

MOTS CLÉS: Modèle écosystémique, récifs coralliens, Ecospath with Ecosim, impact de la pêche, prédateur-proie

INTRODUCTION

Coral reef ecosystems are characterised by, and dependent upon, intricate linkages among habitats, species, and trophic levels. These valuable ecosystems have historically provided income and cheap protein sources but they can be lost if the component resources are not managed sustainably. In 1931, 1403 fishermen using 711 vessels landed 1397 metric tonnes (3,080,100 pounds), primarily, of reef fishes. (Jarvis 1932). Commercial landings for the island peaked in 1979 at 2540 tonnes (5.36 million pounds) and declined to a low of 757.4 t (1.67 million pounds) by 1988 (Appeldoorn et al. 1992). In 1989, 1822 fishermen (30% increase) with 1107 vessels (56% increase) landed only 1045.5 t (2,305,004 pounds) or 75% of the 1931 catch and less than 50% of the 1979 landings (Appeldoorn et al. 1992, Matos and Sadovy 1990). In recent years, fishing pressure from tournament and other recreational fishers in Puerto Rico has also increased (Rodríguez-Ferrer et al. 2005) although means are not in place to assess effects on fish stocks. Resource extractions have been difficult to quantify precisely and additional disturbances, including coral diseases and bleaching, watershed and coastline alterations, overfishing, global warming and ocean acidification (Waddell and Clarke 2008), may further limit coral reef ecosystem productivity. Analytical tools, capable of characterizing the complex ecological linkages and the myriad disturbance effects, are needed to foster sustainable management (Hill 2004). Here we report on an Ecopath model (Guénette and Hill 2009), linking species or species groups through trophic relationships, intending to highlight progress, initial analyses of relationships, and the need for additional collaborations.

MODEL STRUCTURE

The model depicts the coral reef ecosystem of La Parguera, located on the southwest coast of Puerto Rico and encompassing 147 km^2. The modelled system extends from the shoreline to the mapped shelf edge offshore; La Parguera's coastline is lined with mangroves and is protected by a series of coral reef platforms, as described in Guénette and Hill (2009). Coral reef ecosystems are heterogeneous blends of habitats and most species, both sessile and mobile, exhibit some affinity for specific habitat types (Williams 1991). From a modeling perspective, we needed to characterize the structure with a manageable number of habitat types, and, from an ecological perspective, account for diverse species distributions. Three habitat schemes were examined (described in Cerveny 2006, Kendall et al. 2001, Prada 2002) and coalesced into a reduced number of habitat categories that combine elements of geomorphology and habitat type (Table 1). All locations where available geo-referenced biotic surveys (primarily corals and fish) had been conducted were then overlain on the model habitats in GIS and attributed to a particular habitat type.

We used the Ecopath with Ecosim software (EwE) (Christensen and Walter 2004) to construct the model, describing the foodweb interactions of functional groups (composed of a single species or of a group of species) and thus providing a snapshot of the ecosystem for the chosen year (2000, in this case). Input values for the model, *i.e.*, biomass, production and consumption rates, and diet composition, were chosen based on an examination of available data from local research when possible and other published values when necessary. The principle behind this ecosystem modelling approach is that biomass and energy are conserved on a yearly basis (Walters et al. 1997). This does not, however, imply that the model is at equilibrium and would remain the same through time. Migrations and biomass imports/exports can be used to characterize an open system and biomass accumulation can be used to reflect the ongoing changes in population biomass (declines or increases). Additional details of the modeling approach and the resultant model are fully described in Guénette and Hill (2009) but here we use only a few elements to draw attention to certain aspects of our modeling experience.

The La Parguera model is composed of 49 functional groups of fish, 1 of turtles, 10 of invertebrates, and 2 of primary producers. The model was focused on commercial species, their prey and their predators, to enable evaluation of fisheries management scenarios. Fish, not considered separately for their role in the reef fishery, were grouped according to their dominant habitat preference (pelagic, forereef, (other) reef, lagoon, vegetation, or ubiquitous); their diet preferences (e.g., piscivore, invertivore, herbivore); and their production. Except for primary target species, named by family groupings, the name of fish functional groups is generally composed of up to 4 terms:

i) The habitat they are associated with;
ii) Their body size (Large, Medium, Small);
iii) Their diet preferences; and
iv) Exploited groups are signalled by adding "commercial" to their names (e.g., grunts and grunts comm).

Primary target species groups considered separately were the snappers, grunts, (large) wrasses, parrotfish, groupers, grouper seabass, porgies, mojarras, squirrelfish, goatfish, trunkfish and boxfish, triggerfish, barracuda, halfbeaks, mullet, and herring. Finally, 8 groups of fish, mostly commercial species, were divided into juvenile and adult stanzas to account for ontogenetic changes in diet or habitats.

The resulting structure of the modelled fish community is characterised by two species/groups linked with mangroves (mullet and bonefish), seven linked with reefs and lagoons, and seven groups found on the forereef or the "wall of mouths" (*sensu* Hamner et al. 1983). Most grunts and similar species are commuters, moving between vegetated lagoons and reef sites or mangroves daily, and can thus be found in multiple habitats in one day (Hill 2001). Parrotfish, a diverse group of essential herbivores, contains species often found on forereefs and in seagrass but also those that can be found on inner or outer reefs, so they were placed with the ubiquitous and commuters groups. Finally, most pelagic species such as halfbeaks, herring, barracudas and sharks, move freely across or, generally, above the reef. Many groups of commercial species include species with quite diverse habitat preferences and are thus classified in the ubiquitous group.

MODEL EVALUATION

Once a model has been balanced a variety of tools can be used to evaluate it. Generally Ecopath modellers enter biomass, production, consumption, and diet of included species and the model calculates the Ecotrophic Efficiency, (EE_i), the proportion of the biomass of group i (a value between 0 and 1) that is consumed or used in the system. A high value means that most of the group's total production goes to predation and fishing mortalities. Our balanced model shows EE values ranging from a low of 0.007 for squirrelfish (group 17) to almost 1 for groups such as wrasses, mojarras, herring and juvenile grunts. EE values are relatively low for several functional groups, irrespective of their exploitation status. For example, parrotfish comm. adults (group 13), characterized by large biomass and production/biomass ratio, feeding mainly on benthic producers, is fished using several gears and is preyed upon by six large predators present on the reefs and in the wall of mouths (Reef L pisc, groupers, grouper seabasses, barracudas, sharks and jacks; Figure 1). Nevertheless, only 7% of biomass is consumed within the model (EE = 0.07), and similarly, its juvenile stanza presents EE = 0.28. The same applies to the non-commercial parrotfish (group 15, EE = 0.031). The explanations may form the basis for competing hypotheses.

Imprecision in the current methods of identifying species and functional groups actually eaten by any given predator renders the results of some simulations difficult to interpret. Uncertainty in diet compositions can be reflected in a model's trophic relationships. For instance, parrotfish comm. adults (group 13), in spite of their large biomass, account for less than 5% in the diet of a few predators that are generally not very abundant in the ecosystem: sharks, jacks, snappers, groupers, grouper seabasses, reef L piscivores and invertivores, and barracudas. While the group contains large-bodied species that are no longer abundant in the La Parguera system (*Scarus guacamaia, S. coeruleus* and *S. coelestinus*) it also contains common large parrotfishes (*S. vetula and S. viride*) that should suffer predation in the system. If not the adults, certainly juveniles could be considered as suitable and vulnerable prey. One might hypothesize that this is an indication of faulty diet composition or that a diminished biomass of large piscivores in 2000 resulted in less predation mortality

Table 1. Surface area and percent of habitat types represented in the modelled study area.

Habitat	**Percent**	**Surface (km^2)**	**Description**
Basin Patch Reefs	24.6	36.20	Various types of patch reefs found between the 3 reef lines, generally surrounded by sand bottoms, may be aggregated or individual patch reefs.
Macroalgae beds	6.4	9.46	With greater than 80% coverage by macroalgae (such as *Halimeda, Penicillus, Laurencia, Udotea*)
Mangrove Edge	0.1	0.18	Shoreline and island root zone, shaded areas within 4 m of roots
Mid-shelf colonized hard-bottom	28.9	42.60	typically with sand channels, especially "Marta's Limestone Reefs"
Reef Rubble	0.2	0.27	Benthic coverage by broken pieces or fragments of coral. Fragments have potential to move with waves. May have matrix of sand or seagrass
Sand Flats	13.0	19.16	Sand bottom with less than 10% vegetative cover; depth less than 5 m
Seagrass Beds	15.3	22.51	Seagrasses *Thalassia, Syringodium and Halodule*, monoculture or mixed; covering more than 10% over sand bottom, OR more than 30% over macroalgal bottom
Shallow reef zones	0.8	1.15	includes coral reef zones shallower than 3 m: backreef, submerged reef top, forereef - all having underlying coral structure and coral live or dead on surface.
Shelf-edge reefs	4.5	6.60	Shelf edge reefs, typically continuous high relief reef, possibly spur and groove with sand channels, e.g., polygon extension to the west approximated in GIS based on depth
Shelf-edge slope	1.2	1.75	Shelf edge habitat seaward of shelf edge reef, depth typically 30 down to about 50m
Intermediate to deep forereef	3.5	5.14	Forereef zones mainly of inner and intermediate (possibly outer shelf reefs) affected by wave action, depth from 3 m to bottom of forereef.
Basin mud bottom	1.2	1.78	Fine grain mud bottoms wither between inner - intermediate or between intermediate - outer shelf reefs
Patch reefs in backreef seagrass	0.3	0.46	seagrass habitats with invert patch reefs - coral, live or dead, sponges, gorgonians - almost all are predominantly in backreef areas. Buffered backreef 15m in GIS to produce polygons
Total km^2		147.31	

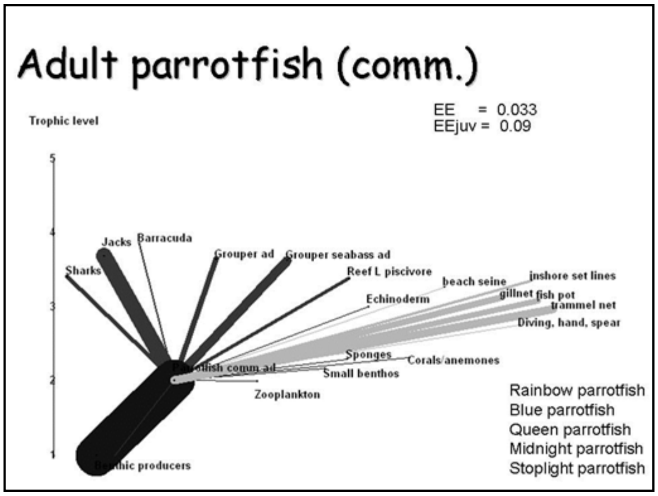

Figure 1. Parrotfish adult commercially exploited (group 13), at trophic level 2.1 (marked with a white dot), its links to prey (in black) and predators (in grey) displayed at their trophic levels on the y axis. The strength of the link is proportional to its width.

than expected (Sadovy 1999, and references therein). In a similar vein, squirrelfish, also with low predation pressure, may not be a prey sought after by many predators as suggested by the model's diet matrix or their predators were not considered in the model. In a model of Grenada and the Grenadines, squirrelfish and similar species were found to be prey for large pelagics (tuna, billfish, mahi mahi), mackerels, bathypelagics, sharks, groupers and snappers (Mohammed 2003). Opitz (1996) produced a similar list of predators for her general Caribbean model. It is possible that our spatial limitations have excluded some of the predators for squirrelfishes or that squirrelfishes were not identified properly in available diet studies. Nevertheless, in spite of their expanded list of predators, the EE for this group is also low (0.197) in the Grenada model. Such analyses provide the foundation for additional ecological studies and hypotheses to further the understanding of the modelled ecosystem.

MODEL IMPROVEMENTS

Additional improvements can be made by improving the data upon which the model is built. Recreational and ornamental fishing are largely lacking. Commercial landings are notoriously incomplete but review with additional local experts may provide more detailed interpretations. In our initial efforts, examination of catch per gear showed that misreporting is pervasive in the data set. For example, in 2000, there was no catch of spiny lobster reported in lobster pots and there were numerous cases of species like conch being reported from hook-and-line and trap gears. A closer examination of the commercial data and the addition of recreational and ornamental catches would be recommended in the next round of modelling and for time series reconstruction. The model, even though preliminary, suggests that prey-predator relationships should be clarified and perhaps, would benefit from a comparison with earlier times, when large predators were more abundant. By nature, diet composition data are fraught with problems, including lack of seasonal sampling and detailed prey identification. These lead one to underestimate common prey or overlook rare prey. Examples given by Guénette and Hill (2009) demonstrate the imprecision in the available data, including nearly complete paucity of data for entire functional groups. For some groups of lower trophic levels such as corals and anemones, the production (= total mortality) is not well explained by the model (EE = 0.24) mainly because of the low predation that has been included in the model, *i.e.*, few direct predators and no fishing mortality. Other sources of mortality caused by increased temperature and other environmental factors such as sedimentation, that have not been considered in the present model, would likely play an important role in the future dynamic version. One of the main benefits in the creation of an Ecopath model is that it provides the means to assess what is known about the relationships between species, with appropriate steps to assess the plausibility of the linkage structures.

Comparisons could also be made with other previously constructed models of similar systems if the structures are somewhat compatible. The closest model for comparison is the model of the Caribbean shelf model built by Opitz (1996). It includes the shelf of Puerto Rico, British and US Virgin Islands for a total of 1000 km^2, and ignored fishing at a period that is assumed to be from the 1970 - 1980s judging from data sources. The author obtained EEs ranging from 0.3 (for large parrotfish) to 0.98. The relatively low EE for parrotfish, even after a reduction in their biomass, was deemed unlikely by the author, and attributed to gaps in the diet compositions. The total biomass (excluding detritus) in the Opitz model (1996) amounted to 2848 t/km^2, 5.6 times higher than in the present model (502 t/km^2). Differences occur at all trophic levels but important differences are noted for large sharks/rays (top predators) that amounted to 0.3 t/km^2 in the Opitz model and 0.162 in our model and benthic producers amounting to 1300 t/km^2 in the Opitz model and 248 t/km^2 in ours. The models are not directly comparable because of the very different structures and study areas, but these differences generate interest in comparing the present model and biomass data to earlier data in terms of ecosystem structure and the influence of fishing and environmental changes over the last 30 years.

This model constitutes the first step in a research plan that proposes to develop a tool for the region that can be used to test various management policies. One accomplishment of the model construction is identification of information gaps that can shape future research priorities and data collection planning. At this stage, we have not included marine birds and marine mammals for lack of data although birds could be a non-negligible source of mortality for some fish. We know from personal experience (R. Hill) that both manatees and bottlenose dolphins frequent the area modelled but there are no reliable estimates on abundances or biomass of either. The next step in the current modelling work should be to build a model for the earliest time possible, e.g. for the early 1970s, and compile time series from that period to the present. Ecological data and estimates of landings by all fisheries (commercial, recreational, aquarium trade) should be included. The objective would be to reconstruct past changes in ecosystem structures due to fishing and environmental factors (e.g., increases in temperature, urchin disease/dieoff) in order to add credibility to the model's predictions of future changes.

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