

# Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system

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**Abstract.** The worldwide decline of coral reefs threatens the livelihoods of coastal communities and puts at risk valuable ecosystem services provided by reefs. There is a pressing need for robust predictions of potential futures of coral reef and associated human systems under alternative management scenarios. Understanding and predicting the dynamics of coral reef systems at regional scales of tens to hundreds of kilometers is imperative, because reef systems are connected by physical and socioeconomic processes across regions and often across international boundaries. We present a spatially explicit regional-scale model of ecological dynamics for a general coral reef system. In designing our model as a tool for decision support, we gave precedence to portability and accessibility; the model can be parameterized for dissimilar coral reef systems in different parts of the world, and the model components and outputs are understandable for nonexperts. The model simulates local-scale dynamics, which are coupled across regions through larval connectivity between reefs. We validate our model using an instantiation for the Meso-American Reef system. The model realistically captures local and regional ecological dynamics and responds to external forcings in the form of harvesting, pollution, and physical damage (e.g., hurricanes, coral bleaching) to produce trajectories that largely fall within limits observed in the real system. Moreover, the model demonstrates behaviors that have relevance for management considerations. In particular, differences in larval supply between reef localities drive spatial variability in modeled reef community structure. Reef tracts for which recruitment is low are more vulnerable to natural disturbance and synergistic effects of anthropogenic stressors. Our approach provides a framework for projecting the likelihood of different reef futures at local to regional scales, with important applications for the management of complex coral reef systems.

**Key words:** connectivity; coral reef dynamics; coral reef management; decision support tool; ecosystem model; Meso-American Reef system.

## INTRODUCTION

In the face of increased chronic anthropogenic stress and climate change, the rate of decline of marine ecosystem health is set to accelerate (Halpern et al. 2008). The biodiversity and functioning of coral reef systems around the globe is at particular risk (Hoegh-Guldberg et al. 2007), and the loss of ecological goods and services associated with coral reef ecosystems is likely to have serious social, economic, and cultural

consequences for millions of people in coastal populations (Moberg and Folke 1999, Cesar et al. 2003). There is a critical need to extend existing coral reef management approaches and to adopt novel, cross-disciplinary, and multi-scale methods (ITMEMS 2006, Mumby and Steneck 2008, Sale 2008). Key steps toward improving coral reef management include: (1) understanding the effects of synergistic stressors and then acting to minimize multiplicative impacts; (2) identifying reef areas that are inherently vulnerable to stress and designing management strategies that explicitly consider differences in vulnerability; and (3) considering feedbacks between ecological and human systems. These are

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important considerations for building and maintaining resilience in reef systems (Nyström et al. 2008).

Models are fundamental tools in decision support (Van Kouwen et al. 2008), and stochastic simulation models are of particular value because they facilitate the projection of potential future outcomes under alternative resource management scenarios. However, modeling coral reef systems is inherently difficult given that they are complex systems with myriad processes acting across a broad range of scales in space and time (Hatcher 1997, Dizon and Yap 2006). In distilling this complexity to design models targeted for decision support, it is important to identify the indicators of reef state that are of most interest to reef managers. These include: hard coral and algal covers; fish biomass; biodiversity; disease prevalence; and the abundance of “special interest” species such as turtles (Kramer 2003, McField and Richards-Kramer 2007). Projecting changes in these variables and identifying potential nonlinear responses to linear changes in disturbances and the magnitude of anthropogenic forcings informs both decision making for management and general understanding of coral reef dynamics.

Simulation models of coral reef ecosystems have been used to examine ecological responses to changes in the intensity and nature of fishing, grazing pressure, disturbance events (storm damage, coral bleaching, and crown-of-thorns starfish outbreaks), nutrification, and sedimentation (McClanahan 1995, McCook et al. 2001, Mumby 2006, Mumby et al. 2006). Limitations of existing models with respect to their application in decision support include: (1) they are usually designed to address research questions for reefs in particular biogeographic regions (e.g., the western Atlantic, Indo-Pacific, or East Africa) and are not readily portable between reef systems, (2) they are not generally instantiated using base maps of the existing location and state of reefs and so cannot resolve real-life spatiotemporal dynamics; and (3) they do not use spatially resolved information to describe larval connectivity. A noteworthy exception is Gray et al.’s (2006) hybrid model for the North-West Shelf of Western Australia, although this modeling framework was not targeted specifically for coral reef systems.

Connectivity of larvae and other suspended particles in marine systems has received significant attention in recent years (Chérubin et al. 2008, Paris and Chérubin 2008, Jones et al. 2009) and is critically important for effective knowledge-based management and conservation. Questions regarding coral reef dynamics and management often relate to connectivity between reefs at regional scales in the order of tens to hundreds of kilometers. For example, will fishing on one reef deplete neighboring reefs of recruits? Will pollutant sources affect nearby and distant habitats? Here, we present a biophysical model of a coral reef system that addresses the issues of geographic portability, spatially resolved larval connectivity patterns, and the need to consider

processes across multiple spatial scales. The model describes dynamics of benthic (corals and algae) and consumer (fish and sea urchins) functional groups from local-scale reef patches ( $500 \times 500$  m) up to regional-scale reef tracts ( $\sim 1000$  km).

Two key objectives in developing our model were: (1) to maintain an underlying model structure sufficiently generic to be portable between biogeographic regions supporting coral reefs, but which will still capture ecological dynamics of interest to coral reef management, i.e., a “minimum realistic” model (*sensu* Fulton et al. 2003); and (2) for model components and outputs to be understandable for nonexperts. Our model is non-equilibrium, and emergent dynamics of interest to research and management are not hardwired into the system. The framework permits us to examine emergent behaviors at a range of spatial and temporal scales. The objective of our model in terms of management applications is to make generic predictions for reef dynamics over timescales of years to decades and to identify trends that manifest at subregional to regional scales. We are not attempting to predict local-scale dynamics at particular sites (which requires the development of local models parameterized for specific sites).

We present a demonstration of our regional-scale model based on a parameterization for the Meso-American Reef (MAR) system. The dynamic history of this region provides a broad range of questions for scenario modeling. Over the past 50 years the MAR has been subject to hurricanes, disease impacts, and spatial gradients in human pressure such as the southward expansion of coastal development in the eastern Yucatan, increased tourism in Belize, and the impacts of sedimentation from coastal runoff in Honduras (Arrivillaga and Garcia 2004). We validate the model using a dual approach; first, we examine how the model behaves over long time series in the absence of forcings (fishing, hurricanes, disease, nutrification, and sedimentation) to assess whether the emergent coral reef structures bear any resemblance to real “healthy” coral reefs in the region. We then compare simulated historical trajectories of reef community structure based on known forcings with measured intermediate and end points of the system. Both the model validation process and emergent behaviors provide useful insights in terms of coral reef function and dynamics.

## METHODS

Our regional-scale model comprises multiple instantiations of a local-scale mean-field model of coral reef dynamics (Fung 2009) that are connected by larval transport (Fig. 1). The behavior of the local model has been evaluated in detail; it realistically captures coral-macroalgal “phase-shift” transitions that are characteristic of coral reefs (Knowlton 1992, Mumby et al. 2007b). Since our regional-scale model is designed to be used in decision support applications for coral reef systems, it is hereafter referred to as CORSET (Coral

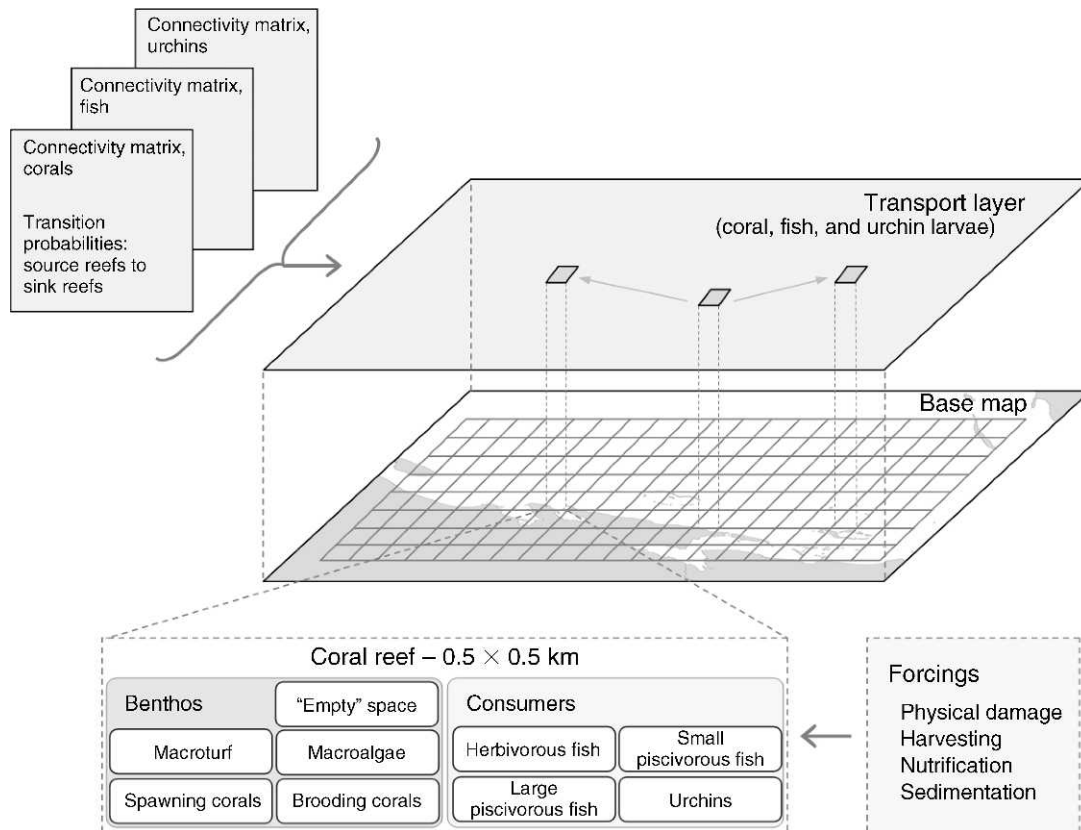


FIG. 1. Structure of the regional model: Coral Reef Scenario Evaluation Tool (CORSET). Eight mean-field equations describing local-scale interactions between functional groups (see Appendix A) are instantiated in each reef cell of a gridded base map. Reef cells are connected through larval transport, which is defined by connectivity matrices of transition probabilities for (spawning) coral, fish, and sea urchin larvae. Fishing, pollution, and disturbance are modeled as external forcings.

Reef Scenario Evaluation Tool; Melbourne-Thomas et al. 2011). CORSET is implemented in the open-source object-oriented Python Programming Language (version 2.5; Python Software Foundation, Hampton, New Hampshire, USA).

#### Model components

Local-scale dynamics in benthic cover and consumer biomass for a shallow (~5–20 m depth) coral reef habitat are simulated using difference equations that are updated over weekly time steps. The set of equations is instantiated in each  $500 \times 500$  m reef cell of a gridded base map. Nine functional groups are modeled: brooding corals, spawning corals, macro turf, macroalgae, grazed epilithic algal communities (EAC), herbivorous fish, small-to-intermediate piscivorous fish, large piscivorous fish, and sea urchins (Table 1). Macro turf refers to ungrazed algal turfs greater than ~2–4 mm in height. The grazed EAC functional group represents areas of reef that are covered by cropped algal turf (less than ~2–4 mm in height), typically growing on dead coral or non-geniculate coralline algae that exerts a constant growth pressure, but is maintained at a low canopy height by fish and sea urchin grazing. The key functional

differences between macro turf and grazed EAC are: (1) EAC can grow into macro turf if grazing pressure is sufficiently reduced, (2) the recruitment rate of coral onto macro turf is lower than the rate onto grazed EAC, and (3) the growth rate of coral over macro turf is lower than the growth rate over grazed EAC. Other benthic organisms such as soft corals, sponges, ascidians, and clams are assumed to make nonsignificant contributions to the dynamics we are attempting to capture and so are not modeled. These organisms, together with sand patches, implicitly contribute some fixed (non-dynamically variable) proportion of actual benthic space. For simplicity, and because of the spatial scale of reef cells ( $500 \times 500$  m), growth of benthic groups across cell boundaries and movement of fish between reef cells are not modeled. We have considered only those fish groups that are reef-associated. The three fish functional groups we model include varying proportions of commercially important species depending on the reef system to which CORSET is applied.

Our aim in defining local-scale ecological processes was both to capture the key dynamic processes of coral reef systems and to distill a set of interactions that are readily parameterized for reefs in different biogeograph-

TABLE 1. Definitions of functional groups modeled, with example taxa for the Caribbean.

Functional group	Description
Brooding corals	Hermatypic coral species with internal brooding of planula larvae followed by release of planulae (e.g., <i>Agaricia</i> spp., <i>Porites astreoides</i> ).
Spawning corals	Hermatypic coral species with broadcast spawning and external fertilization of gametes (e.g., <i>Acropora cervicornis</i> , <i>Acropora palmata</i> , <i>Montastrea annularis</i> ).
Macroturf	Fast-growing, filamentous algae that form patches greater than ~2–4 mm canopy height (e.g., <i>Ceramium</i> spp., <i>Enteromorpha</i> spp.).
Macroalgae	Green, red, and brown algae with larger thallus size and greater structural complexity than macroturf (e.g., <i>Dictyota</i> spp., <i>Lobophora variegata</i> ).
Grazed epilithic algal communities	Benthic cover characterized by non-geniculate coralline algae and dead coral skeletons. For purposes of the model, the most important feature of this functional group is that it is covered by fine algal turf less than ~2–4 mm in height. The low canopy height of this fine turf is maintained by grazing.
Herbivorous fish	Reef-associated fish that feed on epilithic algal communities, macroturf, and macroalgae (e.g., families Acanthuridae, Scaridae).
Small-to-intermediate piscivorous fish	Fish that predate on herbivorous fish and are <60 cm in length. Some fish in this functional group remain small-to-intermediate throughout their lifetime (e.g., some fish from families Lutjanidae, Serranidae), while a certain proportion grow into large piscivorous fish.
Large piscivorous fish	Fish that predate on herbivorous fish and small-to-intermediate piscivorous fish and are ≥60 cm in length (e.g., fish from families Carangidae, Lutjanidae).
Sea urchins	Grazing sea urchins (e.g., <i>Diadema antillarum</i> ).

ic regions. Equilibrium behavior and parameter sensitivity of the local-scale system of equations have been examined in detail for an analogous, continuous-time (differential equations) system (Fung 2009). This continuous-time system (from which our discrete-time system was derived using Euler's method) is outlined in Appendix A together with parameter values specific to the western Atlantic region. Where the values derived for model parameters are ranges based on empirical observations, CORSET selects values from that range at random, i.e., assuming a uniform distribution. We used uniform distributions because of a lack of information regarding the detailed shape of distributions for ecological parameters. In this way, parameter values are randomly selected for each cell and can vary from year to year (to represent interannual variability in ecological processes). Parameters that are defined as yearly rates are scaled to suit the weekly updating interval in the model.

In selecting an updating interval of one week, we faced a trade-off between model run time and mathematical rigor. Small updating intervals reduce the number of mathematical constraints required to keep the model within the biological domain, but are associated with a nonlinear increase in computational cost. We found that CORSET behaved equivalently under daily, weekly, and fortnightly updating intervals, but that monthly and yearly updates were associated with dynamic instability. A weekly updating interval was selected as the optimal compromise between mathematical rigor and computational cost. Weekly updating confers flexibility in event scheduling, although for simplicity and consistency, the version of CORSET presented here does not include seasonality in growth processes, reproduction, recruitment, or disturbances.

#### Recruitment scheme

Recruitment dynamics are modeled explicitly in CORSET, as opposed to Fung's (2009) local-scale representation in which recruitment occurs at fixed rates. The recruitment scheme comprises three connected processes: larval production, larval dispersal (including transport and settlement), and post-settlement processes. Yearly larval production is determined by the standing stock (proportional cover for corals and biomass for fish and urchins) in each reef cell. Because published values for larval production by corals, fish, and sea urchins are uncertain and variable, CORSET is tuned by varying larval production parameters within acceptable ranges derived from the literature (see Appendix B).

Larval dispersal is defined by transition probabilities in the form of connectivity matrices. For the MAR system instantiation of CORSET presented here, connectivity matrices for fish, spawned coral, and sea urchin larvae are derived from Lagrangian stochastic models that incorporate physical (eddy perturbation and diffusion) and biological (vertical movement and mortality) processes (Paris et al. 2007). Connectivity matrices can be generated using proxies such as drifter data for reef systems for which sophisticated connectivity information is lacking. However, there is strong evidence that oversimplified representations of larval transport, in particular the representation of larvae as neutrally buoyant particles, typically leads to overestimates of transport distances (Cowen et al. 2000, 2006). Given progress with several global ocean circulation models (e.g., Smedstad et al. 2003, Weijs et al. 2003, Chassignet et al. 2007, Oke et al. 2008), we envisage that highly resolved hydrodynamic simulations coupled with particle tracking models, which provide connectivity



TABLE 2. Biological parameters used for larval dispersal simulations.

Larvae	Pre-competency (d)	Maximum competency (d)	Mortality (d <sup>-1</sup> )	Spawning season (Caribbean)	Vertical migration	Sensory zone†
Coral larvae (spawning species)	5 <sup>(1,2)</sup>	30 <sup>(1,3)</sup>	0.25	August <sup>(1,4)</sup>	...	...
Fish larvae	15 <sup>(5)</sup>	40 <sup>(6)</sup>	0.1 <sup>(6)</sup>	May <sup>(6,7)</sup>	after 30 d <sup>(6)</sup>	~9 km <sup>(6,8)</sup>
Urchin larvae	30 <sup>(9)</sup>	65 <sup>(10,11)</sup>	0.2	June <sup>(12,13)</sup>	...	...

Note: Superscripts indicate sources: 1, Baums et al. (2006); 2, Hughes et al. (2002); 3, Richmond and Hunter (1990); 4, Mumby et al. (2007a); 5, Paris et al. (2005); 6, Paris et al. (2007); 7, Cowen et al. (2000); 8, Cowen et al. (2006); 9, Eckert (1998); 10, Karlson and Levitan (1990); 11, Morgan and Shepherd (2006); 12, Iliffe and Pearse (1982); 13, Hernandez et al. (2006).

† Sensory zone defines the distance within which larvae can detect, and begin moving toward, settlement reefs.

estimates as output, will soon be available for most, if not all, coral reef regions of the world.

Dispersal of larvae in the MAR region was simulated using linked hydrodynamic and particle tracking modules (Chérubin et al. 2008, Paris and Chérubin 2008). The grid resolution for hydrodynamic data, generated with the three-dimensional Regional Ocean Modeling System (ROMS), was 2 km. Particle tracking was conducted separately for “generalized” reef fish larvae, spawned coral larvae, and sea urchin larvae considering the biological characteristics specific to these groups (Table 2). We defined a “generalized” fish larva to represent both herbivorous and piscivorous fish larvae. As in Paris et al. (2007), we applied a 9-km sensory buffer zone for larval fish denoting their ability to sense and swim toward settlement habitat on reefs (Fisher et al. 2000, Simpson et al. 2005, Gerlach et al. 2007). Fish larvae were also able to migrate vertically from the surface to deeper layers once they reached an age of 30 d, with vertical probability distributions for larvae based on field observations (see Paris et al. 2007). Larval mortality for all groups was included in the particle tracking scheme as a constant process assigned stochastically among larvae in a particular simulation. The larval transport simulations we conducted to inform CORSET provided a unique opportunity to explore differences in patterns of connectivity between functional groups in a coral reef system. Furthermore, we were able to evaluate potential ecosystem-level consequences of these connectivity patterns.

Connectivity matrices for the MAR define transition probabilities between 152 reef polygon “nodes” (source and settlement reefs), with average dimensions of 5 × 10 km (Fig. 2B). Of these polygons, 143 contain reef cells at the 500 × 500 m resolution. It was necessary to eliminate 30 polygons as source nodes because of an artifact of domain truncation at the northern boundary of the modeled system; eliminated source nodes acted as sink nodes only. Mapping of the 500 × 500 m reef cells to polygons was used to accumulate spawned larvae at source nodes and to distribute transported larvae evenly between reef cells within sink nodes (i.e., the model divides larvae arriving at a particular sink polygon equally between all reef cells in that polygon).

The model assumes that settlement of coral larvae is limited by the availability of appropriate settlement

habitat (grazed EAC and, to a lesser extent, macro turf). Brooded coral larvae are assumed to settle within natal reef polygons given short average dispersal periods for the larvae of coral species in this group (on the order of 4 d; Fadlallah 1983). Brooding and spawning coral larvae suffer mortality during the first year following settlement, after which they recruit to adult coral cover. Settled fish and sea urchin recruits are subject to density-dependent post-settlement mortality above a predefined threshold of recruit density (Jones 1990), and fish recruits suffer additional post-settlement mortality in reef cells with ≤10% coral cover (Feary et al. 2007, Holbrook et al. 2008). As for corals, fish and sea urchin recruits enter modeled stocks after one year. The derivation of post-settlement parameters for coral, fish, and sea urchin recruits is detailed in Appendix B.

#### Forcing scheme

We use the term forcings to refer to modeled changes in fishing pressure, hurricane events, disease and bleaching events, nutrification (sensu Szmant 2002), and sedimentation. The scheduling of forcings in CORSET is flexible. For example, hurricanes can be modeled with a defined long-term frequency, but where year-to-year occurrence and category strength are random. Alternatively, hurricanes can be scheduled to occur in particular years with predefined category strengths and to affect particular subregions of the model domain. Here, hurricanes refer to tropical cyclones with maximum sustained wind speeds of ≥33 m/s (Nyberg et al. 2007). Hurricane forcings are modeled as a loss of coral and algal cover (Table 3). Based on Gardner et al.’s (2005) definitions for zones of influence for hurricanes, high-category hurricanes affect a greater proportion of reef cells than low-category hurricanes. Category 4 and 5 hurricanes are assumed to affect all cells within a reef tract (or subregion), category 3 hurricanes affect two-thirds of cells, and category 1 and 2 hurricanes affect one-third of reef cells.

As for hurricanes, disease and bleaching events in CORSET can be set to occur randomly or, in recreating known events, be scheduled to affect particular reef cells at predefined time steps. Coral bleaching and disease forcings invoke a loss of coral cover, while disease in sea urchins results in a decrease in sea urchin biomass. Fishing pressure can be scheduled to increase or

decrease over time in a given model run in particular cells or subregions of the model domain. Total fishing pressure ( $f$ ) is apportioned between herbivorous, small-to-intermediate piscivorous, and large piscivorous fish (see Appendix A).

Nutrification and sedimentation forcings are modeled by scaling ecological processes at the local scale (Table 3). In reef cells affected by nutrification, the growth rate of macroalgae increases and coral larval production decreases. In sedimentation-affected cells, coral growth and the survival of coral recruits decrease while coral mortality rate increases. Reef cells affected by these parameter forcings can be identified in association with nutrient and/or sediment point sources or alternatively the proportion of nutrification/sedimentation-affected cells can increase or decrease over time for a given model run. The model framework provides the capability to include sediment transport by ocean currents; however, sediment transport has not been included in model runs presented here. CORSET does not currently model seasonality in forcings; fishing, nutrification, and sedimentation forcings act year round, while hurricanes and bleaching/disease events occur mid-year.

#### *Meso-American Reef system instantiation*

The spatial extent of this instantiation was  $326 \times 632$  km and a total reef area of  $1342 \text{ km}^2$  was modeled ( $5368 \text{ } 500 \times 500 \text{ m}$  reef cells; Fig. 2). Here, reef area refers to generic coral reef habitat (in the approximate depth range 5–20 m; see Plate 1); the model does not resolve the variability or distribution of different coral reef habitat types within the MAR since our intention is to make broad predictions at regional and subregional scales (and not to predict local-scale dynamics). Reef locations in the MAR region are derived from The Millennium Coral Reef Mapping Project's geomorphologic classification of coral reefs (from 30-m Landsat imagery; IMaRS 2004) and include only those classifications with a high probability of being living coral (forereef, reef flat, barrier reef pinnacle, and shallow terrace, as in Burke et al. [2004]). CORSET assumes that all reef locations in the model domain can support coral cover and that a given reef community will respond in a broadly similar way to a given major forcing.

To facilitate implementation of forcing schedules, the region was divided into five subregions following Kramer and Kramer's (2002) eco-regional planning scheme for the MAR. To validate this instantiation we present model output under two forcing schemes or scenarios. In the first, with all forcings switched off, we assess whether the model is able to produce stable long-term dynamics in which reefs are recognizable as being in a "healthy" state. In the second we use predefined schedules for fishing, hurricanes, disease, bleaching, nutrification, and sedimentation that mimic the known sequence, location, and magnitude of these events. The intention is to assess the capacity to predict the known

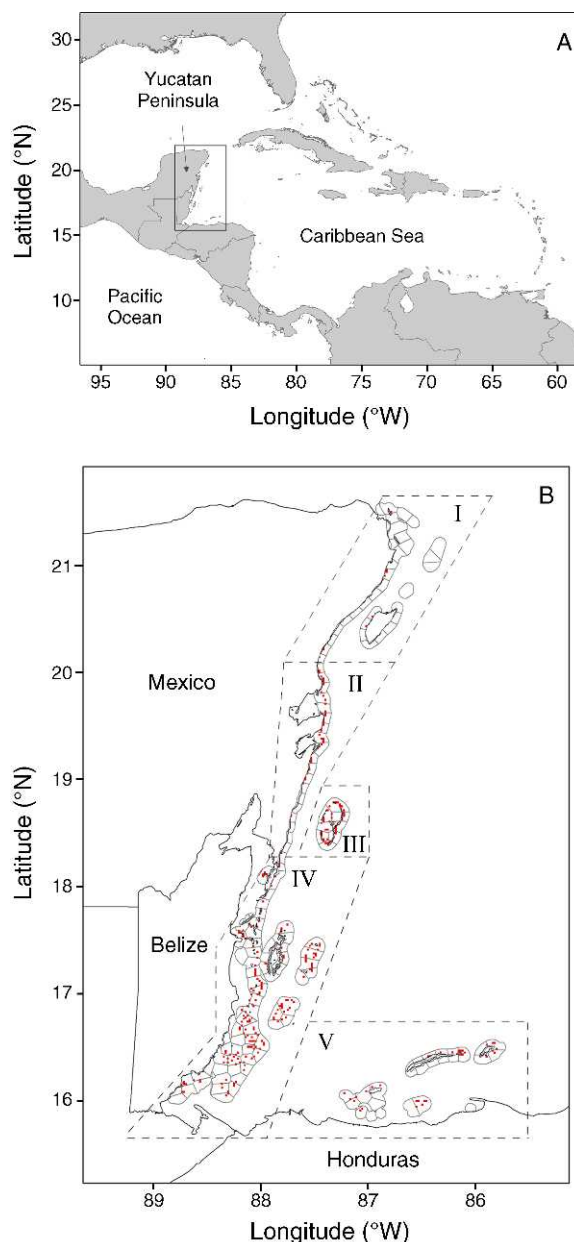


FIG. 2. Spatial extent of the region modeled for the Meso-American Reef system instantiation of the Coral Reef Scenario Evaluation Tool (CORSET). Larval sources and sinks were defined by 143 polygons that enclose  $5368 \text{ } 500 \times 500 \text{ m}$  reef cells (indicated in red). Reef cell locations were extracted from reef distribution maps from the University of South Florida's Institute for Marine Remote Sensing Millennium Coral Reef Mapping Project (IMaRS 2004). Areas delineated by dashed lines indicate the extent of the five subregions: I, II, III, IV, and V.

structure of particular reef areas from a known history of forcings.

To test whether CORSET could capture dynamics typical of a "healthy" reef in the MAR we compared mean trajectories from five runs of the model (in the

TABLE 3. The effects of hurricane, nutrification, and sedimentation forcings on ecological processes in the Coral Reef Scenario Evaluation Tool (CORSET).

Parameter	Derived value(s)	Sources
Factor by which coral cover is reduced by a hurricane disturbance	0.002–0.7	1, 2, 3, 4, 5
Factor by which macroalgal cover is reduced by a hurricane disturbance	0.9	6
Scaling factor for growth rate of macroalgae under nutrification	2–7	7, 8, 9, 10, 11
Scaling factor for coral larval production under nutrification	0.75–1.0	12, 13
Scaling factor for coral growth rate under sedimentation	0.7	14
Increase in coral mortality rate (per year) under sedimentation	0–0.2	15
Scaling factor for survival of coral recruits under sedimentation	0.4	16
Recruitment rate of coral onto macro turf under sedimentation	0	17

Note: Sources are: 1, Bythell et al. (1993); 2, Cheal et al. (2002); 3, Lirman (2003); 4, Gardner et al. (2005); 5, Wantiez et al. (2006); 6, Mumby et al. (2006); 7, Lapointe (1989); 8, Lapointe and O'Connell (1989); 9, Larned and Stimson (1996); 10, Larned (1998); 11, Schaffelke and Klumpp (1998); 12, Loya et al. (2004); 13, Ward and Harrison (2000); 14, Cortes and Risk (1985); 15, Nugues and Roberts (2003); 16, Babcock and Smith (2000); 17, Birrell et al. (2005).

absence of all forcings) with indicator values from the Healthy Reefs Initiative (HRI) Reef Health Index for the Meso-American region (HRI 2008). Five model runs were taken as sufficient because variability in model output between runs was small (due to the parameter selection method described above). Recent observations of reef state in the MAR were used as initial conditions for this “healthy reef” scenario (García-Salgado et al. 2006). We then simulated historical trajectories based on schedules of known and estimated past forcings for the MAR from 1980 to the present (Table 4) and compared these trajectories with observations of benthic cover and consumer biomass values from ecological surveys in the region (Arias-González 1998, UNESCO 1998, Almada-Villela et al. 2002, Steneck and Lang 2003, Roy 2004, García-Salgado et al. 2006, Newman et al. 2006, Brown-Saracino et al. 2007, Marks and Lang 2007, McField et al. 2008; J. E. Arias-González, *unpublished data*). We assumed nominal human impact to reefs in the MAR prior to 1980 and initial conditions for historical trajectories were set within the range for healthy MAR reefs (HRI 2008) in the absence of other information. The increase in coastal development in Meso-America over the past 30 years was modeled as a progressive increase in the number of reef cells affected by nutrification and sedimentation forcings across the

entire region. Given evidence that dissolved nutrients and sediments can be transported significant distances from land-based sources (Andréfouët et al. 2002, Chérubin et al. 2008, Paris and Chérubin 2008, Carilli et al. 2009b, Soto et al. 2009), we assumed that these forcings affected offshore atolls as well as reefs adjacent to the coast.

Data for historical fishing pressure on functional groups of fish modeled in CORSET is lacking. Reports indicate that there has been a steady increase in fishing pressure in the MAR region since 1980 and that large piscivores have been preferentially targeted (Koslow et al. 1994, Harborne et al. 2001, Arrivillaga and Garcia 2004). This increase was represented in our historical scenario as a progressive increase in total fishing pressure from 10% to 100% of the most recent available estimates of fishing pressure for the region (Koslow et al. 1994, Arias-González et al. 2004) over 30 years. We did not consider differences in fishing pressure between reserve and non-reserve areas as our aim was to examine broad trends in model trajectories. Note however that it would be straightforward to use our model to examine more detailed scenarios of marine protected area placement.

We modeled the 1983–1984 Caribbean-wide sea urchin mortality event as a 90% reduction in urchin

TABLE 4. Chronology of modeled forcings for the Meso-American Reef (MAR) system, for the period 1980 to the present.

Year(s)	Subregions affected	Forcing
1980–2007	entire region	increasing fishing pressure and nutrient/sediment inputs from coastal development <sup>(1,2,3)</sup>
1983–1984	entire region	urchin mortality event <sup>(4)</sup>
1986–1990	IV	decline in coral cover due to white-band disease <sup>(5)</sup>
1988	I	Hurricane Gilbert (category 5)
1998	I, II, III, V	coral bleaching event <sup>(3,6)</sup>
1998	IV, V	Hurricane Mitch (category 5)
2000	IV	Hurricane Keith (category 3)
2001	IV, V	Hurricane Iris (category 4)
2002	I	Hurricane Isidore (category 3)
2005	I	Hurricanes Wilma and Emily (category 4)
2007	II, III	Hurricane Dean (category 4)

Notes: Spatial delineations for subregions I–V are indicated in Fig. 2B. Hurricane categories (at the time they intersected reefs in the MAR) were derived from NOAA National Hurricane Center (NHC) archives. Superscripts indicate sources: 1, Koslow et al. (1994); 2, Arrivillaga and Garcia (2004); 3, McField et al. (2008); 4, Lessios (1988); 5, Aronson and Precht (2001); 6, Steneck and Lang (2003).

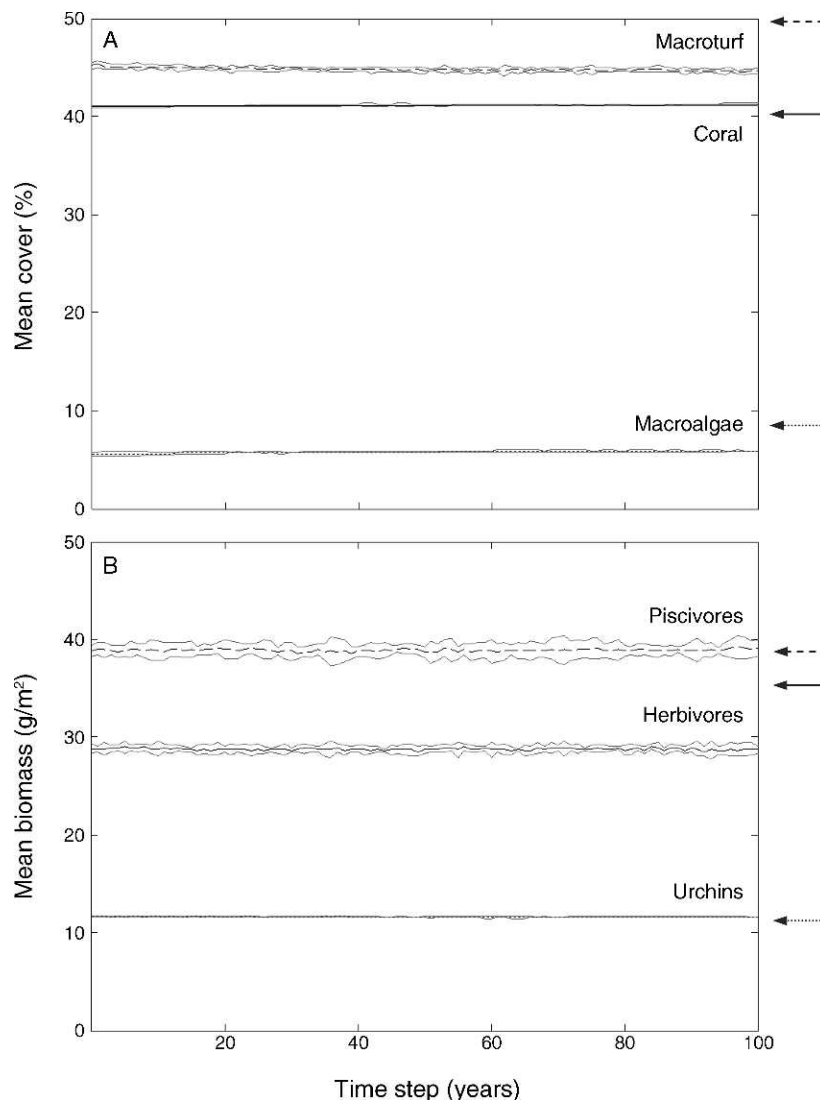


FIG. 3. Model trajectories for (A) benthic and (B) consumer functional groups over 100 years in the absence of forcings (the “healthy reef” scenario). Mean values and 95% confidence intervals from five model runs are presented (confidence intervals indicate variability between runs rather than spatial variability across the region). Equilibration time steps (from initial conditions to quasi-equilibrium) are not shown. Values for piscivores are the sum of model outputs for small-to-intermediate and large piscivorous fish. Arrows indicate expected values for healthy reefs in the Meso-American Reef (MAR) region.

biomass (Lessios 1988) and the decline in coral cover between 1986 and 1990 on the Belize Barrier Reef (subregion IV), which is presumed to have been due to mortality caused by white-band disease (Aronson and Precht 2001), as a 20% reduction in coral cover. The 1995 Caribbean coral bleaching event was not included in the historical scenario since this event caused minimal coral mortality in the MAR; corals recovered despite widespread bleaching (Koltes et al. 1998). We modeled the 1998 bleaching event as 20% overall coral mortality in subregions I, II, III, and V and 50% mortality in subregion IV, based on reported levels of mortality following the event (Steneck and Lang 2003, McField et al. 2008).

## RESULTS

### “Healthy reef” scenario

Model trajectories for benthic and consumer functional groups were stable over long time series (100 years) in the absence of stressors and disturbances (Fig. 3), and the system can be assumed to have converged to (quasi)equilibrium. Average values across the region at equilibrium approximate indicators for reefs of “good” to “very good” health in the MAR (HRI 2008), i.e.,  $\geq 20\%$  coral cover ( $\geq 40\%$  = “very good”) and  $\geq 36$  g/m<sup>2</sup> herbivorous fish biomass ( $\geq 48$  g/m<sup>2</sup> = “very good”). While predicted herbivorous fish biomass was slightly lower than expected, there is still sufficient grazing pressure to constrain algal overgrowth of coral. We



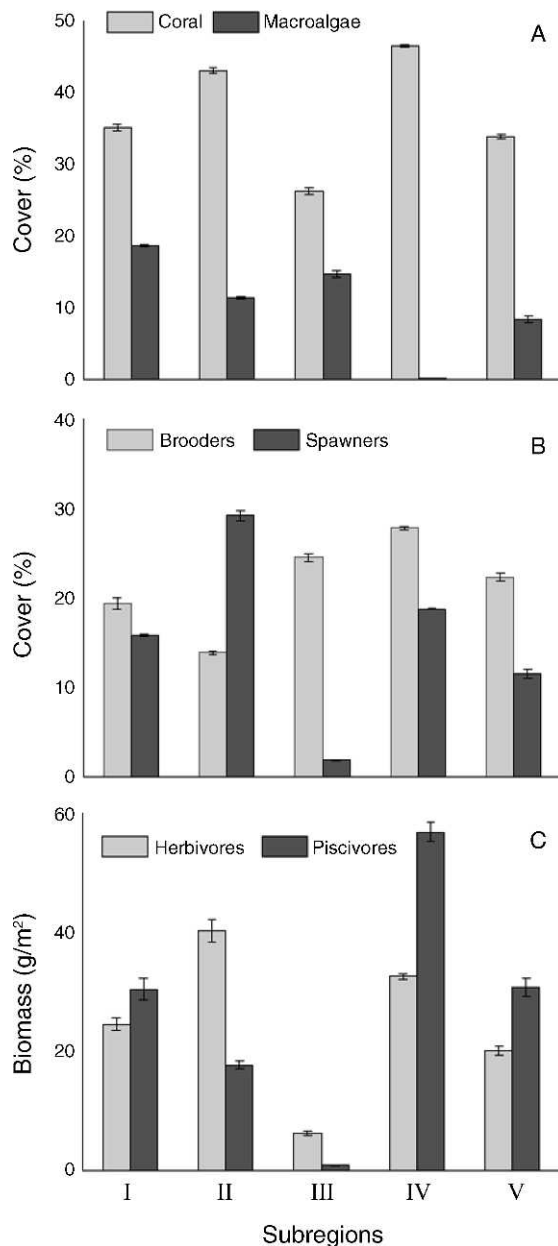


FIG. 4. Average endpoints from the “healthy reef” scenario in each of the five Meso-American Reef (MAR) subregions for benthic and consumer groups from five model runs of 100 years (error bars indicate 95% confidence intervals). Means were taken across subregions for: (A) coral (brooding and spawning corals combined) and macroalgal covers; (B) brooding and spawning coral covers; and (C) herbivorous and piscivorous fish biomass (sum of small-to-intermediate and large piscivorous fish biomasses). There are pronounced differences in predicted community composition between subregions.

tested “healthy reef” scenarios with low-frequency hurricanes (once every 20 years and once every 10 years) and found that these also give stable regional average coral covers of ~40%.

Empirical indicators are not available for algal cover, piscivorous fish biomass, or sea urchin biomass;

however, data for 11 survey sites in Belize (Brown-Saracino et al. 2007) indicate that at reef locations with high mean coral cover ( $\geq 40\%$ ), mean macroalgal and macroalgal covers were 50–80% and 8–15%, respectively. Modeled values for algal cover (Fig. 3A) were at the low end of these ranges. The maximum predicted value for piscivorous fish biomass in the region,  $39 \text{ g/m}^2$  (Arias-González 1998), is assumed to be representative of a healthy reef state and is similar to modeled biomasses for this functional group. Values for sea urchin biomass reported by Brown-Saracino et al. (2007) are in the range  $36\text{--}258 \text{ g/m}^2$ , mostly comprising *Echinometra* spp. However, these values are much higher than biomass estimates for the MAR ( $10\text{--}40 \text{ g/m}^2$ ) reported by Newman et al. (2006), who found *Diadema antillarum* to be the dominant sea urchin species. Our simulated estimates for sea urchin biomass (Fig. 3B) were closer to values reported by Newman et al. (2006). We note that since there is some competition for algal resources between herbivorous fish and sea urchins in the model (based on evidence from Hay [1984] and Carpenter [1990]), we expect that at high herbivore biomass and low algal cover, sea urchin populations will be relatively low.

There was pronounced spatial variation in benthic cover and consumer biomass across the modeled region, with variability arising both within and between subregions (Figs. 4 and 5). This variability was driven primarily by differences in self-recruitment and external larval supply among reefs and could not have been predicted a priori because of the complex nature of recruitment in CORSET. With over  $12 \times 10^3$  possible larval connections between reefs for each of the three dispersed groups (spawning corals, fish, and urchins) and the potential for cascading downstream effects of low or high recruitment (e.g., low recruitment to a particular reef cell will lead to reduced larval output, which will then have consequences for downstream reef dynamics, and so on), the nature of spatial variability cannot be anticipated from model inputs. The model predicted macroalgal cover to be close to zero in Belize (model subregion IV) compared with ~10% average macroalgal cover in other subregions (Fig. 4A). The ratio of brooding to spawning coral cover predicted by CORSET was also spatially variable (Fig. 4B). Due to the structure of the model, brooding corals will be more successful in reef areas to which the supply of spawning coral larvae is low. CORSET predicted this to be the case for the offshore atoll Banco Chinchorro (subregion III), where arrival rates for larvae from spawning corals were only 30% of average rates for the entire MAR region. From connectivity matrices for the MAR, we identified northern Belize and Honduras (subregions IV and V) as the primary source reefs for exogenous supply of coral larvae to Chinchorro.

Average piscivorous fish biomass was notably higher in Belize than in other subregions, whereas total fish biomass was low at Banco Chinchorro (Fig. 4C). Larval

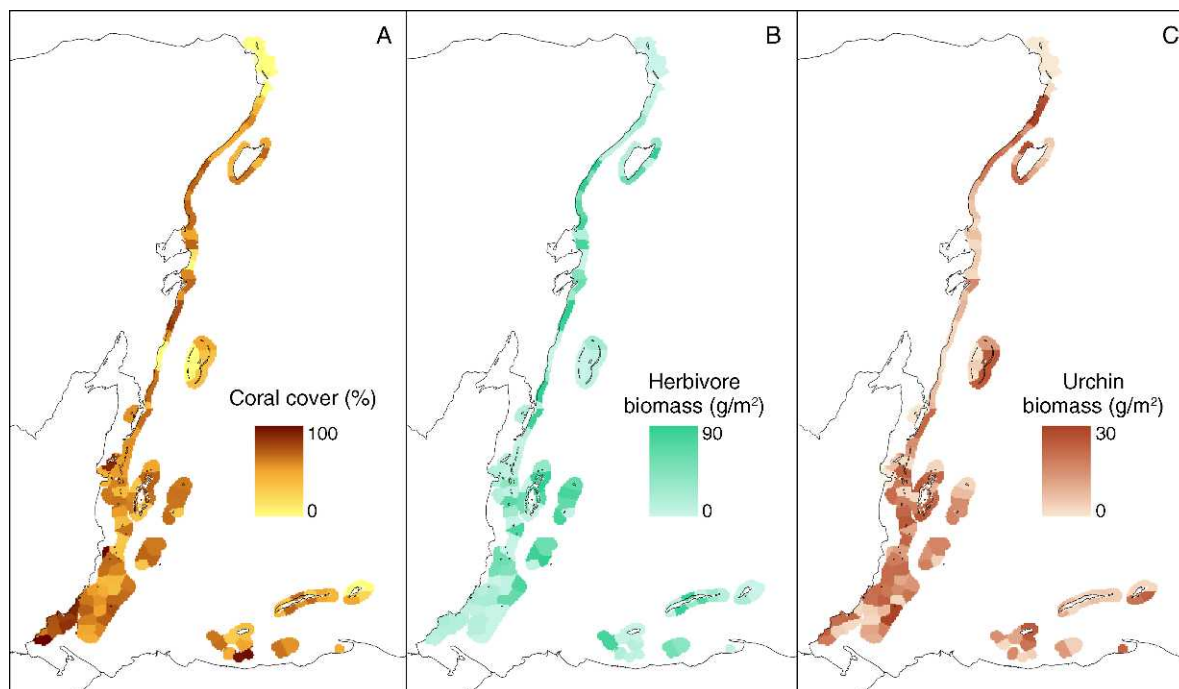


FIG. 5. Spatial variation in modeled (A) coral cover, (B) herbivorous fish biomass, and (C) sea urchin biomass across the Meso-American Reef (MAR) region for the “healthy reef” scenario. For visualization purposes, values displayed are averages across cells within polygons at the final time step of a 100-year model run. Spatial variability within the region is pronounced and results from variability in larval supply and how this affects “downstream” dynamics directly and indirectly.

dispersal simulations predicted low settlement rates of fish larvae on Chinchorro; total settlement for this subregion was only 10% of mean values for the MAR region and Honduras was the predominant exogenous source of fish larvae. The reported abundance of piscivorous fish families at Chinchorro is low, a fact generally attributed to overfishing (Loreto et al. 2003). While our result suggests that there may be other ecological factors at play, namely limited larval supply, CORSET considers only reef-associated piscivorous fish species. Visitations of pelagic predators may have been frequent at Chinchorro in a pristine state.

Patterns of larval connectivity in the MAR were remarkably different between functional groups (Fig. 6). These patterns are the complex outcomes of oceanographic processes and the behavioral characteristics of the larvae themselves. In larval dispersal simulations, sea urchin larvae could spend up to 65 d in the water column and were not competent to settle for the first 30 d of this period (Table 2). This resulted in patchily concentrated arrival of sea urchin recruits to sink locations (Fig. 6C), which is reflected as hotspots of modeled adult biomass (Fig. 5C). In contrast to sea urchin larvae, simulations indicated strong self-recruitment for fish larvae (Fig. 6B, upwards diagonal of matrix), an observation that is increasingly common from field studies and modeling approaches that consider behavioral characteristics of fish larvae (Wolanski et al. 1997, Jones et al. 2005, Cowen et al. 2006). The strength of self-recruitment for

coral larvae was intermediate between that of fish and sea urchins. Predicted larval supply to the northern part of the MAR was depauperate for both corals and fish; sensitivity analyses indicated that this feature is not an artifact of the elimination of some Mexican reefs as larval sources (as described in *Methods*). Comparison of the modeled recruitment ratio for brooding to spawning corals with published values for the Caribbean region indicated that the modeled ratio was within the expected range. The mean ratio for the Caribbean ranges from 3 to 46 for new recruits (Smith 1992, Langmead and Sheppard 2004), while the ratio from CORSET is between 7 and 20.

#### *Historical trajectories*

Model trajectories from 1980 to the present for the five MAR subregions showed reasonable correspondence with available data points for benthic and consumer functional groups (Figs. 7 and 8). CORSET captured the widespread decline in coral cover and increase in algal cover in the MAR over the past 30 years, which has been described qualitatively (e.g., Arrivillaga and Garcia 2004) but is not well documented in quantitative terms. The impacts of hurricane and bleaching events are clearly evident in model trajectories for coral and algal cover (Fig. 7) and it appears that the modeled effects of chronic stressors (fishing, nutrification, and sedimentation) may have hampered recovery of coral cover following disturbance events. Data points



PLATE 1. Example of a shallow coral reef community from Akumal, in the north of the Meso-American Reef region. Photo credit: J. R. Garza-Perez.

for 2004–2005 (García-Salgado et al. 2006) are from sites within marine protected areas, so may reflect healthier reef states than average.

The biomass of large piscivores declined over the simulated time series; however, data are not available to verify modeled biomass for this functional group separately. Our estimates of historical fishing pressure in Belize may have been too conservative as CORSET overpredicted herbivorous and piscivorous fish biomass in this subregion (Fig. 8). Modeled historical piscivorous fish biomass was highly variable between reef cells in Belize, as reflected in large confidence intervals for piscivore biomass in this subregion. Model outputs indicated slightly better recovery of sea urchins in subregions I, III, and IV than in subregions II and V following the major urchin disease mortality event in the early 1980s.

#### DISCUSSION

##### *Model validation for the Meso-American Reef system: implications for coral reef management in the region*

Coral reefs are complex multi-scale systems, with inherent properties of emergence, self-organization, and unstable equilibria that can be difficult to capture using models, but which nevertheless have significant implications for the management and conservation of reef ecosystems. In our regional-scale model (CORSET) we represent a complex reef system using a minimal set of biophysical processes and ecological interactions. We asked two questions of the model using an instantiation for the MAR system: Could it simulate the expected

quasi-equilibrium state of a healthy reef system in the absence of human impacts or disturbance? How would the model respond to a scenario representing our best interpretation of disturbance events and anthropogenic impacts that have affected reefs in the MAR over the past 30 years? Despite its relatively simple structure, CORSET realistically captures broad dynamics for the MAR since 1980. Moreover, our examination of the model's behavior under the "healthy reef" scenario provides insights into inherent differences between subregions of the MAR that may influence real-world dynamics for this reef system.

The spatial variability we observed from the model at local, subregional, and regional scales (Figs. 4 and 5) is unpredictable; it arises from the complex nature of larval connectivity and cascading downstream effects of low or high recruitment. The dispersal and recruitment of marine larvae is fundamental to understanding, modeling, and managing marine ecosystems (Gaines and Lafferty 1995, Sale et al. 2005, Grober-Dunsmore and Keller 2008), yet the study of these processes is a developing science. Here, by explicitly including larval connectivity information in our regional-scale model from sophisticated particle transport simulations that include key elements of larval behavior influencing transport, we are able to directly evaluate some of the potential consequences of larval connectivity patterns across a range of spatial scales.

Our results indicate that reefs at the northern extreme of the MAR model domain receive fewer fish and coral larvae relative to more southerly reefs (Fig. 6). These differences, if real, might confer vulnerability to



repeated disturbance events. In our historical scenario, hurricane and bleaching events that affected reefs in the northern Mexican Caribbean between 1980 and the present were intermittent compared with consecutive disturbance events in Belize and Honduras (Table 4, Fig. 7). However, the frequency of coral bleaching events and the frequency of intense Atlantic hurricanes are likely to increase in coming decades (Donner et al. 2009, Bender et al. 2010). Results from the historical scenario we examined also suggest that the presence of multiple chronic stressors may have hampered recovery of coral populations from disturbance events during the past 30 years (as has been demonstrated from coral growth records in the MAR region; Carilli et al. 2009a). CORSET can be used to decouple confounding effects of disturbance, coastal development, and fishing on reef systems and to assist the design of management strategies that minimize synergistic impacts.

The coral reef community composition predicted by CORSET for the offshore atoll Banco Chinchorro was distinct from other subregions in two respects: the dominance of brooding corals over spawning corals and a relatively low fish biomass (both herbivorous and piscivorous fish). Results from our larval transport simulations for the MAR indicate that the supply of larvae from spawning coral species to Chinchorro is low compared with other subregions and that the primary source reefs for supply of coral larvae to Chinchorro are in northern Belize and Honduras. If results from CORSET translate to real-world dynamics, then damage to reef systems in these “source” locations, particularly in Honduras where further changes in land use practices could lead to severe sedimentation of adjacent reefs (Burke and Sugg 2006), may have significant consequences for the resilience of reefs on Banco Chinchorro. Hence, although the direct impact of sediments from Honduran river inputs is likely to be low on Chinchorro (Paris and Chérubin 2008), indirect impacts ostensibly have the potential to be quite large given modeled larval connectivity strengths. This is an example of how CORSET might be used to examine the potential ecological consequences of scenarios relating to land use change in the MAR region.

Overfishing has generally been cited as the cause of low piscivorous fish biomass on Chinchorro (Loreto et al. 2003). However, our results suggest that exogenous larval supply and standing stocks of herbivorous and piscivorous fish may be naturally low for this atoll. CORSET does not consider the contributions of fish spawning aggregations or juvenile fish nursery habitats to recruitment dynamics. Spawning aggregations of the

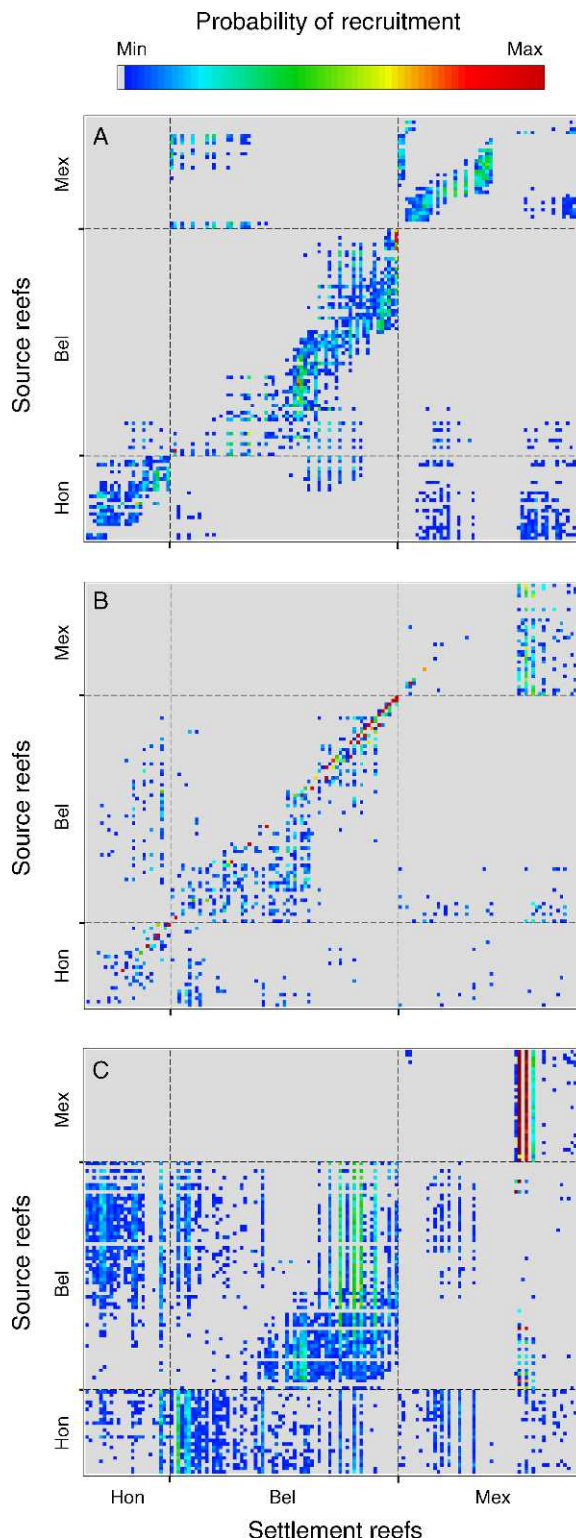


FIG. 6. Matrices of transition probabilities between source reefs and settlement reefs for (A) coral, (B) fish, and (C) sea urchin larvae. The matrix for coral larvae applies to spawning corals only; brooded coral larvae settle locally. Values are standardized relative to the maximum recruitment probability

for each group. Dashed lines indicate spatial delineations for source and settlement reefs in Mexico (Mex), Belize (Bel), and Honduras (Hon). Self-recruitment (represented on the upward diagonal axis of each plot) is strongest for fish and weakest for sea urchins. Predicted coral and fish larval supply is depauperate for some Mexican reefs.



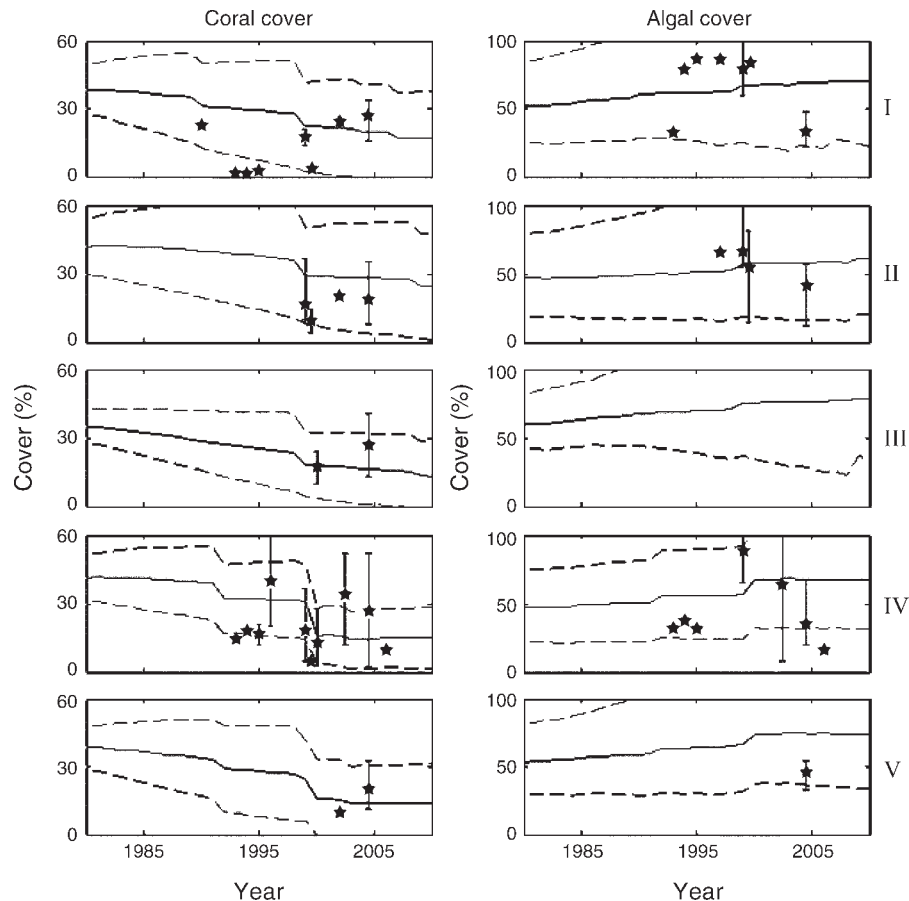


FIG. 7. Comparison of model trajectories for coral and algal cover in the five Meso-American Reef (MAR) subregions from 1980 to the present with empirical observations. Solid lines indicate mean trajectories from five model runs, and dashed lines indicate 95% confidence intervals for coral and algal cover across all reef cells within each subregion. Vertical bars and stars indicate minimum–maximum ranges and average values from empirical observations, respectively. Algal cover refers to macroalgal and macro turf covers combined. Empirical estimates of algal cover in subregion III were not available.

Nassau grouper *Epinephelus striatus* occur throughout the MAR region, including Chinchorro. These aggregations play a key role in population dynamics for *E. striatus*, and there is significant evidence that spawning routes and aggregation sites are highly vulnerable to overfishing (Aguilar-Perera and Aguilar-Dávila 1996, Heyman and Requena 2003). Availability of juvenile nursery habitats, particularly mangrove forests, has been shown to increase the biomass of commercially important fish species in the Caribbean (Mumby et al. 2004). We advocate consideration of features such as spawning aggregations and juvenile nursery habitats, in tandem with our approach, in designing management strategies for reef systems.

#### Limitations and assumptions

Communicating limitations and identifying sources of uncertainty are important considerations in designing and applying complex systems models, particularly where models are intended for use in environmental decision making (Ascough et al. 2008). Key limitations

and sources of uncertainty in our approach are discussed here under three categories (summarized in Table 5): (1) the limitations of using data from larval dispersal simulations, (2) parameter uncertainty, and (3) simplifying assumptions.

Despite being highly informed by physical and biological data, connectivity patterns indicated by larval dispersal simulations should be interpreted with some caution unless validated by data from genetic or tagging approaches. Transport simulations for passive particles in the MAR derived from ROMS have been validated through comparison with ocean color satellite data (Chérubin et al. 2008), but it is important to also include behavioral features of larval particles in estimating connectivity because, typically, estimates of transport of passive particles exaggerate larval dispersal distances (Cowen et al. 2000, 2006). However, connectivity strengths for active larval particles have been shown to be highly sensitive to assumptions regarding biological parameters, particularly larval survival and vertical migration (Paris et al. 2007). In addition, the transport

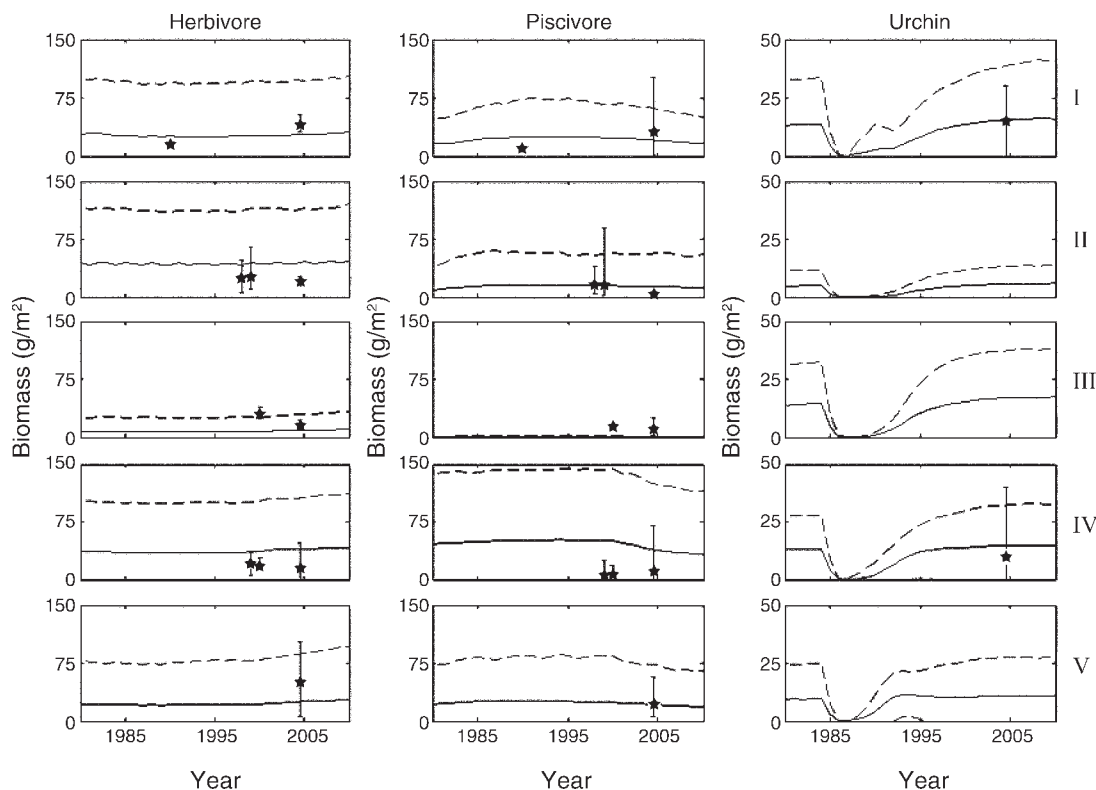


FIG. 8. Comparison of model trajectories for herbivorous fish, piscivorous fish, and sea urchin biomass in the five Meso-American Reef (MAR) subregions from 1980 to the present with empirical observations. Solid lines indicate mean trajectories from five model runs, and dashed lines indicate 95% confidence intervals for fish and sea urchin biomass across all reef cells within each subregion. Vertical bars and stars indicate minimum-maximum ranges and average values from empirical observations, respectively. Piscivorous fish biomass refers to the sum of small-to-intermediate and large piscivorous fish biomasses. Empirical estimates of sea urchin biomass in subregions II, III, and V were not available.

simulations used here to inform CORSET were based on hydrodynamic simulations for only a single year. Given that larval connectivity in nearshore systems has been shown to have a stochastic component in nature (Mitarai et al. 2008, Siegel et al. 2008), we would have greater confidence in interpreting connectivity patterns and model output from CORSET given information from dispersal simulations over multiple years.

Sensitivity analysis provides a means to assess the implications of parameter uncertainty, and a summary

of results from a detailed sensitivity analysis for CORSET is provided in Appendix C. Modeled reef state was most sensitive to rates of coral growth, coral mortality, and piscivorous fish mortality and to rates of coral larval production. While there is some uncertainty in the estimation of all parameters in CORSET, estimates of larval production are particularly uncertain as published data for these values are both sparse and variable and it is likely that larval production differs between biogeographic regions (e.g., because of differ-

TABLE 5. Summary of the limitations and key assumptions of the Coral Reef Scenario Evaluation Tool (CORSET).

General categories	Specific issues
Uncertainty regarding larval connectivity patterns	CORSET relies on connectivity matrices that may be difficult to obtain and/or validate. In particular there is a need to: <ul style="list-style-type: none"> <li>• validate connectivity data derived from larval dispersal simulations</li> <li>• explore sensitivities to assumptions regarding biological parameters used in dispersal simulations</li> <li>• capture temporal stochasticity in larval connectivity</li> </ul>
Parameter uncertainties	<ul style="list-style-type: none"> <li>• uncertainty in the estimation of larval production parameters</li> <li>• uncertainty regarding the nature of spatial variability in parameter values</li> </ul>
Simplifying assumptions	<ul style="list-style-type: none"> <li>• the selection of an appropriate set of functional groups</li> <li>• the use of uniform distributions for parameter values</li> <li>• the lack of seasonality in growth, reproduction, and disturbance</li> <li>• assumptions regarding the characteristics of coral reef habitats and the impacts of forcings (e.g., fishing pressure and nutrification/sedimentation) across the Meso-American Reef region</li> </ul>

ences in species compositions). Given the likelihood that larval production is region-specific, the sparseness of published estimates, and the fact that the model is sensitive to larval production parameters (at least for corals), we tuned the model by varying larval production within acceptable ranges derived from the literature (see Appendix B). Because information is not available on the nature of spatial variability in parameters for the MAR, we assumed random spatial variability in local model parameters. However all forcing parameters and connectivity information was entered in a spatially explicit manner. Notably, CORSET is amenable to input of systematic inter-reef differences in parameter values where such information is available.

As in any modeling study, we have made a range of simplifying assumptions, the key ones being: (1) the selection of functional groups to model; (2) use of uniform distributions for parameters; (3) lack of seasonality in growth, reproduction, and disturbance; and (4) assumptions regarding reef habitat characteristics in the MAR and the spatial variability of major forcings. Selection of functional groups was based on the minimum suite of groups we believed was necessary to capture essential coral reef structure and ecological processes on coral reef systems worldwide, acknowledging that species compositions can be very dissimilar across regions. We selected nine functional groups for which we were able to define a set of interactions that can be parameterized for reefs in different biogeographic regions and which together provide a useful representation of reef state. The local model that defines interactions among these nine functional groups is arguably the most complex yet developed for coral reefs, but is nonetheless a gross simplification of dynamics among the myriad species that inhabit coral reefs. The inclusion of invertivorous fish as a 10th functional group may be appropriate for regions where this group is economically important, given that the model is intended as a decision support tool. Additionally, some management questions may extend to other habitats that are ecologically or functionally linked to coral reefs in some way, e.g., seagrass and mangrove habitats, but which are not currently captured in CORSET. Nonetheless, the architecture of CORSET is structured such that additional habitats and functional groups can be incorporated in a modular fashion.

We used uniform distributions for parameters in the absence of other information regarding the shape of distributions for ecological parameters in CORSET. This may exaggerate or dampen dynamics unrealistically if our parameter ranges (estimated largely from empirical observation) are larger than the typical range for ecological processes on coral reefs. Seasonality was not represented in CORSET because, with a focus on management at subregional scales, the model is intended for simulations over decadal timescales and parameter values represent yearly averages rather than seasonal processes. A disadvantage of this approach is that in real

reef systems ecological thresholds need only be crossed for short periods for them to have long-term consequences; CORSET is limited in its ability to resolve this kind of dynamic change.

Finally, we have made simplifying assumptions about the characteristics of coral reef habitats and the impacts of forcings such as fishing pressure and nutrification/sedimentation across the MAR region. Our approach assumes that all reef cells in the model domain can support coral cover. This is reasonable given the high quality of source data for our MAR base map (i.e., 30-m Landsat imagery; ImaRS 2004) and the fact that only geomorphological classifications with a high probability of being living coral (forereef, reef flat, barrier reef pinnacle, and shallow terrace) were included in the base map (as in Burke et al. 2004). However, our approach is not able to resolve the diversity of reef habitats within the MAR (which according to Kramer and Kramer [2002] is substantial) beyond emergent differences in community structure as determined by differing abundances of modeled functional groups. The spatial representation of major forcings in our historical trajectories, in particular fishing pressure and nutrification/sedimentation impacts, is also simplistic. While the impacts of these forcings do vary in space and time in the model, limited information was available regarding systematic differences in the impacts of these forcings over the MAR region during the past 30 years. As a result, we have been reasonably cautious in our interpretation of spatial patterns in reef state that emerge from the model. While our use of simplifying assumptions is appropriate for the general purposes of demonstrating CORSET, testing the model's behavior and assessing broad-scale patterns in model results, the model architecture allows more realistic patterns of reef distribution and anthropogenic impacts to be built into future instantiations.

Despite these caveats, CORSET was nonetheless able to realistically capture broad dynamics for the MAR and to reproduce changes in variables that are of interest to coral reef managers and other stakeholders. Some of the issues we have raised in relation to limited data availability can possibly be overcome using alternative approaches such as Bayesian belief networks (BBNs; e.g., Wooldridge and Done 2004, Wooldridge et al. 2005, Renken and Mumby 2009), although BBN approaches are perhaps less transparent for non-scientist end users and existing BBN applications for coral reef systems are not spatially explicit. Importantly, the most robust management and associated decision support will attempt to utilize a toolbox of several model types. Even with its limitations, the behavior of CORSET indicates that it would be a useful component of that toolbox.

#### *Potential management applications*

CORSET provides an adaptable framework for scenario projection to support decision making in relation to the conservation and management of coral

reef systems. Potential applications include identifying the synergistic effects of multiple disturbance events that occur simultaneously or sequentially (for example, the degree to which nutrification and sedimentation hamper recovery of coral cover following hurricane disturbances) and the effects of chronic anthropogenic disturbances and/or stressors. CORSET can be used to estimate the likelihood of potential reef futures under different management strategies and hence evaluate risks associated with different courses of action. For example, it could be used to assess whether it is more risk averse to prioritize regulation of fishing activity over coastal development. Our model could also facilitate comparisons of the effectiveness of particular management approaches between regions. Important applied questions such as these are sensibly focused at spatial scales well beyond the scope of conventional experimental and observational approaches.

While the emphasis of our study, and of previous efforts to model coral reefs (e.g., McClanahan 1995, McCook et al. 2001, Mumby 2006, Mumby et al. 2006, Melbourne-Thomas et al. 2011), has been on biophysical scenarios and responses, scenario projection is arguably most informative for management and policy making when it addresses linked biophysical-socioeconomic dynamics (e.g., Gray et al. 2006, Shafer 2007) and captures both socioeconomic and biophysical indicators of reef state (Hatzioles 2006, McField and Richards-Kramer 2007). Agent-based modeling approaches have been applied successfully to model populations of marine resource users and to evaluate strategies for managing multiple extractive activities (Gray et al. 2006). The forcings we applied in our study to recreate an historical scenario for reefs in the MAR (physical damage, harvesting, nutrification, and sedimentation) can be used as “pipes” for information transfer between CORSET and an agent-based socioeconomic model. As a stand-alone model or in tandem with a dynamic socioeconomic model, CORSET has important applications as a tool for decision support in the management of coral reef systems. In the near future we can hope to see scenario projection integrated with existing approaches for vulnerability assessment, marine reserve design, and reef state visualization to inform the difficult task of effective management of complex coral reef systems.

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## APPENDIX A

The local-scale ecological model (*Ecological Archives* A021-064-A1).

## APPENDIX B

Recruitment parameters (*Ecological Archives* A021-064-A2).

## APPENDIX C

Summary of results from sensitivity analysis for CORSET (*Ecological Archives* A021-064-A3).