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PRIMARY RESEARCH PAPER

Trophic models and short-term simulations for the coral reefs of Cayos Cochinos and Media Luna (Honduras): a comparative network analysis, ecosystem development, resilience, and fishery

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Abstract We analyzed the trophic functioning of two Caribbean coral reefs with different disturbances, comparing their biomass flows, ecosystem development, and resilience. Cayos Cochinos is a protected reef impacted by tourism, artisanal fisheries, and continental river discharges, while Media Luna is an isolated reef located near to a lobster industrial fishery zone. Ecopath models were built to (1) estimate the ecosystem status-related properties; (2) evaluate the system recovery time; and (3) assess the fishery effects on species and functional groups. Our results indicate that the biomass of both systems is dominated by macroalgae (>75%), mainly at Cayos Cochinos that exhibit greater total system throughput. We show that the harvest of herbivores and coastal eutrophication causes increase in macroalgal biomass. The Media Luna ecosystem appears to be more mature and organized ($Pp/R = 1.6$, $FCI = 6.95\%$), but is also less resistant to fishery impact ($SRT = 10.79$ and 21.72 years using bottom-up and top-down flow-control mechanisms, respectively) than Cayos Cochinos ($SRT = 9.30$ and 16.89). The benthic autotrophs, phytoplankton, and soft corals are the most important functional groups to the trophic functioning, resilience, and development of these ecosystems. However, fishery simulations also show that snappers and spiny lobster reduce the resilience of Cayos Cochinos and Media Luna, respectively.

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Introduction

Coral reef ecosystems present higher values of gross primary production and biodiversity than any other ecosystem on the planet (Connell, 1978), as well as providing ecosystem services for over 100 countries (Salvat, 1992; Moberg & Folke, 1999). However, these ecosystems are being degraded by natural and anthropogenic impacts, such as bleaching, disease, eutrophication, sedimentation, and overfishing (Wilkinson, 2000, 2008; Graham et al., 2007; Mumby, 2014). In Honduras, coral reefs are distributed in patches around the Bahía Islands and the archipelagos of Cayos Cochinos and Honduran Mosquitia (Wilkinson & Souter, 2005). The Cayos Cochinos archipelago is part of the Mesoamerican Barrier Reef System (MBRS) and contains one of the first protected marine areas established in this country, the Natural Marine Monument Archipelago of Cayos Cochinos (SINAPH, 2003). However, fish (i.e., groupers and snappers), spiny lobsters (*Panulirus argus* (Latreille, 1804)), and queen conch (*Strombus gigas* Linnaeus, 1758) were intensively exploited before the protection of Cayos Cochinos and are still extracted today by local artisanal fishermen of the archipelago (Tewfik et al., 1998; Sibaja-Cordero, 2009). Furthermore, the archipelago is an important international tourist destination throughout the year, with hotel services established some 40 years ago and a majority of international tourists. Unfortunately, no consistent records are available regarding the number and types of tourist in Cayos Cochinos (Andraka et al., 2004; ICF, 2011). To date, there have been no studies designed to assess the socio-ecological impact of tourists on this reef ecosystem (ICF, 2011), although studies have been performed on the marine and terrestrial taxonomy, geology, community structure, and coral cover of the Cayos Cochinos reef (Rodríguez-Zaragoza et al., 2012). During the rainy season, this area is susceptible to sedimentation and eutrophication because of the rivers that discharge off the coast of Honduras (Prouty et al., 2008; Carilli et al., 2009). River plumes are transported by the bifurcation of the Caribbean current and impact upon processes such as larval dispersal, recruitment, and productivity at Cayos Cochinos and other MBRS reefs (Andréfouët et al., 2002; Soto et al., 2009). The Honduran Mosquitia is used by both local people and industrial fishing fleets (Chollet & Stoyle, 2014). These reefs, which are not under government protection, lie approximately 60 km from the coast, and the eutrophication generated by the continental rivers does not affect this area, since the river plumes are transported by the Caribbean current from East to Northwest ensuring they do not reach the archipelago. Fishermen visit these islands for extended periods (i.e., August-February) in order to fish for spiny lobster (*P. argus*). During this period, the fishermen live in boats and the lobsters caught are stored and transported by other fishing boats. The size of the artisanal fishery at Media Luna has diminished; however, Castellon & Sarmiento (2002) reported that around Media Luna, there is a high exploitation of *P. argus* using industrial fishery practices. To date, no studies have evaluated the effects of this important fishery on the Honduran Mosquitia coral reefs. The only scientific study published from the Honduran Mosquitia was carried out by Hay (1984), who evaluated the effects of algal and seagrass consumption by herbivores in the Becerros and Media Luna reefs, showing the high incidence of seaweed and seagrass consumption in these coral reefs. With this study, and the current observations by Chollet & Stoyle (2014), it is possible to infer that the Media Luna reef was not affected by the high mortality of *Diadema antillarum* (Philippi 1845) and overfishing of herbivorous fishes, due mainly to the high observed density of parrotfish (*Scarus coelestinus* Valenciennes 1840 and *Scarus guacamaia* Cuvier 1829) and *D. antillarum*, which have remained in greater abundance than other reefs at Honduran Mosquitia and MBRS (e.g., Mohammed, 2003; Vidal & Basurto, 2003; Arias-González et al., 2004). Herbivore activity can be used as an indicator of changes in the state of coral reefs (Bellwood et al., 2004). Hughes et al. (1987) demonstrated that the absence of herbivores, mainly parrotfish and the sea urchin *D. antillarum*, caused a rapid increase in macroalgal coverage and significantly reduced the growth of corals and their associated community structures.

In recent years, the study of ecosystems has been oriented toward improving our capacity to understand trophic relationships among different components of the ecosystem rather than simply assessing the dynamics of isolated populations (Scotti et al., 2007). Macrodescriptors, or emergent properties that allow changes to be detected within ecosystems, have been proposed based on the foundations of systems ecology (e.g., Costanza, 1992). Ulanovicz (1986, 1997) developed a framework called *Ascendency* to assess the level of development and organization of ecosystems (Costanza & Mageau, 1999). *Ascendency* estimates two fundamental attributes of ecosystems: their size and level of organization. Using these attributes, it is possible to compare ecosystems subjected to different levels of human activities (Monaco & Ulanowicz, 1997; Ortiz & Wolff, 2002; Arias-González et al., 2004; Pinnegar & Polunin, 2004), such as the direct and indirect effects following disturbances, and *system recovery time* (as a measure of system resilience) can be estimated (e.g., Patrício & Marques, 2006; Ortiz et al., 2013, 2015). Several coral reef ecosystems have been studied using multispecies trophic models (e.g., Arias-González, 1998; Arias-González et al., 2011; Alva-Basurto & Arias-González, 2014); however, this type of study has never been conducted for the coral reefs of Honduras. For this reason, our objective was to compare the resistance and resilience to fisheries of two different coral reef systems: Cayos Cochinos, a semi-protected site with riverine inputs, and the Media Luna reef, an unprotected and isolated site with an industrial lobster fishery. We used *Ecopath with Ecosim* software to build two balanced mass trophic models, and to estimate the following ecosystem status-related properties: *Ascendency*, food web topology, biomass flows across trophic levels, and pathway (ecological) redundancy. This latter would be defined as the existence of functional groups of species with similar trophic functions in the systems (sensu Lawton, 1994). The species and functional groups that were most affected by fisheries were also evaluated.

Materials and methods

Study areas

We compared two study areas. The first was the Natural Marine Monument Archipelago of Cayos Cochinos, a protected area within the MBRS, located between the northern coast of Honduras and the Bahía Islands in the Caribbean Sea (Fig. 1). The archipelago is composed of two wooded islands and thirteen coral cays, with a total area of 485 km^2 (Andraka et al., 2004). The benthos mainly consists of macroalgae, seagrass, corals, and sandy patches, and the live coral cover has values from 7 to 17% (Rodríguez-Zaragoza et al., 2012). To the north of this archipelago, deep areas of between 30 and 100 m characterize the seafloor, whereas the southern coast only reaches depths of 30 m (Bermingham et al., 1998). In this area, the fishery is primarily focused on fish for self-consumption (Sibaja-Cordero, 2009), and species such as *S. gigas* and *P. argus* are overexploited (Tewfik et al., 1998; Castellon & Sarmiento, 2002; Salas et al., 2011). The second study area is the Media Luna reef, a portion of the Honduran Mosquitia located approximately 60 km off the Northeast Honduran coast facing Nicaragua, with a total area of 218 km^2 (Fig. 1). The deepest area of this site does not exceed 20 m, so that only shallow coral reefs are present. Reef habitat is currently dominated by fleshy macroalgae, followed by the corals *Acropora palmata* (Lamarck 1816), *Orbicella* spp., and *Siderastrea* spp; total live coral cover ranges from 4% to 16%, according to our estimates based on field data. Unfortunately, only limited information exists relating to this archipelago since the Mosquitia area has not yet been scientifically explored (Chollet & Stoyle, 2014).

Selection of model compartments and data sources

Species and functional groups used for the construction of trophic models for both study areas were selected based on their economic importance and functional roles within ecosystems. The *Ecopath with Ecosim* (*Ewe*) input parameters—biomass (*B*), catches (*Ca*), turnover rates (*P/B*), consumption rates (*Q/B*) and diet composition—were obtained from the field (for fish, corals and macroalgae; Appendix C Supplementary Material) and from the scientific literature. Model functional groups included piscivorous fish, groupers, snappers, benthic-pelagic carnivorous fish, mackerel, benthic carnivorous fish, omnivorous fish, zooplanktivorous fish, herbivorous fish, and parrotfish. Invertebrate species were classified as large benthic carnivores, *P. argus* (spiny lobster), stony corals, soft corals, medium benthic omnivores, benthic filter feeders, benthic detritivores, small benthic omnivores, zooplankton, benthic autotrophs, phytoplankton, and detritus. All groups were linked to detritus, as this material consisted of microorganisms and organic matter (Sorokin, 1973). Because of the nutritional importance of zooxanthellae (symbiotic microalgae living in the

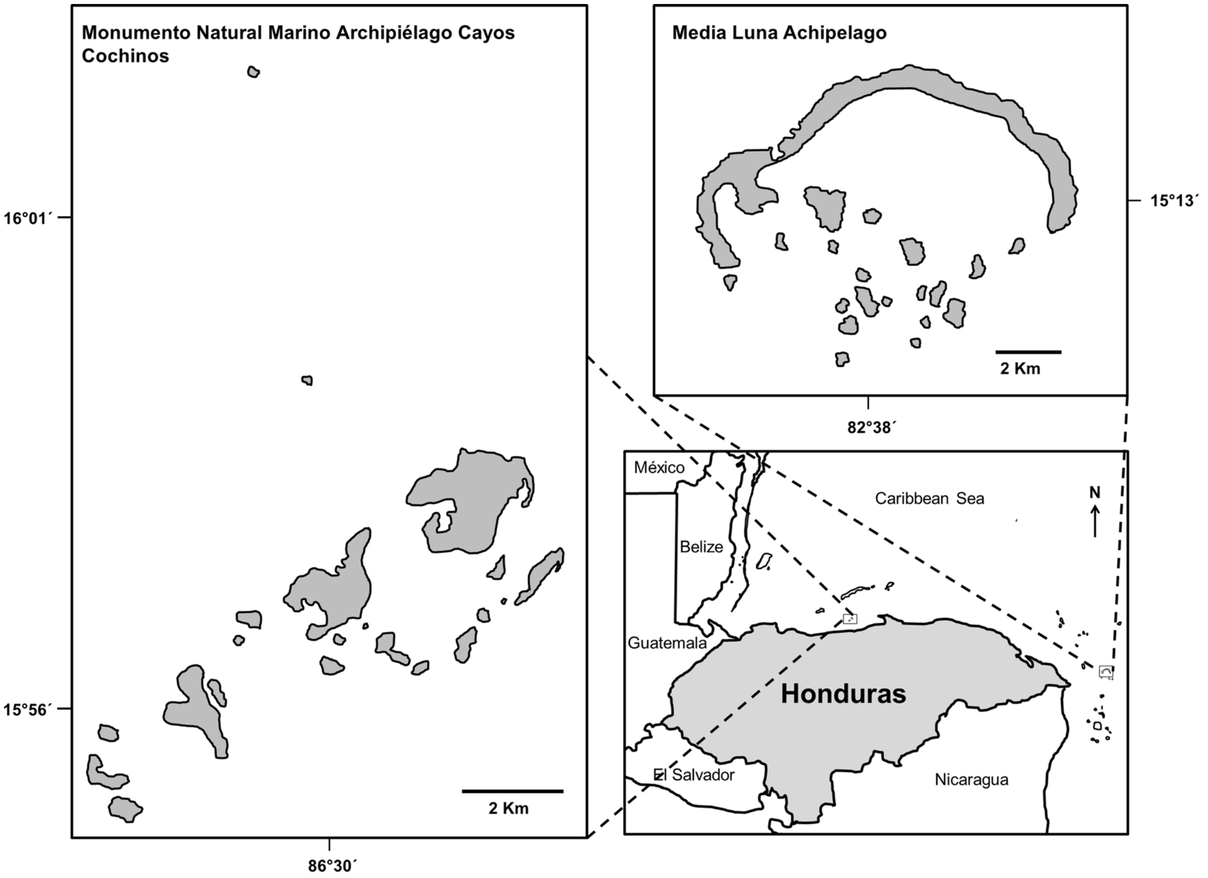


Fig. 1 Locations of the study areas in central north and northeast of Honduras: Natural Marine Monument Archipelago of Cayos Cochinos and Media Luna Archipelago

coral tissue) to corals (Pearse & Muscatine, 1971), they were included in the stony coral group, as per Liu et al. (2009). To prevent erroneous comparisons among systemic macrodescriptors, both models were built using a similar number of components. It is known that grouper fishes play an important ecological and economic role in Caribbean reefs. However, we elected not to include this functional group in the Media Luna reef, because they are not recorded in the visual census at this site. In addition, there are no fisheries data with which to infer the possible biomass based on mortality. Appendix A Supplementary Material lists the species within each functional group, the matrix diet composition, and the data sources used for both study areas.

Ecopath and Ecosim modeling approaches

Trophic mass balance models were constructed using the software *EwE*. *Ecopath* was initially built following the approach of Polovina (1984) and was subsequently expanded by Christensen & Pauly (1992) and Walters et al. (1997). *EwE* estimates the biomass and food consumption of species and functional groups, in addition to the ecological macrodescriptors proposed by Odum (1969) and Ulanowicz (1986, 1997) that include *Primary production/community respiration* (*Pp/R*), *Primary production/biomass* (*Pp/B*), *Total system throughput* (*TST*), *Ascendency* (*A*), *Development capacity* (*C*), *Ascendency/Capacity (A/C)*, and *Overhead/Capacity* (*Ov/C*) ratios. *Throughput* is a measure of system metabolism and describes the size or vigor of this ecosystem. *Ascendency* integrates size with organization (*average mutual information*) of the system; organization represents the number and diversity of interactions between system components. *Development capacity* quantifies the maximum limit of *Ascendency*, and *A/C* is a ratio of the organization of ecosystems. Finally, the *Ov/C* ratio is a measure of system resistance (redundancy) to disturbances (Ulanowicz, 1986, 1997). *Ecopath* describes the flows of matter and energy in an ecosystem at steady state at a particular time, whereas Ecosim is used to perform dynamic simulations based on balanced *Ecopath* models. These simulations represent changes in the flow of biomass over time in response to a disturbance; using the simulations, the propagation of changes in ecosystem food webs can be estimated. *EwE* enables the comparison of ecosystems of different sizes, geographical locations, and levels of complexity (e.g., Monaco & Ulanowicz, 1997; Arias-González et al., 2004; Griffiths et al., 2010). More details and *EwE* referred equations are shown in Appendix B Supplementary Material.

Balancing and calibrating models

For model balancing, the following two criteria were verified: (1) the *ecotrophic efficiencies* (*EE*) <1.0 (Ricker, 1968) and (2) *gross efficiency* (*GE*), which must be physiologically acceptable, with magnitudes <0.3 (Christensen & Pauly, 1993). When these criteria were not met, the biomass and *P/B* values were slightly modified. In the case of the fishes, stony corals, soft corals, and benthic autotrophs, changes were made within ± 1 standard deviation; for the remaining model components, adjustments were made based on values in the literature (e.g., Optiz, 1996; Arias-González et al., 2004; Alva-Basurto & Arias-González, 2014).

Assessment of direct and indirect effects and system recovery time in short-term dynamics

An analysis of direct and indirect trophic relationships was conducted using the routine *Mixed Trophic Impacts* (*MTI*) of *Ecopath* (Ulanowicz & Puccia, 1990), in which the effects of a species or functional group on other compartments of the system were evaluated. The short-term dynamic propagation of direct and indirect effects and the *system recovery time* (*SRT,* as an internal stability/resilience measure) were assessed in response to an increase of total mortality (*Z*) of each compartment equivalent to 30%, considering that *Production* = *Biomass* x Z. It is relevant to indicate that *Z* can be equivalent to just natural mortality [*M*] or *M* + fishing mortality [*F*] for not exploited and exploited species, respectively. This procedure was performed—as a similar perturbation—for each component between the first and second year of the simulation. The propagation of short-term responses was determined by evaluating the biomasses of all the compartments of both model systems in the third year of the simulation, that is, one year after the increase in fishing mortality (sensu Ortiz et al., 2009). As both models (Cayos Cochinos and Median Luna) have more than 20 compartments (species and functional groups), we had to select only the six compartments that presented the strongest effects on the remaining components of each system. This selection was based on a ranking process that assessed the changes of magnitude at the final biomass following a disturbance generated for each species and functional group.

Because historical levels of fishery landings are unknown for either system, we changed the flow-control mechanisms (v_{ij}) that influence the energy transfer rate between two groups and represents top-down, mixed, or bottom-up control (Appendix B Supplementary Material). We performed three flow-control simulations: bottom-up ($v = 1.0$), mixed ($v = 2.0$), and top-down ($v = 6.0$), following the criteria applied by Ortiz (2010) and Ortiz et al. (2013, 2015).

Results

The benthic autotroph group presented the highest total biomass in both systems; biomass was higher at Cayos Cochinos (75% of the total system biomass) than at Media Luna (43%) (Fig. 2; Table 1). With respect to system structure and properties, Media Luna presented lower values of *Pp/R* and *Pp/B* ratios than Cayos Cochinos (Table 2). The *total system throughput* (*TST*) was 220,232 g m^{-2} $year^{-1}$ at Cayos Cochinos and was 71,305 g m^{-2} $year^{-1}$ at Media Luna (Table 2). The Cayos Cochinos ecosystem had a higher *development capacity* (*C* = 627,897 flowbits) and *Ascendency* (*A* = 296,771 flowbits) compared to Media Luna (*C* = 314,370 flowbits, *A* = 96,334 flowbits). Likewise, Cayos Cochinos had a higher degree of development (*A/C* = 47%) and lower resistance to disturbances (*Ov/C* = 53%) than was the case with Media Luna (*A/C* = 31% and *Ov/C* = 69%) (Table 2). Pathway redundancy presented a similar tendency of *Ov/C* ratios (Table 2). The sum of all flow into detritus was higher at Cayos Cochinos

(90,423 g m^{-2} $year^{-1}$) than at Media Luna (17,881 g m^{-2} $year^{-1}$), and Finn's cycling index (*FCI*) indicates that Media Luna reached a higher magnitude (6.95%) compared to Cayos Cochinos. The magnitudes of *average path length* (*APL*), *food web connectance*, and *omnivory index* (*OI*) were also similar for both systems (Table 2). Trophic levels were lower at Media Luna than at Cayos Cochinos as a result of the absence of the groupers functional group, and the mean trophic level of the catch differed between ecosystems, reaching values of 3.6 at Cayos Cochinos and 3.0 at Media Luna (Table 2).

The *Mixed Trophic Impacts* (*MTI*) analysis showed the species and functional groups that induced major direct and indirect effects in the other components were omnivorous fish (OMF), zooplanktivorous fish (ZOF), *P. argus* (SPL), benthic detritivores (DBI), parrotfish (PAF), and soft corals (SFC) at Cayos Cochinos, and omnivorous fish (OMF), herbivorous fish (HEF), benthic-pelagic carnivores fish (BPF), parrotfish

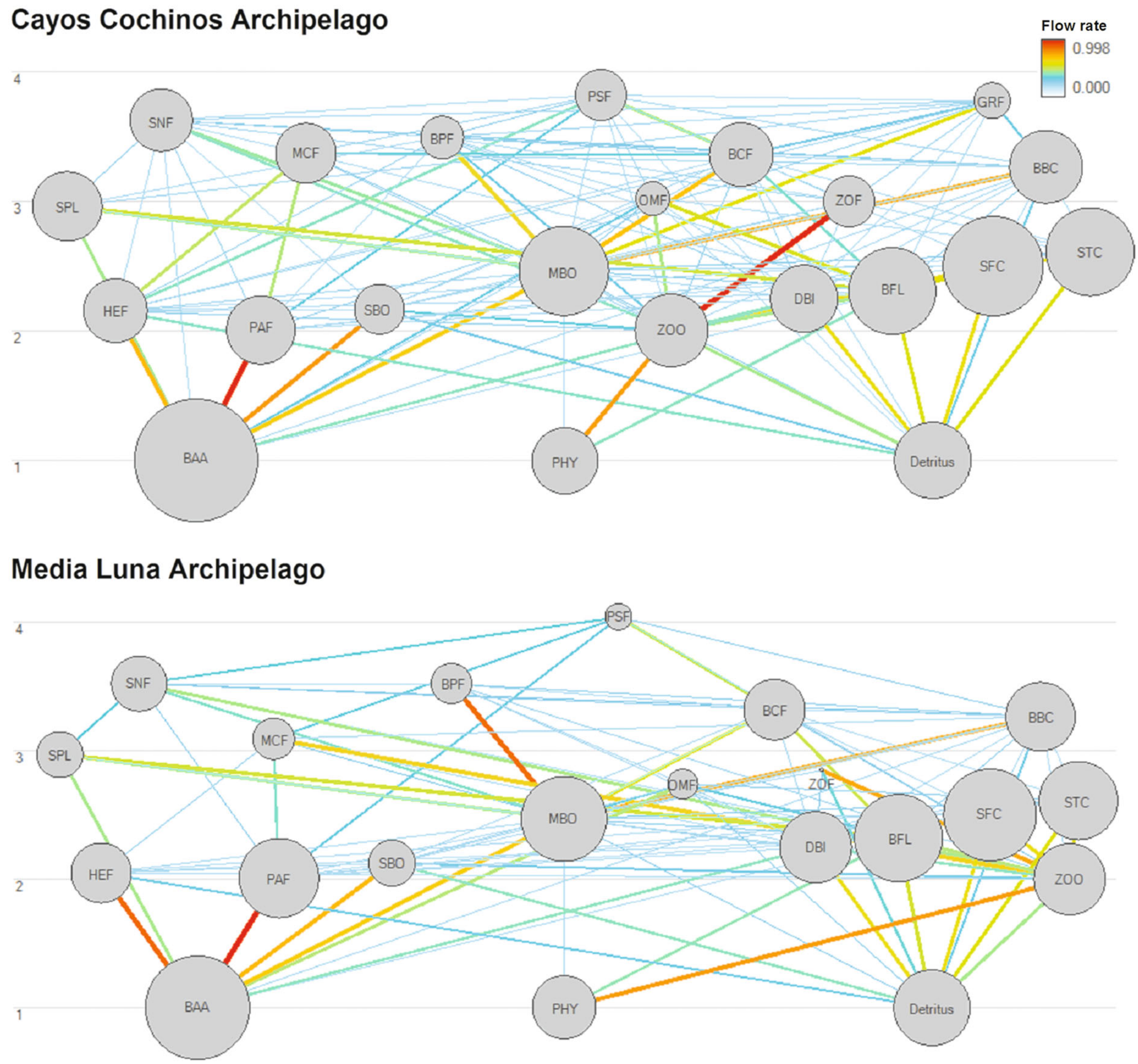


Fig. 2 Food web topology for Cayos Cochinos and Media Luna ecosystems. Vertical position approximates trophic level (*numbers on the left*). The circle size is proportional to the compartment (populations and/or functional groups) biomass (g wet weight m^{-2}). The code in the circle corresponds to the species or functional groups (Table 1)

Table 1 Parameter values entered (in bold) and estimated by Ecopath software for Cayos Cohinos (A) and Media Luna ecosystem (B)

Species/functional groups	*B*	*Ca*	*P/B*	*Q/B*	*TL*	*EE*
A. Cayos Cochinos Model						
(1) Piscivorous fish (PSF)	**9.80**	**4.65E−06**	**0.46**	**1.90**	3.82	0.02
(2) Groupers (GRF)	**2.38**		**0.50**	**4.68**	3.77	0.09
(3) Snappers (SNF)	**27.00**	**8.35E−05**	**1.48**	**7.00**	3.63	0.02
(4) Benthic-pelagic carnivorous fish (BPF)	**4.70**		**2.10**	**17.70**	3.50	0.86
(5) Mackerel (MCF)	**22.00**	**4.67E−09**	**1.86**	**7.00**	3.37	0.02
(6) Benthic carnivorous fish (BCF)	**29.60**	**7.60E−07**	**2.50**	**10.92**	3.36	0.85
(7) Big benthic carnivores (BBC)	**67.32**		**1.43**	**6.40**	3.26	0.91
(8) Omnivorous fish (OMF)	**1.85**		**4.74**	**17.00**	3.03	0.16
(9) Zooplanktivorous fish (ZOF)	**9.60**		**1.90**	**9.94**	3.00	0.60
(10) *Panulirus argus* (SPL)	**52.37**		**2.34**	**8.00**	2.96	0.19
(11) Stony corals (STC)	**263.40**		**2.50**	**8.50**	2.61	0.87
(12) Soft corals (SFC)	**791.04**		**0.08**	**2.50**	2.50	0.30
(13) Medium benthic omnivores (MBO)	**294.30**		**3.50**	**12.00**	2.47	0.97
(14) Benthic filters feeders(BFL)	**246.70**		**3.00**	**12.00**	2.30	0.90
(15) Benthic detritivores (DBI)	**40.16**		**0.80**	**3.85**	2.25	0.89
(16) Small benthic omnivores (SBO)	**9.00**		**4.90**	**125.25**	2.16	0.93
(17) Herbivorous fish (HEF)	**29.61**		**2.50**	**26.45**	2.15	0.88
(18) Parrotfish (PAF)	**47.30**		**2.40**	**20.76**	2.00	0.56
(19) Zooplankton (ZOO)	**72.10**		**63.00**	**215.00**	2.00	0.77
(20) Benthic autotrophs (BAA)	**6300.72**		**13.25**		1.00	0.05
(21) Phytoplankton (PHY)	**37.40**		**409.40**		1.00	0.76
(22) Detritus (DET)	**100.00**				1.00	0.10
B. Media Luna Model						
(1) Piscivorous fish (PSF)	**0.96**		**0.25**	**3.65**	4.04	0.00
(2) Snappers (SNF)	**14.10**		**0.40**	**4.50**	3.52	0.11
(3) Benthic-pelagic carnivorous fish (BPF)	**3.60**		**0.98**	**15.14**	3.52	0.24
(4) Benthic carnivorous fish (BCF)	**24.63**		**0.97**	**10.22**	3.32	0.26
(5) Big benthic carnivores (BBC)	**51.00**		**1.43**	**6.20**	3.26	0.66
(6) Mackerel (MCF)	**4.15**		**2.38**	**9.59**	3.09	0.06
(7) *Panulirus argus* (SPL)	**6.50**	**0.31**	**2.34**	**9.07**	2.97	0.81
(8) Zooplanktivorous fish (ZOF)	**0.02**		**2.43**	**10.96**	2.85	0.00
(9) Omnivorous fish (OMF)	**1.43**		**2.42**	**26.23**	2.74	0.20
(10) Stony corals (STC)	**113.20**		**3.10**	**10.50**	2.61	0.95
(11) Soft corals (SFC)	**392.53**		**0.08**	**9.00**	2.50	0.37
(12) Medium benthic omnivores (MBO)	**215.62**		**2.79**	**9.39**	2.47	0.95
(13) Benthic filters feeders (BFL)	**274.00**		**1.48**	**10.23**	2.32	0.90
(14) Benthic detritivores (DBI)	**65.90**		**0.80**	**3.85**	2.25	0.28
(15) Small benthic omnivores (SBO)	**6.30**		**4.72**	**125.25**	2.13	0.87
(16) Herbivorous fish (HEF)	**21.82**		**0.36**	**24.64**	2.05	0.40
(17) Parrotfish (PAF)	**129.15**		**0.40**	**15.23**	2.01	0.31
(18) Zooplankton (ZOO)	**62.60**		**63.50**	**215.00**	2.00	0.88
(19) Benthic autotrophs (BAA)	**1135.10**		**13.25**		1.00	0.28
(20) Phytoplankton (PHY)	**29.20**		**376.80**		1.00	0.93

Table 1 continued

Species/functional groups	*B*	*Ca*	*P/B*	*Q/B*	*TL*	*EE*
(21) Detritus (DET)	**100.00**				1.00	0.45

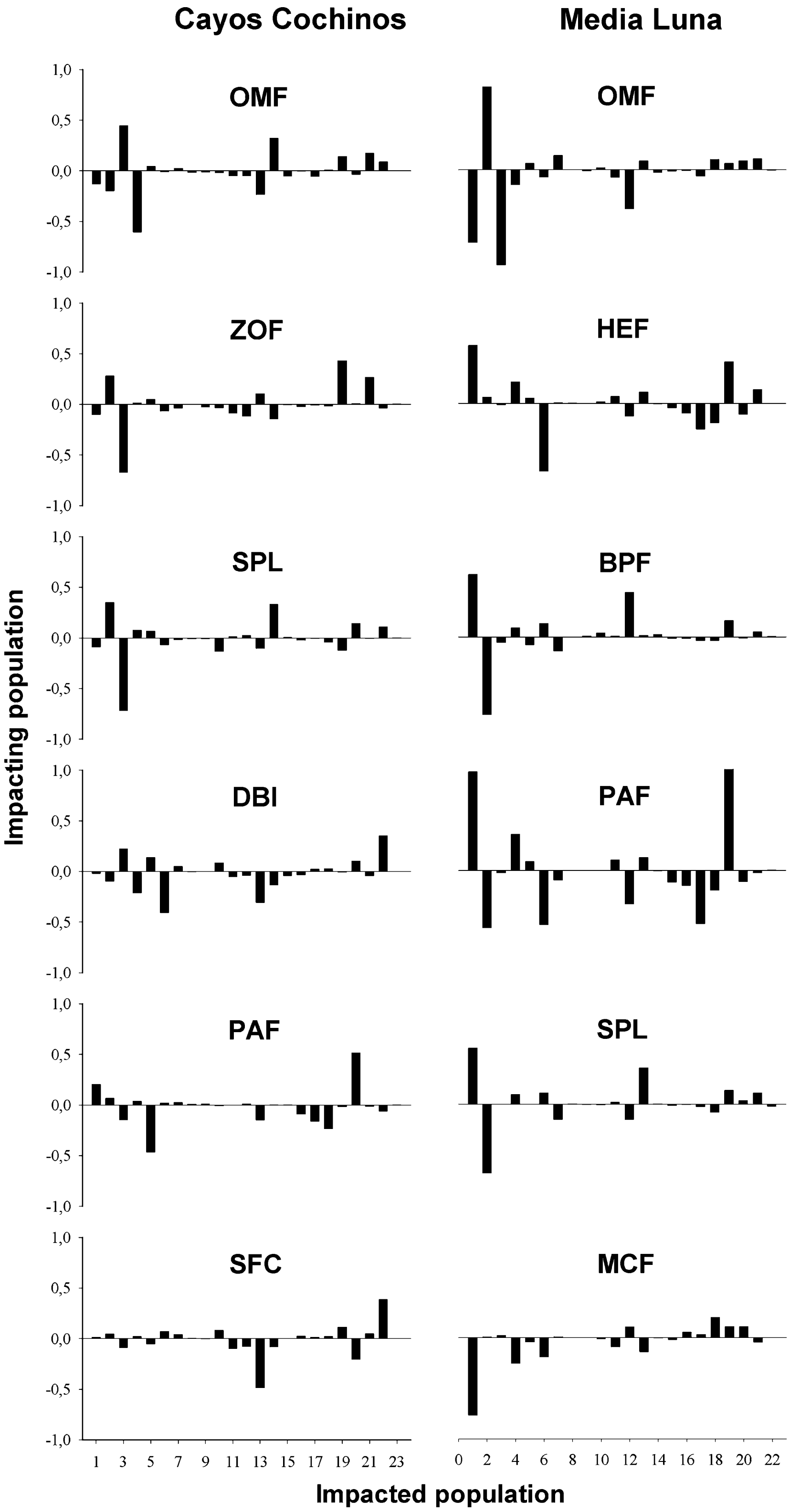
TL trophic level, *Ca* catches (g wet weight m^{-2} $year^{-1}$), *B* biomass (g ww m^{-2}), *P/B* turnover rate ($year^{-1}$), *Q/B* consumption rate ($year^{-1}$), *EE* ecotrophic efficiency

Table 2 Summary statistics after mass balance process by Ecopath and Network Analysis flow indices

Macrodescriptors	Ecosystems	
	Cayos Cochinos	Media Luna
(A) Summary Ecopath statistics		
Sum of all consumption (*Q*) (gm^{-2} $year^{-1}$)	31,013	27,381
Sum of all exports (gm^{-2} $year^{-1}$) (*E*)	81,700	9779
Sum of all respiratory flows (*R*) (gm^{-2} $year^{-1}$)	17,096	16,264
Sum of all flows into detritus (gm^{-2} $year^{-1}$)	90,423	17,881
Total system throughput (*T*) (gm^{-2} $year^{-1}$)	220,232	71,305
Sum of all production (gm^{-2} $year^{-1}$)	106,510	31,684
Mean trophic level of the catch	3.64	2.97
Gross efficiency	1.01E−09	1.20E−05
Total net primary production (gm^{-2} $year^{-1}$) (*P*)	98,796	26,043
Total primary production/total respiration (*Pp/R*)	5.78	1.60
Net system production (gm^{-2} $year^{-1}$)	81,700	9779
Total primary production/total biomass (*P/B*) (gm^{-2} $year^{-1}$)	11.82	10.21
Total biomass/total throughput ($year^{-1}$) (*B/T*)	0.04	0.04
Total biomass (excluding detritus) (*B*) (gm^{-2} $year^{-1}$)	8358	2552
Total catches (gm^{-2} $year^{-1}$)	1.00E−04	3.11E−01
(B) Network Analysis flow indices		
Ascendency (Total) (*A*) Flowbits	296,771	96,334
Overhead (Total) (*O*) Flowbits	331,127	218,036
Capacity (total) (*C*) Flowbits	627,897	314,370
Pathway redundancy (of overhead) (%)	41	49
Ascendency/capacity (*A/C*) (%)	47	31
Overhead/capacity (*O/C*) (%)	53	69
Throughput cycled (exc. Detritus) (gm^{-2} $year^{-1}$)	540	302
Throughput cycled (inc. Detritus) (gm^{-2} $year^{-1}$)	3523	4647
Statistical entropy (*H'*) (Bits)	1.50	3.05
Finńs cycling index (*FCI*) (%)	1.60	6.95
Number of pathways	5805	1491
Average path length (APL) (dimensionless)	6.65	5.65
Connectance index (*CI*) (dimensionless)	0.30	0.26
Omnivory index (*OI*) (dimensionless)	0.21	0.20

(PAF), *P. argus* (SPL) and mackerel (MCF) at the Media Luna reef (Fig. 3). It is notable that omnivorous fish (OMF), *P. argus* (SPL), and parrotfish (PAF) propagated changes in both systems, and the magnitudes of effect were higher in Media Luna (Fig. 3). In the short-term dynamic simulations with *Ecosim*, Cayos Cochinos exhibited major changes under the top-down simulations when the group benthic

Fig. 3 *Mixed trophic impacts* (*MTI*) (direct and indirect) as response to the main impacting functional groups for Cayos Cochinos and Media Luna ecosystems. *Note* the numbers on the x-axis correspond to the species or functional groups of Table 1



autotrophs, snappers, medium benthic omnivores, and benthic filter feeders are fished (Fig. 4). At Media Luna, strong effects were caused by changes to the benthic autotrophs and medium benthic omnivores, especially under the top-down simulations, while smaller to no effects were observed after increasing the mortality of phytoplankton and benthic filter feeders (Fig. 4).

Unfortunately, *system recovery time* (*SRT*) could only be estimated using bottom-up and mixed flow-control mechanisms, as the top-down mechanisms exhibited oscillations (particularly in the Cayos Cochinos model) (Table 3). Likewise, oscillatory responses were also observed for soft corals and zooplankton groups of Cayos Cochinos using the mixed control mechanism. The results obtained from the bottom-up control mechanism suggest that the Media Luna system requires slightly more time to return to its initial condition ($SRT = 10.7$ years under mixed control mechanism) than is the case at Cayos Cochinos ($SRT = 9.3$ years using mixed control).

Discussion

One of the main symptoms of the deterioration of coral reef ecosystems is a significant increase in the abundance of fleshy macroalgae (Jackson et al., 2001; Kramer, 2003; Acosta-González et al., 2013). Fleshy macroalgae hinders coral growth and coral recruitment (Ruiz-Zarate et al., 2003; Bellwood et al., 2004). A loss in coral cover and their three-dimensional structural complexity plays an important role in the settlement potential of fish recruits and provides habitat to many other coral reef organisms (Knowlton & Jackson, 2001; Jones et al., 2004; Graham & Nash, 2013). In Cayos Cochinos and Media Luna, the benthic autotroph group (primarily consisting of fleshy macroalgae) presented the greatest total biomass of all groups. This generally undesirable condition is similar to that reported in several coral reefs of MBRS (Arias-González et al., 2004; Rodríguez-Zaragoza et al., 2012; Acosta-González et al., 2013). In the Caribbean Sea, it has been observed that, with a decline in herbivore populations (e.g., urchins, parrotfish and other herbivorous fish), the cover of fleshy macroalgal species can increase (Hughes, 1994; Jackson, 1997; Jackson et al., 2001; Hughes et al., 2003). These effects are consistent with the results obtained from our *MTI* (Fig. 3; parrotfishes (PAF) and herbivorous fishes (HEF) panels). Likewise, eutrophication and sedimentation promotes the growth of macroalgal species (Lapointe, 1997; Brown, 1997) and limits the growth and recruitment of corals (Bell, 1990; Hunte & Wittenberg, 1992). Eutrophication and sedimentation may affect the coral reef at Cayos Cochinos, given the proximity of the reef to the coast and the sediments, metals, and nutrients (i.e., by products of agriculture) delivered by the Aguan and Papaloteca rivers (Andréfouët et al., 2002; Carilli et al., 2009).

Fig. 4 Dynamical responses of the main impacting functional ▶ group subject to 1 year of increased fishing mortality (between year 1 and 2 of the simulation) under three flow-control mechanisms using *Ecosim*. The biomass responses were obtained for the third year of the simulation. Note: the numbers on the x-axis correspond to the species or functional groups of Table 1

The catches (*Ca*) used in our models were estimates taken from technical reports (Sibaja-Cordero, 2009), and we believe that these were underestimated, since fishing is unregulated in Cayos Cochinos. Even though this activity is practiced exclusively by locals of the archipelago, according to Andraka et al. (2004): (1) Fishes are fished from smaller sizes to the first mature stages, (2) there are few larger or reproductive fishes, (3) overfishing occurs, (4) the fisheries are supported by the recruitment and the rapid growth of some fishes, and 5) the spiny lobster is overexploited. On the other hand, the stock of spiny lobster at Media Luna is shared with Nicaraguan fishermen, and there are no regulations that apply simultaneously to both countries. Despite this limitation, snappers (fished in Cayos Cochinos) propagated the highest impacts of all species when exploited according to our short-term dynamic simulations using *Ecosim* with mixed and top-down controls. The *MTI* also indicates that omnivorous fish, parrotfish, and *P. argus* substantially influenced the other compartments in both systems. Moreover, herbivorous fish also caused major impacts at Media Luna, while parrotfish maintained a strong influence on benthic autotrophs. This herbivory control mechanism has been reported for coral reefs in the Caribbean Sea, where parrotfish and herbivorous fish harvesting provokes a phase-shift from coral to seaweed that affects communities within the ecosystem (Hixon & Beets, 1993; Hughes, 1994; Jackson et al., 2001). Our short-term dynamic simulations partially corroborate this role of the herbivores, and the negative impact on benthic autotrophs generates

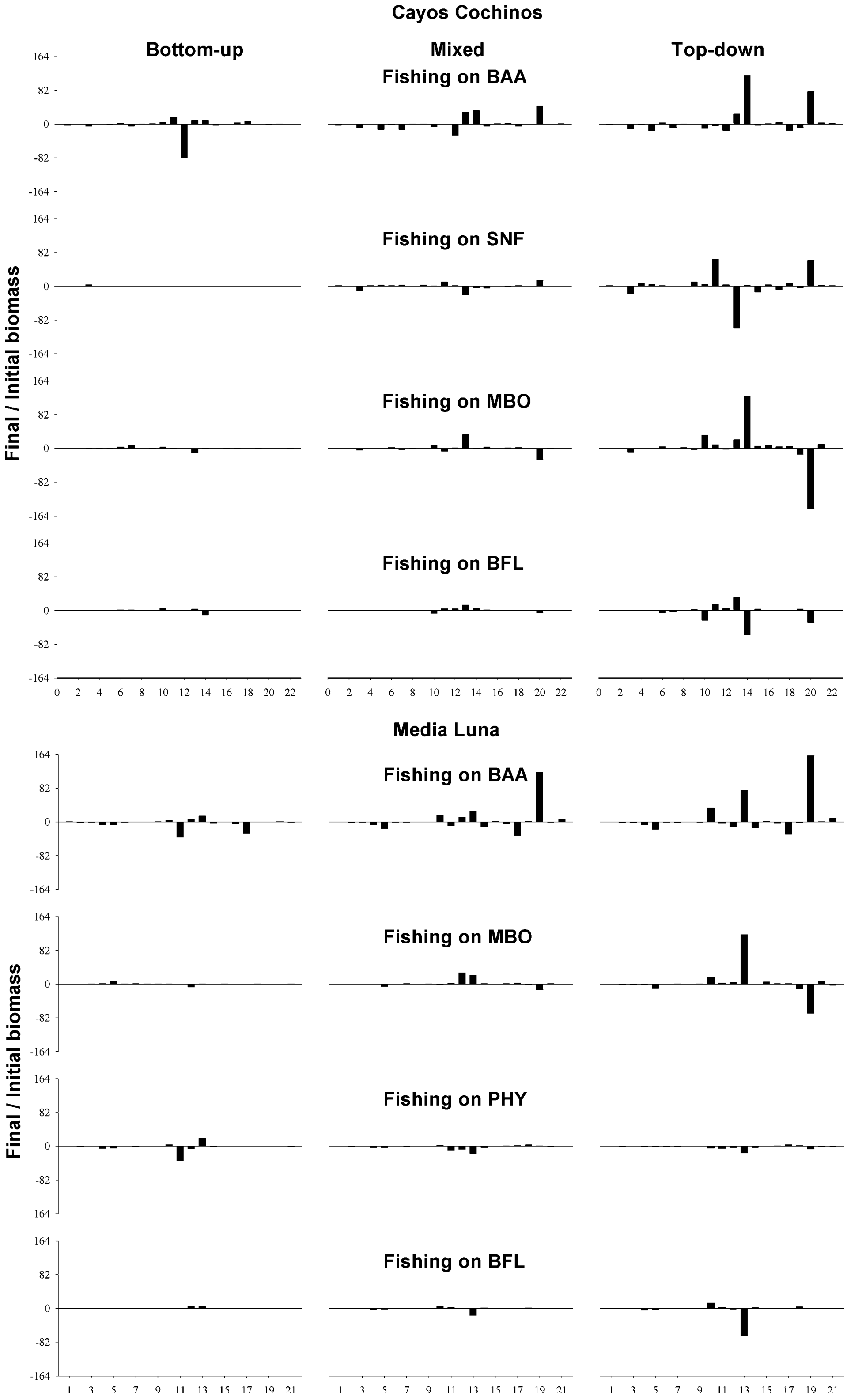

Cayos Cochinos
Bottom-up
Mixed
Top-down
Fishing on BAA
Fishing on SNF
Fishing on MBO
Fishing on BFL
Final / Initial biomass
164
82
0
-82
-164
0 2 4 6 8 10 12 14 16 18 20 22
Media Luna
Fishing on BAA
Fishing on MBO
Fishing on PHY
Fishing on BFL
Final / Initial biomass
1 3 5 7 9 11 13 15 17 19 21

Table 3 Summary of the *system recovery time* (*SRT*) (years) for Cayos Cochinos (A) and Media Luna (B) ecosystems using bottom-up, mixed, and top-down flow-control mechanisms (v)

Ecosystems	Bottom-up control ($v = 1.0$)	Mixed flow control ($v = 2.0$)	Top-down control ($v = 6.0$)
A. Cayos Cochinos model			
Harvest on			
(1) Piscivorous fish	8.90	18.10	Oscillations
(2) Groupers	11.42	14.92	Oscillations
(3) Snappers	10.67	14.30	Oscillations
(4) Benthic-pelagic carnivorous fish	8.67	10.00	Oscillations
(5) Mackerel	7.08	20.25	Oscillations
(6) Benthic carnivorous fish	8.92	14.25	Oscillations
(7) Big benthic carnivores	8.25	12.83	Oscillations
(8) Omnivorous fish	6.83	10.42	Oscillations
(9) Zooplanktivorous fish	7.50	11.80	Oscillations
(10) *Panulirus argus*	7.68	13.08	Oscillations
(11) Stony corals	8.50	16.58	Oscillations
(12) Soft corals	8.50	Oscillations	Oscillations
(13) Medium benthic omnivores	11.75	15.25	Oscillations
(14) Benthic filters feeders	9.67	17.50	Oscillations
(15) Benthic detritivores	8.92	12.58	Oscillations
(16) Small benthic omnivores	6.75	8.92	Oscillations
(17) Herbivorous fish	9.00	14.17	Oscillations
(18) Parrotfish	9.25	13.17	Oscillations
(19) Zooplankton	11.08	Oscillations	Oscillations
(20) Benthic autotrophs	14.17	35.60	Oscillations
(21) Phytoplankton	11.83	47.17	Oscillations
Average	9.30	16.89	–
B. Media Luna model			
Harvest on			
(1) Piscivorous fish	9.10	21.01	37.17
(2) Snappers	10.50	18.75	38.33
(3) Benthic-pelagic carnivorous fish	8.50	11.25	35.83
(4) Benthic carnivorous fish	10.92	21.33	47.30
(5) Big benthic carnivores	10.50	15.83	Oscillations
(6) Mackerel	10.67	22.75	71.30
(7) *Panulirus argus*	11.75	18.17	Oscillations
(8) Zooplanktivorous fish	8.00	5.50	Oscillations
(9) Omnivorous fish	7.58	12.80	Oscillations
(10) Stony corals	11.83	23.83	Oscillations
(11) Soft corals	8.66	40.42	Oscillations
(12) Medium benthic omnivores	13.50	28.17	Oscillations
(13) Benthic filters feeders	12.33	35.42	Oscillations
(14) Benthic detritivores	9.17	17.92	45.33
(15) Small benthic omnivores	7.00	18.00	Oscillations
(16) Herbivorous fish	10.25	18.58	Oscillations
(17) Parrotfish	12.00	30.25	Oscillations
(18) Zooplankton	12.58	34.00	Oscillations

Table 3 continued

Ecosystems	Bottom-up control ($v = 1.0$)	Mixed flow control ($v = 2.0$)	Top-down control ($v = 6.0$)
(19) Benthic autotrophs	17.42	37.35	Oscillations
(20) Phytoplankton	13.50	42.92	Oscillations
Average	10.79	21.72	–

small positive effects on the stony corals at Media Luna reef, mainly in mixed and top-down scenarios.

In theory, the least disturbed ecosystems should be more mature and developed (Odum, 1969; Ulanowicz, 1986). Unfortunately, in this study, the Odum's and Ulanowicz's indices show contradictory trends to indicate which system (i.e., Cayos Cochinos or Media Luna) is more mature and developed. Media Luna appears to exhibit properties of a mature ecosystem, based on a *Pp/R* ratio close to 1 (sensu Odum, 1969; Christensen & Pauly, 1993). This *Pp/R* ratio may be the result of reduced fishing and the lack of riverine inputs in this ecosystem. Additionally, the *Sum of all flow into detritus* (non-assimilated food flows) in Media Luna was considerably lower than Cayos Cochinos. In addition, *Finn's cycling index* (*FCI*) indicates that energy is best used in Media Luna reef. As a consequence of natural and human disturbances, Cayos Cochinos may be a less mature or organized ecosystem, and in turn may be more resistant than the Media Luna reef to perturbations. However, *A/C* ratio and *Ov/C* ratio indicate that the opposite is true. This may be because Cayos Cochinos is a larger system in terms of flow—i.e., *Total system throughput (TST)*—than Media Luna and other coral reefs of the Caribbean Sea (e.g., Mohammed, 2003; Vidal & Basurto, 2003; Arias-González et al., 2004). This is mainly explained by the high accumulation of benthic autotroph biomass that possibly benefited from low herbivory and nutrient supplementation from the Aguan and Papaloteca rivers (Carilli et al., 2009). However, Patrício et al. (2004) noted that systems exposed to high levels of nutrients exhibit a marked increase in *TST* as a result of microalgal blooms. This may be also the case of the Cayos Cochinos reef, but with an increase in the fleshy macroalgae. The latter is correlated with a higher value of *Pp/R*. On the other hand, Cayos Cochinos has both shallow and deep habitats that increase its biodiversity and, in turn, that of the prey. This generates a more complex food web topology in terms of *number of pathways*, *average path length*, and *connectance index*. These features perhaps lead to decreased energy cycling and increased system entropy. Nevertheless, the strong influence of *TST* on *Ascendency* may be negatively correlated with ecosystem maturity (Christensen, 1995). According to *Pp/R*, *sum of all flow into detritus* and *FCI*, Media Luna should therefore be more mature or organized, but less resistant to the impact of fisheries than Cayos Cochinos.

The functional groups, benthic autotrophs, phytoplankton, and soft corals, are the compartments that contributed most in terms of *Ascendency* (sensu Ulanowicz, 1997), suggesting they are the most important to the structure and trophic functioning of both systems. These results correlated with the short-term simulations of *Ecosim*, since these functional groups were the most important for increasing the *System recovery time* (*SRT*), mainly in the mixed scenario. Furthermore, the short-term *Ecosim*'s dynamic simulations also show that in Cayos Cochinos and Media Luna, other species and functional groups increased their *SRT*. For example, when total mortality is increased by 30% in snappers at Cayos Cochinos and in *P. argus* in Media Luna (actually exploited in both reefs), the systems take over 10 years to recover. It is important to note, however, that Cayos Cochinos also takes less time to recover than Media Luna in both the bottom-up scenario and mixed scenario. So this indicates that Cayos Cochinos should be the most resilient system. The most of simulations for *SRT* using a top-down control mechanism showed oscillatory responses, which is explained by the non-linear Lotka-Volterra's behavior of this control (see Walters & Martell, 2004).

This study represents the first attempt to quantitatively estimate trophic interactions of two coral reef ecosystems in the southwestern Caribbean off the Honduran coast. We show that the Media Luna reef is the more mature or organized system, but is less resistant and resilient to the impact of fisheries than Cayos Cochinos. We therefore suggest the implementation of new management strategies in Cayos Cochinos that address not only the exploitation of natural resources, but also other processes, such as the increase of sediment input during the rainy seasons, in order to control seawater eutrophication and fleshy macroalgal blooms. In both reefs, it is also necessary to establish ecosystem-based fishery management strategies, adopting bans for target fish species and spiny lobster, mainly in the Media Luna reef that has no current government protection. However, and despite the fact that *Ecopath with Ecosim* were used to generate models to assess the trophic functioning and development and organization of ecosystems, the limitations of this theoretical framework are well-known. We also therefore suggest that future research should aim to clarify the relative importance of bacteria, DOM, and POM in trophic webs, particularly in the Cayos Cochinos ecosystem. Likewise, these studies should be complemented with the use of qualitative and/or semi-quantitative models that include other types of ecological relationships, as well as the identification of keystone species complexes to further the knowledge regarding ecosystem resistance and resilience under a conservation view.

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