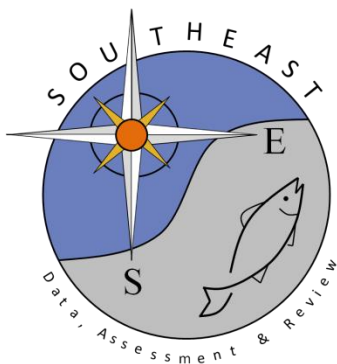


A trophic model of the coral reef ecosystem of La Parguera, Puerto Rico: synthesizing fisheries and ecological data

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A trophic model of the coral reef ecosystem of La Parguera, Puerto Rico: synthesizing fisheries and ecological data

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ABSTRACT.—La Parguera, Puerto Rico, a well-studied Caribbean reef system, is showing signs of overfishing and thus, is a good candidate to evaluate fishery policy scenarios using ecosystem modeling. The first steps taken to build a plausible ecosystem model of the La Parguera reef system using Ecopath with Ecosim software included synthesizing fisheries and ecological data then balancing and analyzing trophic relationships for the year 2000. The model is centered around species of commercial and ecological importance in the ecosystem, grouped by habitat preferences. Model construction identified gaps in available data (e.g., diet compositions, metrics of fishing effort, incomplete landings) and balancing raised interesting ecological questions. Some groups, such as parrotfish are so underutilized as prey that the accuracy of biomass estimates and our understanding of predator-prey relationships are questioned. Apparent shortcomings in estimates of primary production relative to consumer biomass generated questions of whether estimates are inaccurate or whether the system is highly subsidized by importation from outside ecosystem boundaries. Although details are not directly comparable because of different structures, 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 found to be accurate, point out the need for further study of the roles fishing and environmental change have played in reshaping this system over the last 30-40 years. This modeling effort defined future data needs, generated hypotheses for further coral reef research, and provided a starting point towards evaluation of fishery management scenarios in an ecosystem context.

KEYWORDS.—Caribbean, ecosystem model, Ecopath with Ecosim, fisheries impact, predator-prey

INTRODUCTION

Puerto Rico's coral reef ecosystems support commercial and recreational fishing and a booming tourist industry for both local and foreign tourists. These systems are characterised by, and dependent upon, intricate linkages among habitats, species, and trophic levels to maintain their high productivity and value. The extractive and non-extractive values of coral reefs in eastern Puerto Rico, have been estimated at \$4.2 million per linear kilometre of reef-lined coast, totalling \$1.8 billion per year (ETC (Estudios Técnicos Inc) 2007), however, these resources can be lost if the ecosystem is not managed sustainably. Over the three-year period beginning 1999, the number of recreational fishers participating in tournament fishing activities in Puerto Rico increased by 30.3% and although all types of recreational fishing are believed to have increased, no

long-term data are available to assess the impacts of these activities (Rodríguez-Ferrer et al. 2005). In most of the smaller coastal communities in Puerto Rico, fishing on coral reef resources has been a dominant and traditional source of income and, as in many tropical settings, fishing provides an invaluable source of inexpensive animal protein (Agar et al. 2008). In 1931, 1403 fishermen using 711 vessels landed 1397 metric tonnes (3,080,100 pounds) (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). Slight increases

were seen from 1989 until the present but they have been minor compared to the earlier peak. The results of these resource extractions have been difficult to quantify and additional disturbances, including diseases, bleaching, watershed and coastline alterations, overfishing, global warming and acidification of the oceans (Waddell and Clarke 2008), may further limit coral reef ecosystem productivity. Sustainable management of coral reef ecosystems and associated fisheries requires tools to characterize the complex ecological linkages and the myriad disturbances affecting productivity and value of the reef system.

Given their economic and ecological importance, coral reef ecosystems in Puerto Rico have been the subject of numerous scientific studies although basic fisheries data are still found insufficient to conduct conventional stock assessments on exploited species (Appeldoorn et al. 1992, SEDAR 2008). Conventional stock assessment methods generally require more data than is available from the multi-gear, multi-species fisheries typical in tropical reef fisheries but attempts have been made in the U.S. Caribbean (Puerto Rico and the US Virgin Islands) because of recognition that improved management of both stocks and essential fish habitats is needed. Fishery statistics that are available show the classic signs of overfishing: reduced total landings, declining catch per unit effort (CPUE), shifts to smaller fish, and recruitment failures (Appeldoorn et al. 1992). Unfortunately, the key metric, change in CPUE over time, is not reliably available for most species. Decreases in mean body lengths in landed species from 1985-1990 suggested overfishing of many target species but translating the findings into practical management terms or policies has been difficult. Applying similar logic in a more rigorous analysis, a recent alternative approach used single-species length-based assessments to show that 16 out of 23 species in the highly valued snapper-grouper complex were already overfished in the 1980s; and, although the average lengths have increased slightly since then, these species are still overexploited (Ault et al. 2008)

As a complement to single-species assessment, and given the increasing recognition that multiple stressors require an ecosystem-based management approach (Wilson et al. 2006a), ecosystem modeling is a useful tool to characterize fishery ecosystems. Well designed models can account for species interactions through the food-web (exploited and unexploited species), evaluate the effect of system stressors, and test the effects of fisheries management scenarios. Ecopath with Ecosim (Christensen and Walters 2004) is widely used to build ecosystem models in both data-poor and data-rich systems. The Ecopath model, the first step in the process, is a snapshot of the ecosystem for a given period that describes the trophic interactions and the magnitude of fisheries in the system. In the second step, Ecosim, the dynamic simulation module, can predict changes in the ecosystem under different fishery policy scenarios, using fishing effort or mortality or environmental changes as drivers. In the third step, Ecospace (Pauly et al. 2000, Walters et al. 1999, Walters et al. 1998) can be used to test spatial dynamics of an EwE model. The utility of this approach has been demonstrated for coral reef ecosystems in the Caribbean and in the Pacific (e.g., Ainsworth et al. 2007, Bozec et al. 2004, Christensen and Pauly 1993, Opitz 1996, Zeller et al. 2003). These ecosystem models succeeded in providing a credible structure for complex coral reefs, synthesizing ecological and fisheries data, and assessing the impact of fisheries using network analysis. Only a few models attempted to develop management scenarios for coral reefs and ecosystem-based management (e.g. Ainsworth et al. 2008) although there are several examples set in other tropical ecosystems (e.g. Arias-González et al. 2004, Arreguín-Sánchez et al. 2008, Gribble 2003, Okey et al. 2004, Zetina-Rejón et al. 2004).

This work represents the first step of the modeling process; namely, it draws together ecological and fisheries data and develops a trophic model of the coral reef ecosystem of La Parguera, Puerto Rico for the nominal year 2000. The paper presents the steps to build and balance the model. It describes the resulting model and identifies the missing pieces of information necessary

to better understand the functioning of this ecosystem, including the role of fishing and other factors. It is a preliminary approach to developing models that can serve as useful tools for ecosystem-based fisheries management in the US Caribbean.

MATERIALS AND METHODS

Study area

The model depicts the coral reef ecosystem of La Parguera, located on the south-west coast of Puerto Rico and encompassing 147 km² (Figure 1). The modelled system extends from the shoreline to the mapped shelf edge offshore and from Cayo Romero in the east to Margarita reef in the west. The coastline of La Parguera is lined with mangroves and is protected by a series of coral reef platforms. An inner platform of intermittent emergent reefs borders and parallels the shoreline. Several reef crests have been colonized by red mangroves (*Rhizophora mangle*) providing additional fish habitat in the prop roots. Backreef areas are typically

sand bottom with mixed seagrasses, and small patch reefs, soft coral fields, and/or isolated hard corals. A second, mid-shelf line of reefs, about 1 km offshore, and the outer shelf reefs, about 3 km offshore (e.g., Media Luna, Turrumote), both have a mix of habitats similar to the inner reef line. A fourth line of submerged reefs occurs at the edge of the insular shelf, up to 8 km offshore. These shelf-edge reefs rise to a depth of approximately 15-20 m below the surface, mainly with a typical spur-and-groove configuration. Since they are not emergent, they do not offer the same sheltering effects as the three inshore reef lines. Deeper areas (~20-40 m) between the shelf-edge, outer, and inner reefs offer additional habitat (e.g., algal flats, deep patch reefs) not found in the shallower strata.

The ecosystem is not homogeneous and most species, both sessile and mobile exhibit some affinity for specific habitat types. Most studies have measured biota relative to particular habitat types or area. In order to use data from a diverse set of research

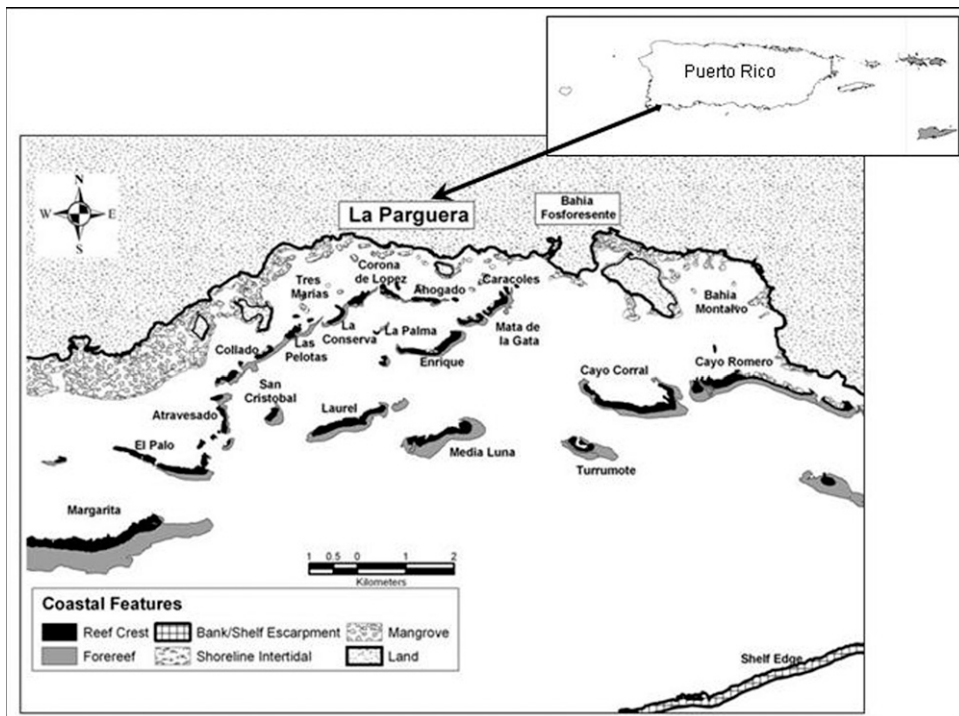


FIG. 1. Location of the study area, La Parguera, in Puerto Rico.

or monitoring studies our model needed to account for differences in the way species were distributed but also to attribute species to a manageable number of habitat types. Three habitat schemes were examined (described in Cervený 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 A1). Existing habitat schemes and maps were not entirely suitable for our modeling purposes, so elements of the available habitat characterizations were selected to allow us the means to effectively group and separate species. Existing habitat maps were brought into a geographical information system (Geographic Information System – GIS) (using ESRI ArcGIS® 9.2). Habitat polygons were selected or redrawn based on our criteria. For example, all shallow reef zones (shallow forereef and backreef) were combined and middle and deep forereefs were combined. In addition, buffers were generated to represent habitats not clearly differentiated in the GIS layers available: a 4 m buffer was created between mangroves and seagrasses to represent the prop root habitat accessible to most fish species (and researchers) and a 15 m buffer, termed “Patch reefs in backreef seagrass” was created between shallow backreef and seagrass habitats in the inner shelf areas where such habitats important as nursery areas (Hill 2001), are known to exist (R. Hill, personal observation). The original NOAA benthic maps contained a large area of unknown habitat so benthic habitat maps developed from sidescan sonar data from Prada (2002) were incorporated into the project, converted to the same modeling habitat scheme, and added to the project. This provided additional shelf-edge and inshore areas mapped to a finer resolution with accompanying fish surveys. Areas that bordered the shelf-edge, extending to 50m depths (generally the limit of current deep diving operations, and the waters overlaying them) were denoted as shelf slope reefs. All locations where georeferenced biotic surveys (primarily corals and fish) had been conducted were then overlain on the model habitats and attributed to a particular habitat type.

Model structure and data

We used the Ecopath with Ecosim software (EwE) (Christensen and Walters 2004) to construct a model of the ecosystem that describes the foodweb interactions of functional groups (composed of a single species or of a group of species). The Ecopath model, a snapshot of the ecosystem for a given year (2000, in this case), accounts for each functional group i , and is formally written:

$$P_i = F_i + B_i * M2_i + E_i + BA_i + P_i * (1 - EE_i)$$

where P_i is the total production rate (t/km²/year) of i , F_i is the total fishery catch rate (year⁻¹) of i , B_i is the biomass of group i (t/km²), $M2_i$ is the total predation rate (/year) on group i , E_i the net migration rate (/year) (emigration – immigration), BA_i is the biomass accumulation rate (/year) for i , while $P_i * (1 - EE_i)$ is the ‘other mortality’ rate (/year) for i (equivalent to $M0_i$). EE_i is 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. The predation rate is a function of all predators consuming prey i , their rate of consumption per unit of biomass (Q/B_i , /year) and the proportion of prey i in their diet. The production per unit of biomass (P/B_i , /year) is the sum of predation (natural mortality, M) and fishing mortality (F). The principle behind this ecosystem modeling 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 account for an open system and biomass accumulation can be used to signal the ongoing changes in population biomass (declines or increases).

Only 4 of the 5 parameters (B , P/B , Q/B , P/Q , EE) are initially entered in Ecopath, the fifth one being estimated by Ecopath. For instance, in absence of information on biomass for a group one can set EE to a reasonable value based on ecological considerations and obtain an estimated value of biomass. The model is also able to incorporate

multiple life history or ontogenetic stages (stanzas) for species with complex life histories (e.g. grunts, snappers, and groupers in this model). The stanzas (here, juvenile and adult groups) are linked and their respective P/B, Q/B, and growth are calculated from a baseline estimate for a leading group (the adults in our case). Growth for each stanza is calculated following the von Bertalanffy growth curve and assuming stable survivorship through ages (Christensen and Walters 2005).

The model is composed of 49 functional groups of fish, 1 of turtles, 10 invertebrates, and 2 of primary producers. Given the objective of evaluating fisheries management scenarios, the model has been organized around commercial species, their prey and their predators. Fish that have not been considered separately for their role in the reef fishery have been grouped according to their dominant habitat preference: pelagic, forereef, (other) reef, lagoon, vegetation, and ubiquitous; their diet preferences (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 4 terms: 1. the habitat they are associated with; 2. their size (Large, Medium, Small); 3. their diet preferences; and 4. exploited groups are signalled by adding commercial to their names (e.g., grunts and grunts comm). Primary target species groups considered separately are the snappers, grunts, (large) wrasses, parrotfish, groupers, grouper seabass, porgies, mojarras, squirrelfish, goatfish, trunkfish and boxfish, triggerfish, barracuda, halfbeaks, mullet, and herring (Table A2). Finally, 8 groups of fish, mostly commercial species (Table A2) were divided into juveniles and adults to account for ontogenetic changes in diet or habitats.

Pelagic habitat taxa include jacks, wahoo, mackerels, and the "wall of mouths" invertivores (*sensu* Hamner et al. 1988) which are found windward of the reef preying on incoming plankton and nekton. Forereef species prefer more exposed reefs although some also may be found in more protected reef zones. The reef habitat species are more closely associated with rocky

or coral reefs, mainly because of the benthic structure they provide. Lagoon species can be found on all sorts of bottom types but mainly inhabit protected waters. Vegetation species are specifically associated with vegetated bottoms whether seagrass or macroalgae. Ubiquitous species can be found in all sorts of habitats and are often more mobile species. For these various groupings, we make the assumption that most fish species are more dependent on structure than exact taxa-provided habitat, and that these species may use several habitats at different times of day or periods of the life cycle. Their actual biomass distributions vary across the habitats where they have been sampled, which is particularly important for later Ecospace modeling.

Fish parameters

Catch data for the period 1983-2003 were obtained from the NOAA TIP database for statistical areas 360-362 (Lajas: La Parguera, Papayo, Salinas) and 370-371 (Cabo Rojo: Pitahaya and Bahia Sucia). Catches of large pelagics such as tunas, swordfish, large offshore sharks, dolphinfish and trashfish (PR DNER Fishery Category) were ignored because they are not generally found in the model area or, in the case of trashfish, could not be attributed to specific functional groups. Fish reported as First, Second and Third Class fish in commercial statistics were allocated to functional groups according to the classification of Matos and Sadovy (1990) (see Table A3).

With the multigear and multispecies nature of the fisheries, landing statistics are often difficult to analyze. For example, different species, from different habitats, taken with different gears may be reported together on the same reporting form and attributed to the main gear used on the trip. For this reason it was deemed necessary to reapportion the species into nominal fisheries. For our purposes, all conch are taken in the conch fishery. Line, trap, and net fisheries were divided into shallow or deep fisheries based on the species they reportedly caught, e.g., deep water snapper on deep water lines, nets, or traps and shallow water snapper species on shallow water lines, nets,

and traps. This reinforces the ecological distinctions and trophic interactions between the species although it does not improve the difficult task of assessing fishing effort used to obtain the catch. Within each functional group, these catches were attributed to a specific gear in the same proportion as they were observed in the statistics. Catches used in the present model are shown in Table A4. Finally, recreational catches, probably important for some species, have not generally been taken into consideration at this time. Given the probable importance of sport fishing for adult groupers (group 26), we added an additional catch for the recreational fishery equal to the total commercial landings (0.04 t/km^2) for these species to help balance the model.

Biomass data for fishes and benthos were collected from multiple sources, the primary ones being Coral Reef Ecosystem Studies-UPRM (CRES) permanent forereef transect surveys, NOAA's National Marine Fisheries Service paired benthic and fish transect surveys, and NOAA's National Ocean Service transect surveys. CRES surveys were conducted from 2003 through 2008 on six fore-reef and two shelf-edge sites. Three replicate transects were established at each of three nominal depths (5, 10, 15 m) on the fore-reef sites and three replicate transects were established for each of the shelf edge sites (20 m). Biomass estimates from this dataset were calculated from fish abundance and size estimates of samples taken from 2003-2007. NOAA Fisheries' surveys have monitored benthic composition, coral disease, and fish assemblages with randomly placed transects at specific sites (offshore, Turrumote, Pinnacles) in La Parguera from 1997 to 2008. Fish data consist of abundance and size estimates. Since 2000, the Biogeography Branch of NOAA's National Ocean Service has conducted over 1,000 benthic and fish surveys in La Parguera. Survey sites were spatially random and stratified by habitat type, and matched fish abundance and size estimates with benthic surveys and measures of rugosity. Data from 2000-2002 were examined for the model (Table 1). In some instances, biomass data from 2001 or 2002 were used to improve the generality of the data based on increases in

sample numbers or detrending data from numbers of samples. Additional sources of data included Cross Shelf Habitat (CSH) fish surveys (K. Cerveny, UPRM, unpublished data) and side-scan sonar mapping with matched fish survey data (Prada 2002 and M.C. Prada, UPRM data).

The biomass was averaged for each habitat (Table A1) to take into account the variable numbers of transects surveyed and account for inter-habitat density differences. Total biomass for the study area ($Biom_i$) is the sum of the biomass of species i and habitat h multiplied by the percentage of the surface area occupied by each habitat in the study area ($prop_h$, see Table A1).

$$Biom_i = \sum_h Biom_{i,h} * prop_h$$

The biomass for the study area was calculated separately for juveniles and adults when necessary, using size at first maturity as the cut off between the two stanzas (Table A5 for values and Box A1 for methods of calculations). Adult biomass was assumed to be more reliable than that of juveniles, which may be more susceptible to being under- or over-estimated because of their size and behaviour. Thus, the biomass of juveniles estimated in the survey is presented for information only (Table 1). For consistency, in EwE, the biomass of one group, we chose the juveniles, is derived from adult biomass and juvenile mortality.

Fish natural mortality was derived using empirical equations as described in Box A1. Fishing mortality was calculated as the ratio of catch/biomass (C/B) unless biomass estimates were absent or smaller than the corresponding catch ($C/B > 1$, in italics in Table 1), in which case, F was estimated using a multiplier of natural mortality to account for the perceived level of exploitation: 0.5 for species that are not overfished, 1 for fully exploited and 2 for overexploited species (see Table 1). The ratio of Production/Consumption (P/Q) was obtained from Opitz (1996).

Recent studies in La Parguera have examined stomach contents from fishes as they move from one habitat to another, serving as transport vectors for nutrients (Clark et al. this volume, B. Roque, UPRM, unpublished data). Diets from these local studies were

TABLE 1. Parameters used to build the initial Ecopath model: Biomasses, landings, natural mortality (M) derived by Pauly's and Hoenig's equations, and value used, fishing mortality (either derived from the ratio catch over biomass (C/B) or a multiplier of M), production per unit of biomass (P/B), production per consumption (P/Q) and consumption per unit of biomass (Q/B). (see text for further explanation).

Functional group	Biomass (t/km ²)			Catch 2000 (t/km ²)	P/B (/year)	C/B (/year) ^e	M mult. <i>b</i>	Natural mortality (M/year)			Q/B (/year)	EE
	2000	2001	2002					value retained <i>a</i>	Hoenig	Pauly		
1 Sharks/rays	0.0000	0.0000	1.7324	0.0236	0.26	0.014		0.24	0.24	0.34	0.16	
2 Jacks	11.9008	11.7261	12.4109	0.0217	0.40	0.002		0.40	0.40	0.53	0.22	
3 Wahoo <i>f</i>				0.0001	0.24		0.5	0.16			0.20	
4 Mackerels				0.0205	0.47		0.5	0.32	0.32	0.41	0.23	
5 WoM invertivore	0.4488	0.3147	0.9637	0.0023	0.69	0.005		0.69	0.69	0.69	0.28	
6 Snappers inshore adult	0.4745	0.1685	0.1762	0.1842	0.68	0.388		0.29	0.29	0.42	0.23	3.55
7 juv	1.3513	1.4452	2.1182	0.0146	0.59	0.011		0.58			0.23	
8 Snappers deep				0.0290	1.06		1	0.53	0.58	0.53	0.20	0.80
9 Grunts adult	0.0431	0.0000	0.0221	1.39e-05	0.46	3.22e-04		0.46	0.46	0.69	0.25	1.85
10 juvenile	0.0867	0.0136	0.0398	0.0000	0.92	0.000		0.92			0.25	
11 Grunts comm adult <i>c</i>	0.1958	0.1958	0.3984	0.0676	0.65	0.346		0.31	0.31	0.55	0.24	2.94
12 juv	5.4008	1.5473	1.3626	0.0000	0.62	0.000		0.62			0.24	
13 Parrotfish comm adult	1.7696	2.8982	4.0179	0.0651	1.04	0.037		0.64	0.64	0.74	0.25	5.35
14 juv	0.4576	1.0761	1.7535	1.39e-05	1.29	3.03e-05		1.28			0.25	
15 Parrotfish adult	4.8290	4.0215	6.4384	0.0000	0.92	0.000		0.92	0.92	1.01	0.25	2.91
16 juvenile	3.1372	4.1866	4.3531	0.0000	1.84	0.000		1.84			0.25	
17 Squirrelfish	4.6905	4.8162	4.6628	0.0083	1.89	0.002		1.89		1.89	0.25	
18 Wrasse adult <i>c</i>	0.0743	0.0743	0.0006	0.0297	0.66	0.400		0.26	0.26	0.41	0.25	2.60
19 juvenile	0.0025	0.0173	0.0629	0.0000	0.52	0.000		0.52			0.25	
20 Goatfish	0.2930	0.6294	0.8118	0.0219	0.91	0.075		0.83		0.83	0.28	
21 Trunkfish and boxfish <i>cn</i>	0.0483	0.0483	0.0391	0.0699	1.25	1.447	0.5	0.60			0.28	0.90
22 Forereef M piscivore <i>gn</i>				0.0000	0.83			0.60	1.20	1.20	0.20	
23 Forereef M invertivore <i>cg</i>	0.1724	0.1724	0.4245	0.0000	0.83	0.000		0.83	1.95	1.95	0.25	
24 Forereef S invertivore <i>g</i>	0.8495	0.7494	0.7208	0.0000	0.83	0.000		0.83			0.28	
25 Herring <i>h</i>	0.0196	0.0095	0.2076	0.0011	1.55	0.054		1.50			0.20	
26 Grouper adult	2.0012	2.2904	2.2629	0.0371	0.21	0.019		0.19		0.32	0.22	1.84
27 juvenile	0.1353	0.5278	0.3154	0.0146	0.48	0.108		0.37	0.19		0.22	
28 Grouper seabass adult	0.1377	0.1745	0.2108	0.0054	0.36	0.039		0.32	0.32	0.47	0.21	1.63
29 juvenile		0.0620	0.0490	0.0000	0.64	0.000		0.63			0.21	
30 Reef L piscivore <i>i</i>	0.0192	0.1378	0.0755	0.0000	0.30	0.000		0.30			0.24	
31 Reef S piscivore <i>j</i>	0.0110	0.0696	0.0720	0.0000	0.84	0.000		0.83			0.25	
32 Reef L invertivore	0.0557	1.7368	0.2517	0.0000	0.71	0.000		0.71		0.71	0.24	
33 Triggerfish	0.6651	0.9623	1.2463	0.0220	0.67	0.033		0.63		0.63	0.25	

(Continued)

primarily used (NOAA/UPR database). The diets of species not covered by these studies were taken from Fishbase and other literature sources citing data from the same geographical area. Suitable diets taken from Fishbase were averaged by species when necessary and kept separate from those of the NOAA/UPR database for comparison purposes in further steps. Regardless of the provenance of the diet composition, fish prey were often identified to the larger groups or families (Clupeidae, Labridae) and often only labelled as finfish or unidentified fish. This forced us to rely on expert judgement/knowledge, and other ancillary data. Unidentified fish were allocated to a group of prey using fish size, spatial co-occurrence, and known behaviour (R. Appeldoorn and M. Nemeth, University of Puerto Rico-Mayagüez, R. Hill, personal observations).

Turtles

Turtles, while known to be present, are not well documented in the study area. Their natural mortality (0.12 /year, Bjørndal et al. 2003) and Q/B (8.87 /year, Bjørndal 1980) was based on *Chelonia mydas*. Diet was assumed to be composed of macroalgae (67%) and sponges (33%) to account for both included species. In absence of a biomass estimate, EE was set at 0.7.

Invertebrates

The natural mortality for spiny lobster (*Panulirus argus*) was estimated at 0.22/year, assuming a longevity of about 20 years and using Hoenig's equation (Box A1). This species is known to be highly targeted and was probably overfished in 2000 and thus $F=2*M$, for a P/B of 0.67 /year, and EE is set at a high value (0.97). The production/consumption ratio (P/Q) was set at 0.15, a value similar to that calculated from Opitz (1996) and based on a detritivorous diet.

Conch (*Strombus gigas*) natural mortality is difficult to estimate given the ontogenetic changes in natural mortality rate (e.g., Appeldoorn 1988a) and thus the literature proposes estimates that vary considerably among studies. We used Appeldoorn (1987) estimates of mortality from a local mark-recapture experiment spanning 1983-1985.

The author estimated M (1.05/year) by using the mortality measured without fishing minus the dispersion rate ($=0.481$), using a dispersion model. Fishing mortality was calculated from 3 periods of fishing activity and amounted to 1.14/year. The population was deemed overexploited at the time and we assumed that the level of exploitation remained the same although the management regime changed in 1997, including size limits, daily bag limits and closed seasons (spawning season) (Graciela García-Moliner, Caribbean Fisheries Management Council, pers. comm.). P/Q was set at 0.15, a value typical for herbivorous species. It was assumed that fishery mortality and predation are important to explain most of the mortality in this ecosystem and thus $EE=0.95$.

P/B and Q/B for squids/octopus were set as the average values of 3.02/year (range of 2.63-3.4) and 10.22/year (range of 9.43-11.4) respectively (Arreguin-Sanchez et al. 2000, Buchan and Smale 1981). Values of P/B for shrimps and crabs ($=2.14$ /year) were approximated using a longevity of 2 years and Hoenig's equation. Q/B was set at 0.15/year (Jarre-Teichmann and Guénette 1996). Sea urchins (mainly *Diadema*) were separated from the other echinoderms because of their specific life history and their predatory habits on benthos. P/B (1.1/year) and Q/B (3.7/year) were taken from Opitz (1996). Echinoderms' P/B (1.1/year) and Q/B (3.7/year) were taken from Opitz (1996). P/B (3/year) and Q/B (44.95/year) for small benthos are the average of values for snails, chitons, small benthic arthropods, and clams found in Opitz (1996).

Corals/anemones

P/B was taken from Bozec et al. (2004) for stony corals. Q/B was the average of estimates for stony corals (7.3/year) (Bozec et al. 2004) and for octocorals (1.1/year) (Ainsworth et al. 2007), based on a world average. The biomass of a coral type c in habitat type h is calculated as:

$$Biom_{hc} = surf * \%cover * DW * conversion * rugosity$$

where $surf$ is the surface area of habitat; $\%cover$ is the percentage of live coral; DW

is the dry weight per square meter which is 136 g/m² for stony corals (McClanahan 1995) and 16.52 g/m² for octocorals (Alcolado 1990); *conversion* is the conversion ratio from DW to WW, 1:5.2 for stony corals (McClanahan 1995) and 1:4.44 for octocorals (Opitz 1996); *rugosity* is calculated as the ratio of contoured distance to linear distance across the surface for stony corals only (McClanahan and Shafir 1990). The resulting biomass for La Parguera is thus estimated at 67.62 t/km², composed of 62.24 t/km² of stony corals and 5.39 t/km² of octocorals (Table A6).

Plankton

P/B and Q/B for zooplankton were taken from Opitz (1996) at values of 40/year and 165/year respectively. We assumed that their mortality was well explained by the model and thus EE was set at 0.95. Although important, the estimate for phytoplankton leaves something to be desired and should be updated in the next version. In absence of better data specific to La Parguera, an estimate for Puerto Rico's EEZ was obtained from the Sea Around Us project (<http://www.seaaroundus.org/>). The estimate is derived from the SeaWiFS database and amounts to a value of 334 mgC/m²/day. Assuming a conversion ratio of C:WW of 1:10 (Pauly and Christensen 1995) and 365 days of productivity, the productivity amounts to 1219 g/m²/year, which is probably an underestimate given that the open seas are less productive than coastal waters. For comparison, Opitz (1996) used a value of 2800 g/m²/year. The biomass was obtained by dividing the production by a P/B of 70/year (Opitz 1996) which yields a biomass of 35 g/m². To balance the model the original value was doubled bringing us closer to Opitz's estimate.

Benthic producers

The biomass of benthic producers includes seagrasses (*Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*), calcareous algae, and macroalgae and was derived from the average densities reported for Culebra, on the east coast of Puerto Rico (Hernández-Delgado et al. 2002), which amounted to 248 g/m² (range 140-417). All

of the major components were measured and reported together and their ranges generally fall near those previously measured in past studies of La Parguera. This may be an overestimate if the areas of the study, near the Luis Peña Channel Natural Reserve have higher densities of benthic producers than La Parguera. No recent studies were available. Future revisions of the model should examine these values and perhaps the variations in benthic production across different habitat types. The P/B ratio was assumed to be 13.25/year based on Opitz (1996).

Detritus

A preliminary estimate of detritus biomass (D , in gC/m²) was obtained from Pauly et al. (1993):

$$\text{Log}_{10}D = -2.41 + 0.954\text{Log}_{10}(PP) + 0.863\text{Log}_{10}(E)$$

where PP is primary production in gC/m²/year and E is the euphotic zone in metres. Using PP of 2438 and an euphotic zone equal to the average depth of La Parguera (20m) the detritus biomass amounts to 9.77 gC/m² and, using a conversion ratio of C:WW of 1:10 (Pauly and Christensen 1995), amounted to 97.7 t/km².

Balancing the model

Using the input values, Ecopath solves simultaneous linear equations and estimates the missing parameters, often the EE value. As long as there are values of EE larger than 1, the model is not balanced since there cannot be more biomass consumed than produced in any given year. The balancing process is done manually by checking inconsistencies in data (e.g. biomass lower than the catch), adjusting biomasses, P/B, and diet composition. The predator-prey matrix of predation mortalities, computed at each step, allows the modeller to identify interactions with exceedingly high predation mortalities and find solutions on a case-by-case basis. In some cases, a predator is too abundant and exerts too much predation on several of its prey, which leads to questioning the validity of either its biomass estimation or the diet composition.

In some cases, the predation rate is too high because the proportion of a prey in a predator's diet is overestimated; the consumed prey biomass expected by the model may then be unrealistically high or may exceed biomass actually available in the system. Indeed, diet compositions are often the preferred means of adjusting values for balancing as they are generally the weakest data in the model since studies tend to be scarce, and several published diet compositions did not completely identify all fish or other prey items found in stomachs.

Model characteristics

The resulting model is evaluated by looking at the biomass distribution by trophic levels, the trophic level of the catch, and the degree of omnivory by trophic level. The omnivory index (OI_i), the variance in the trophic level of a consumer's prey, is a function of the trophic level of the predator TL_i and the trophic level of each prey (TL_j) and their respective proportion in the predator's diet (DC_{ij}):

$$OI_i = \sum_{j=1}^n (TL_j - (TL_i - 1))^2 \cdot DC_{ij}$$

A value of zero indicates a specialized consumer while a value approaching 1 indi-

cates a consumer feeding on many trophic levels. The trophic level of the catch is the sum of trophic level of each group fished, weighted by their respective tonnage. The trophic level of a functional group is calculated by assigning a level of 1 to producers and detritus, and a trophic level of 1 + (the weighted average of the preys' trophic level) to consumers (Christensen et al. 2005). Trophic levels typically range from 1 for producers to 5 for top predators.

RESULTS

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 (Figure 2). 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. Parrotfishes, 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 have been placed with the ubiquitous and commuters groups. Finally, most pelagic species such as halfbeaks, herring,

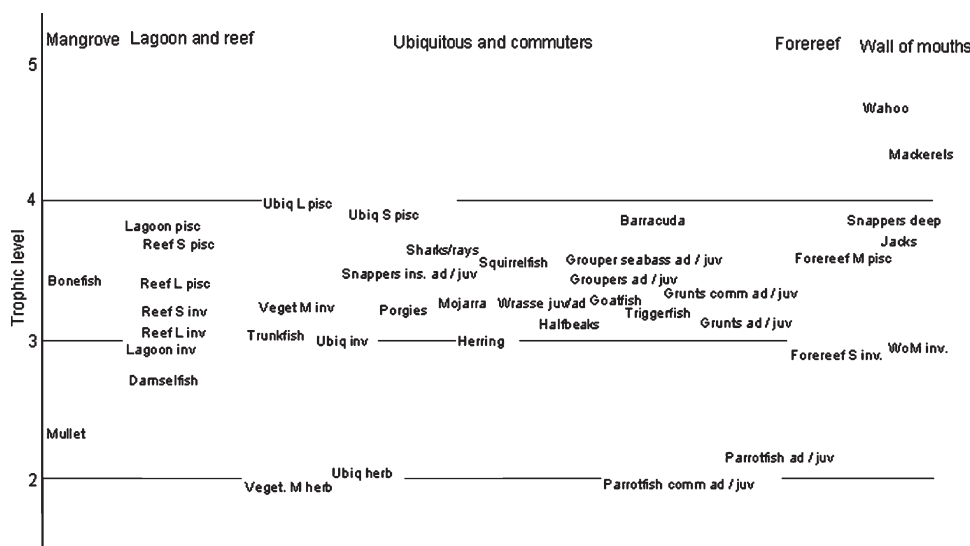


FIG. 2. Distribution of fish functional groups by habitat type and trophic level. Inv=invertivore, herb=herbivore, pisc=piscivore; Veget=vegetation; ad=adult; juv=juveniles.

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.

The balancing process started with the groups at the highest trophic levels with large EE values. Often, solving problems for the high TL groups solves those of lower trophic levels. Several groups around the 3.5 trophic level showed elevated EEs and in turn caused problems for their prey. Modifying the diet composition and biomass as described below solved a large part of the problem. It was not deemed necessary to modify P/B values except for a slight increase for groupers (groups #26-27). However, the biomass of predators of all trophic levels required more primary production than was included in initial estimates in the model study area; the primary production had to be doubled to satisfy the needs of the ecosystem.

Biomass estimates were quite variable among surveys and although the year 2000 estimate was generally used first in the model, adjustments were made based on 2001-2002 (NOS) and 2001-2007 (CRES) survey estimates. Biomass adjustments were necessary for 12 groups (Table 2), of which only 3 were decreased from the initial estimates. Jacks' biomass (group 2) was reduced from 11 to 0.5 t/km² because this group was inflicting very high mortalities on its prey and was likely overestimated. Inshore snappers (group 6) were also reduced slightly to the average of 2000-2002 survey estimates to decrease predation mortalities on their prey. Adult groupers (group 26) were considered overestimated in the survey, especially compared to reported landings (including the increase to account for recreational landings), but still, with a biomass of 0.7 t/km² and increased landings, the EE value only reaches 0.46. Trunkfish and boxfish (group 21) biomass was left to be estimated by the model, assuming an EE of 0.8, because the estimated biomass was smaller than the reported landings. The biomass of Reef L piscivores (group 30) was also increased 4-fold to account for the predation from sharks and groupers, assuming that these cryptic species may be under-

estimated in the surveys. Although the impact of predation on these species is quite large, their importance in the diet of sharks and groupers is relatively small (1 and 2% respectively, Table A7, A8). The biomass of herring, reef S piscivore, mojarras, lagoon piscivore, lagoon invertivore, and vegetation M invertivore were all increased to estimates of 2001-2002, more consistent with the biomass needed to support fishing and predation included in the model.

Overall, changes of 1% or more in the diet matrix were not as frequent as first expected. They affected 19 groups out of 60 while 8 groups necessitated changes of more than 5% (Table A8). The most important groups in this regard are jacks, mackerels, snappers inshore ad and juv, grouper juv, ubiq L pisc, ubiq S pisc, octopus/squids. They are characterized by large biomass – abundant groups preying on less productive groups. For example, the proportion of herring in the diet of mackerels, was decreased by 12% and replaced by predation on jacks (Table A7, A8), a more abundant group likely to be geographically more available to mackerels. In several cases like this, diet compositions were modified to give less importance to fish with low productivity in favour of more productive or abundant fish. For instance, we reduced the predation that jacks (group 2), snappers inshore comm juv (group 7), groupers adult (group 26), ubiq L piscivore (group 44) and octopus and squids (group 51) were exerting on ubiquitous invertivores (group 48, Biom= 0.45 t/km²) and compensated mainly by increasing the importance of the more abundant ubiquitous herbivores (group 49, Biom= 4.6 t/km²) in their diet (Tables 2 and A8). Similarly, the initial high proportion of grunts (group 9) in the diet of ubiquitous S pisc (group 47) had to be removed and replaced by predation on juveniles of groupers (group 27) and parrotfish (group 16) given the relatively small biomass of grunts in the system. As a general rule, it was assumed that predation was more likely to occur on juveniles of many species than on adults.

In the resulting model, wahoo and mackerels are the top predators (TL= 4.67 and 4.35 respectively; Table 2, Figure 2). Fish of trophic level of 3.25-3.75, eating a

TABLE 2. Parameters of the balanced model and initial biomass for comparison for groups that were modified. Trophic level (TL) resulting from Ecopath is compared with values obtained from Fishbase. Numbers in bold were estimated by Ecopath and numbers in bold and italic signal the biomass of juveniles computed by Ecopath. EE values that are questionable are signalled with q.

	Group name	Trophic level	Biomass (t/km ²)	PB	QB	EE	P/Q	Initial biomass	TL from Fishbase	Omnivory index
1	Sharks	3.41	0.169	0.26	1.63	0.9	0.16		3.97	0.826
2	Jacks	3.68	0.5	0.40	1.82	0.782	0.22	11.901	4.17	0.360
3	Wahoo	4.67	0.0014	0.24	1.20	0.8	0.20		4.40	0.267
4	Mackerels	4.35	0.148	0.47	2.04	0.8	0.23		4.50	0.182
5	WoM invertivore	2.9	0.448	0.69	2.46	0.614	0.28		3.08	0.198
6	Snappers inshore adult	3.50	0.42	0.68	3.55	0.72	0.19	0.474	4.09	0.272
7	juvenile	3.42	0.472	0.59	6.44	0.475	0.09	1.351		0.071
8	Snappers deep	3.83	0.088	1.06	5.30	0.8	0.20		4.10	0.396
9	Grunts adult	3.12	0.043	0.46	1.84	0.432	0.25		3.31	0.234
10	juvenile	3.27	0.012	0.92	3.86	0.94	0.24	0.087		0.034
11	Grunts comm adult	3.35	0.196	0.65	2.94	0.568	0.22		3.59	0.155
12	juvenile	3.27	0.16	0.62	5.29	0.435	0.12	5.401		0.034
13	Parrotfish comm adult	2.01	1.77	0.68	5.34	0.071	q 0.24		2.00	0.015
14	juvenile	2.01	0.40	1.29	11.60	0.283	q 0.11	0.457		0.014
15	Parrotfish adult	2.17	4.8	0.92	2.91	0.031	q 0.32		2.00	0.174
16	juvenile	2.06	0.909	1.80	6.58	0.286	q 0.27	3.137		0.065
17	Squirrelfish	3.42	4.69	1.89	7.56	0.007	q 0.25		3.50	0.110
18	Wrasse adult	3.39	0.074	0.66	2.60	0.998	0.25		3.40	0.066
19	juvenile	3.17	0.074	0.52	4.67	0.782	0.11	0.002		0.000
20	Goatfish	3.26	0.293	0.91	3.25	0.280	q 0.28		3.30	0.254
21	Trunkfish and boxfish	3.17	0.113	0.90	3.21	0.800	0.28	0.048	3.08	0.357
22	Forereef M piscivore	3.65	0.021	0.83	4.15	0.900	0.20		4.50	0.439
23	Forereef M invertivore	3.01	0.172	0.83	3.32	0.673	0.25		3.05	0.449
24	Forereef S invertivore	2.92	0.849	0.83	2.96	0.652	0.28		3.11	0.418
25	Herring	3.00	0.2	1.55	7.77	0.963	0.20	0.02	3.30	0.004
26	Grouper adult	3.65	0.7	0.25	1.84	0.455	0.14	2.001	4.04	0.238
27	juvenile	3.45	0.271	0.50	3.93	0.954	0.13	0.135		0.102
28	Grouper seabass adult	3.63	0.14	0.36	1.63	0.361	q 0.22		4.18	0.210
29	juvenile	3.45	0.102	0.63	3.15	0.348	0.20	0.062		0.177
30	Reef L piscivore	3.39	0.11	0.30	1.25	0.949	0.24	0.019	4.17	0.375
31	Reef S piscivore	3.72	0.07	0.83	3.32	0.96	0.25	0.011	3.70	0.100
32	Reef L invertivore	3.15	0.0557	0.71	2.96	0.204	q 0.24		3.50	0.249
33	Triggerfish	3.18	0.665	0.67	2.68	0.202	q 0.25		3.40	0.063
34	Porgies	3.23	0.0857	0.83	3.32	0.580	0.25		3.28	0.237
35	Mojarras	3.25	0.0123	2.32	9.30	0.976	0.25	0.001	3.30	0.059
36	Reef S invertivore	3.23	0.301	1.16	4.15	0.985	0.28		3.42	0.141
37	Damselfish/butterflyfish	2.72	2.958	0.64	2.21	0.234	0.29		2.73	0.404
38	Mullet	2.32	0.09	0.56	2.24	0.955	0.25	0.001	2.25	0.237
39	Lagoon piscivore	3.82	0.08	0.35	1.30	0.909	0.27	0.001	4.20	0.130
40	Lagoon invertivore	2.97	0.21	1.09	3.64	0.971	0.30	0.086	3.10	0.497
41	Bonefish	3.39	0.002	0.51	2.05	0.9	0.25		3.70	0.116
42	Vegetation M invertivore	3.23	0.3	1.08	4.31	0.836	0.25	0.010	3.59	0.073
43	Vegetation M herbivore	2.00	0.0637	0.61	2.45	0.911	0.25		2.00	0.000
44	Ubic L piscivore	3.97	0.897	0.19	0.76	0.042	0.25		4.45	0.348
45	Barracuda	3.86	0.0627	0.32	1.59	0.520	0.20		4.30	0.355
46	Halfbeaks	3.08	0.146	1.17	4.69	0.8	0.25		3.60	0.007
47	Ubic S piscivore	3.90	0.113	0.61	2.44	0.8	0.25		4.40	0.206
48	Ubic invertivore	3.06	0.449	0.80	2.76	0.968	0.29		3.10	0.266
49	Ubic herbivores	2.05	4.647	0.61	2.36	0.276	q 0.26		2.00	0.054
50	Turtles	2.43	0.114	0.12	8.87	0.7	0.01			0.376

(Continued)

TABLE 2. Continued.

Group name	Trophic level	Biomass (t/km ²)	PB	QB	EE	P/Q	Initial biomass	TL from Fishbase	Omnivory index
51 Octopus/squids	3.39	0.129	3.02	10.22	0.95	0.30			0.091
52 Spiny lobster	2.87	0.350	0.67	4.46	0.97	0.15			0.524
53 Shrimps/crabs	2.56	18.246	2.14	10.68	0.95	0.20			0.321
54 Urchins	2.07	4.405	1.10	3.70	0.8	0.30			0.082
55 Echinoderm	3.01	6.557	0.49	3.24	0.8	0.15			0.298
56 Conch	2.12	0.602	2.19	14.60	0.95	0.15			0.124
57 Small benthos	2.17	80.607	2.72	35.28	0.8	0.08			0.147
58 Sponges	2.30	1.825	1.50	5.00	0.8	0.30			0.210
59 Corals/anemones	2.32	67.62	1.10	4.61	0.026	0.24			0.237
60 Zooplankton	2.00	14.078	40	165	0.95	0.24			0.000
61 Phytoplankton	1.00	35.000	70	-	0.771	-			0.000
62 Benthic producers	1.00	248	13.25	-	0.194	-			0.000
63 Detritus	1.00	97.7	-	-	0.626	-			0.273

mixture of fish and invertebrates of medium to low trophic levels, are numerous and constitute 41% of fish groups in the model. It is interesting to note that trophic levels computed by Ecopath, based on diet composition inputs were generally lower than values obtained from FishBase data (Table 2, Figure 4). For instance, the trophic level for sharks and rays was estimated at 3.4, based on the diet composition entered in Ecopath while the average values found in FishBase amounted to 3.97.

The mean trophic level of the catch in the model is 3.1 for a tonnage of 1 t/km², of which 0.18 t/km² consists of snappers (group 6). The total biomass (minus detritus) amounts to 502 t/km²; 6% are fish and 49% are benthic producers. As expected, the biomass decreases as trophic level increases; biomasses of level 1 to 5 are 277, 164, 56, 9, and 1 t/km² respectively. The degree of omnivory (the variance in trophic level of the prey groups used by a consumer) increases from 0 to 0.53 for groups of trophic level ranging from 2 to 2.9 while groups of higher trophic level show a wide range of omnivory. Fish of trophic levels of 3-3.5 with an omnivory index of less than 0.1 are mainly herbivores (e.g. wrasses, urchins) and benthic or planktonic invertivores (herring, halfbeaks, grunts, mojarras). These functional groups are restricted in the choices of prey groups by the very aggregated structure of the plankton and benthos groups in the model (Table 2). Octopus

and squids also fall in this category but this may also result from the lack of knowledge we have of the specific composition of this group in the study area and the limited diet composition. Groups of the same trophic level category with omnivory index between 0.1 and 0.2 (e.g. squirrelfish, bonfish, grunts comm ad) have similar diets but include slightly more prey fish and are sometimes limited to small prey which are aggregated in large functional groups. Fish groups of trophic level higher than 3.5 tend to show higher degrees of omnivory with increases in body size and trophic level. The highest value (0.8) was obtained for sharks/rays which reflects the large array of prey included in their diet.

The balanced model shows low Ecotrophic Efficiency (EE) values ranging from 0.007 for squirrelfish (group 17) to almost 1 for groups such as wrasses, mojarras, herring and juvenile grunts (Table 2). EE values are relatively low for several functional groups, irrespective of their exploitation status (Table 2). For example, parrotfish comm adult (group 13), characterized by large biomass and P/B, 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 3). Nevertheless, the group presents an EE of only 0.07 and its juvenile stanza 0.28. The same applies to the non-commercial parrotfish

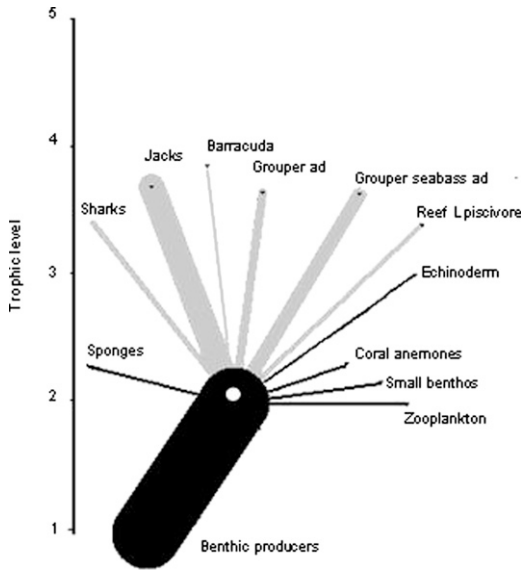


FIG. 3. Parrotfish adult commercially exploited (group 13), at level 2.1 (marked with a white dot), its links to prey (in black) and predators (in grey). The strength of the link is proportional to its width.

(group 15, $EE=0.031$) and grouper seabass (group 28, $EE=0.36$).

Squirrelfish and triggerfish (groups 17 and 33) constitute very abundant groups for which only a few predators could be identified; their mortality is not well explained by the model (EE of 0.007 and 0.202, respectively). Conversely, wrasses (group 18, e.g. hogfish and puddingwife) are not very abundant and constitute a small portion of the diet of abundant functional groups: jacks and groupers (7% each). Although wrasses are not significant in their predators' diet, the predators are responsible for a large predation mortality on large wrasses, presumably preying heavily on juveniles.

DISCUSSION

Reef fish species demonstrate both obligate and facultative habitat preferences with abundances and diversity increasing with complexity in reef habitats thus, habitat can control spatial distributions and

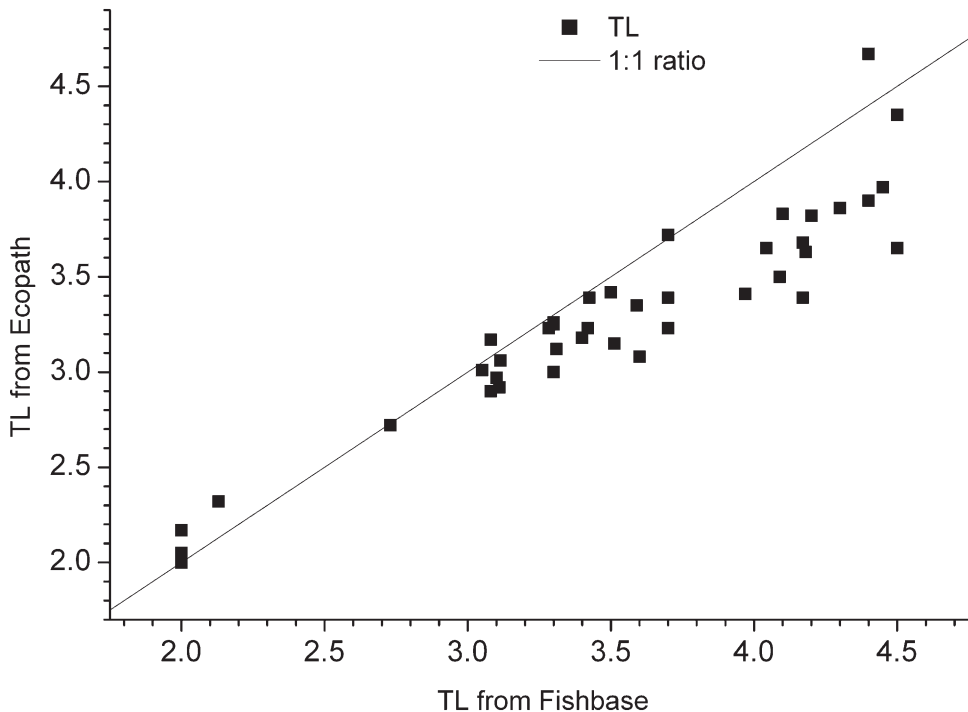


FIG. 4. Comparison of trophic level (TL) derived from Fishbase and from the balanced Ecopath model for fish functional groups.

regulate species interactions (reviewed in Sutton 1983, Williams 1991). The spatial structure of the La Parguera ecosystem model reflects the priority given to exploited groups and their links to habitat, thinking ahead to testing spatially structured fishery scenarios such as marine zoning or reserves. Although several groups were clearly linked with a specific habitat, most were difficult to classify. Some groups are commuters (e.g., grunts) or have large home ranges across habitat boundaries (mackerels) and would defy identifying any strong link with the habitat structures we proposed for La Parguera. A number of species, such as barracudas, are known to have individual territories (Wilson et al. 2006b) but cumulatively, barracuda territories could encompass virtually the entire inshore ecosystem. Furthermore, most exploited groups were aggregates of species that exhibit various degrees of habitat preferences and so the groups ended up being classified as ubiquitous. The contradicting trends between habitat requirements and ontogenetic or diurnal change in habitat for several reef fish has been observed for a long time and constrains the feasibility of completely separating fish into separate habitats (see Opitz 1996). Thus, it is unlikely that a complete classification of fish by habitat can be achieved without producing a totally unwieldy model. If desired, some of the commercial species with specific habitat preferences or critical roles in the fishery or ecosystem, could be split out from their present composite group to test management scenarios in future simulations.

The initial definition of the La Parguera ecosystem mostly assumes a closed system but this may be reconsidered for two reasons. First, pelagic species that live at the edge of the study area, such as the wall of mouths group, likely consume prey species that live outside the area in deep waters. Hamner et al (1988) documented the intense predation pressure of planktivores that feed at the seaward edge of reefs and beyond. Indeed, the large biomass of jacks may be attributed to biomass overestimates or, alternatively, it could be attributed to feeding of this species on pelagic prey offshore of the reef as suggested in Hamner

et al. (1988). The inclusion of 'imported' prey, which we did not consider at this time would have released the excessive predation pressure on the ecosystem. In the case of jacks, the obligatory decrease in biomass from 11 to 0.5 t/km² implies that if the biomass was indeed as high as the survey suggested, at least 90% of its diet would be obtained from the offshore waters, outside the study area. Second, the reef system could be importing primary production from the open ocean as is often the case in clear water reefs. Anecdotal evidence suggests there are episodic nutrient inputs from longshore currents flowing from the east into the La Parguera reef system (R. Hill, personal communication). Without firm data on current primary production we chose to increase the primary production estimates in La Parguera rather than draw from the surrounding open ocean but the importation of production with current flow would constitute a valid alternative. Bozec et al. (2004) found that importation from surrounding waters of plankton, detritus, and prey for some predators was necessary to sustain invertebrates and fish in their model of a New Caledonia atoll.

Input values for the model were chosen based on an examination of available data from local research when possible and other published values when necessary. Biomasses and landings may vary from other models because of the geographic location or the time frame chosen for the model. Natural mortalities and other empirically calculated values also depend on the time frame and the source of available data and were sometimes impossible to obtain because of a lack of basic growth data (e.g. group 21: trunkfish and boxfish). When both maximum age and length at infinity were available comparisons were made between Hoenig (1983) and Pauly (1980), choosing the lower value as the most conservative. Values chosen for the model (Table 1) differ appreciably, for some exploited species (Table A5), from those computed by Ault et al. (2008) for their length-based assessment. Two factors contribute to these differences. Much of the data from Ault et al. (2008) is referenced as coming from data compilations based on research in Florida

and Cuba. As much as possible our sources were from Caribbean studies, occasionally including studies from Cuba. The degree of difference remains to be investigated. Additionally, the maximum age, computed by Ault et al. (2008), is based on the age at which survival reaches 5%, which often differs from the life span calculated in FishBase with equations previously presented. For example, for *Lutjanus vivanus*, the maximum age computed by Ault et al. (2008) is only 9 years but is 32 years in Fishbase; resulting natural mortalities are 0.33/year and 0.14/year respectively. It will be worthwhile to further examine some of the differences that have been detected between the two approaches to see if improvements can be made in the fit of the model.

Additional improvements can be made by including data on recreational fishing catches and reviewing the commercial landings with additional local experts who may be able to help with more detailed interpretations. In our initial efforts, examination of catch per gear has shown that misreporting is pervasive in the data set. For example, in 2000, there is no catch of spiny lobster reported in lobster pots and numerous cases of species like conch being reported from hook-and-line and trap gears. A closer examination of the commercial data would be recommended in the next round of modeling and for time series reconstruction, as would complete recreational fishery removals for all functional groups. As it is, the preliminary model's results pose interesting questions about the present rate of exploitation and population status for some exploited species. For instance, the biomass estimated for conch based on mortality and predation is quite high (0.6 t/km²) compared to the biomass estimated in 1985 (0.11 t/km²) (Appeldoorn 1988b). This estimate should be compared with more recent surveys for this species to verify whether there has been an increase in biomass following the introduction of fishing limitations.

Incomplete diet compositions created uncertainties in the strength of relationships between functional groups (e.g. wrasses vs groupers and jacks). The imprecision in the identification of species and functional groups actually eaten by any given pred-

ators renders the results of some simulations difficult to interpret. Several species are not well explained by the model in spite of importance as commercial species, leading to competing hypotheses. For instance, parrotfish comm (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 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. By contrast, wrasses (group 18, e.g. hogfish and puddingwife) are not very abundant and they constitute a small portion of the diet of abundant functional groups: jacks and groupers (6% each). Although these wrasses are not significant in their predators' diet, the predators are so abundant they are responsible for a large, perhaps excessive, predation mortality on wrasses.

Although the strong link suggested by the diet composition could be real, it could also be an artefact of the imprecise diet composition. Each of these analyses provides the foundation for additional ecological studies and hypotheses to further the understanding of the modelled ecosystem.

According to the scenarios described above, initial balanced-model parameters, such as low EE values may sometimes be justified and deserve further investigation. The model, as preliminary as it is, 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 above demonstrate the imprecision in the available data, including nearly complete paucity of data for entire functional groups. As a further illustration of the evaluation of diet linkages, the high reliance of group 8 (deep-water snapper) on large zooplankton and cephalopods suggested a problem with diet information. Examination showed the diet was principally based on one species (*Rhomboplites aurorubens*). A more detailed review of diet items for the other species of the group listed the same prey species and the data were judged accurate. To the listed prey, myctophids could be added (Michelle Schärer, University of Puerto Rico-Mayagüez, personal communication) but, since myctophids are not generally found in the depths included in the model and the study area, they would have to be handled as imported prey. Finally, 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.

In general, the trophic levels estimated by our Ecopath model are lower than those extracted from Fishbase emphasizing the need to examine diet compositions more closely and the need for more targeted diet samples for some species. In the case of sharks and rays, the diet entered into Ecopath probably includes too much carrion, benthic invertebrates and small fish but this is a result of the diet studies deemed inappropriate. The difference in trophic level could be attributed to the low relative biomass of prey in the model that does not allow for sufficient predation on prey of higher trophic levels. When this occurs, the diet composition would tend to be modified to include more low TL prey during the balancing process, resulting in a lower trophic level estimate for the predator. This could also reflect a real difference between year 2000 and an earlier period. The next step in extending this work to an Ecosim model will be assembly of time series data from a period in the past that can compare some of these relationships through time.

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 km², 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. We have not reduced biomasses in the La Parguera model unless there was a compelling reason to do so, as competing hypothesis about the low EE (too large biomass or low predation because of reduced abundance of predator) remain unresolved. The total biomass

(excluding detritus) in the Opitz model (1996) amounted to 2848 t/km², 5.6 times higher than in the present model (502 t/km²). Differences occur at all trophic levels but important differences are noted for large sharks/rays (top predators) that amounted to 0.3 t/km² in the Opitz model and 0.162 in our model and benthic producers amounting to 1300 t/km² in the Opitz model and 248 t/km² 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 of abundances or biomass of either. The next step in the current modeling 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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