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A discrete mathematical extension of conceptual ecological models – Application for the SE Florida shelf

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ABSTRACT

Conceptual ecological models (CEM) respond to the need for improved management of natural resources due to increasing scale and severity of human impacts. CEMs, like the EBM-DPSER framework, serve as non-quantitative planning tools identifying stressors and drivers on natural systems, effects and biological indicators best suited to show these effects. A disadvantage of CEMs is their non-quantitative nature restraining users from performing sensitivity and quantitative scenario analysis. Here we develop a quantitative extension of a EBM-DPSER model of the SE Florida shelf based on the assumption that the CEM flow diagrams express as digraphs. It was quantified with transition weights from literature research and local data, turning the digraph into a network. The usefulness of the network extension and its underlying weighted adjacency matrix were verified using monitoring data from the Florida Keys Reef Tract. The network extension was then used to explore outcomes of two different management scenarios. Model results suggest that advanced waste water treatment in SE Florida would increase reef diversity and framework growth and could reduce macroalgae cover while increasing coral cover, fish and shellfish abundance and eliminating phytoplankton blooms. Climate change is projected to have an effect on sea level rise, acidification and bleaching but probably with a minor influence on coral cover, reef framework and diversity – which are already low. Tested scenarios show that the modeled impact of regulation processes can vary profoundly even if the number of arcs and vertices in their largest possible out-tree are comparable. Such a tool extends the power of the conceptual model by adding significant new information and the ability to quantifiably test of hypotheses.

1. Introduction

Increasing scales and severity of human impacts on entire ecosystems call for consistently improving and adapting management of natural resources. Environmental threats and/or degradation can span land and seascapes and sometimes encompass several ecosystems, even entire ecozones. The scale of the necessary management interventions calls for the rapid development and use of unified tools. However, understanding of large ecosystems is frequently incomplete, existing knowledge widely scattered, and even if it can be integrated, the resulting information is frequently so complex to quickly become opaque to managers and decision makers. Consequently, easy-to-grasp and rapidly-developed tools for the development of management frameworks are required such as logical processes for synthesizing, organizing, and prioritizing existing knowledge to give science an effective role in supporting planning, assessment, and management (Ogden et al., 2005a).

In response, conceptual ecological models (CEMs) have been formulated (Rodier and Norton, 1992). In their most basic form, these are non-, or semi-quantitative planning tools visualizing drivers and stressors on natural systems, their ecological effects, and resultant biological attributes or indicators of ecological responses (Ogden et al., 2005a). Total System Conceptual Ecological Models (Ogden et al., 2005b) aim to link stressors to changes in ecosystem characteristics via working hypotheses of cause-and-effect relationships. Outputs are insightful graphs demonstrating linkages in ecosystem functioning that can show how management actions might conceivably percolate through the ecosystem (e.g. Harwell et al., 2010). CEMs have variously been used to define risks, screen for (im)plausible hazards, share knowledge aiming at common understanding, communicate with risk managers and stakeholders as well as define life cycles (Suter, 2006). They have also been used as the basis for quantitative models for scenario analysis (Elliott, 2002; Reiter et al., 2013).

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CEMs are frequently expressed as plots in which compartments within the ecosystem (often represented as boxes) are connected by cause-and-effect pathways (often represented as arrows), that are sometimes modified in their weighting. The analogy to graphs in a mathematical sense (Roberts, 1979; Lauritzen, 1996; Harris et al., 2008) is obvious and graphs have been used in conservation and landscape ecology (Cantwell and Forman, 1993; Bunn et al., 2000; Minor and Urban, 2007). Thus, while the CEM can certainly be used as the basis for the development of any type of model, the easiest step toward quantification might be to simply treat the CEM “conceptual” graph as a “mathematical” graph. Graph theory differentiates several distinct types of graphs, primarily based on the type of connection between its components (the “vertices”) whether at all directed, unidirectional, bi-directional and whether loops are present or not. Depending on the type of graph, different mathematical tools are available (Lauritzen, 1996; Minor and Urban 2007; Harris et al., 2008; Moilanen, 2011; Højsgaard et al., 2012; Nagarajan et al., 2013). Graphs developed in CEM are often complex, with bi-directional edges and/or loops and may therefore be analytically complex. A quite intuitive and computationally simple application of even complex graphs is their evaluation by their adjacency matrix (Roberts, 1979; Lauritzen, 1996; Harris et al., 2008), a representation of the interconnectedness of the ecosystem components (the graph’s vertices) as a matrix. Once the CEM is treated as a mathematical graph, a more quantitative exploration of the CEM becomes possible.

Parallel to the development of CEMs, end-to-end ecosystem models like Ecopath with Ecosim (Christensen and Walters, 2004), OSMOSE (Shin and Cury, 2001, 2004), Atlantis (Fulton et al., 2004), InVitro (Gray et al., 2006), SEAPODYM (Lehodey et al., 2003), APECOSM (Maury et al., 2007) and many others have been developed for marine ecosystems. End-to-end models attempt to include all major relevant processes in a system, including human and abiotic components as well as physical and biological processes (IMBER, 2005; Travers et al., 2007). Their spatial and temporal scale often spans several orders of magnitude (Fulton, 2010). End-to-end models are expanding to include multiple trophic levels, nutrients and biogeochemical cycling, a higher number of species groups, climate forcing, environmental variability and impacts of human activities (Fulton, 2010). Fulton et al. (2011) argues that identifying the critical processes, components and scales of a system is needed to obtain an integrated view of system level issues and management options. Therefore end-to-end ecosystem models can be powerful tools for managers, however, they are often forbiddingly complex and not easily adapted “on the fly”.

Here we develop a greatly simplified and easily applied, yet fully quantitative end-to-end ecosystem model of the SE Florida coral reefs based on the mathematical exploitation of a conceptual graph. As a first step, a CEM was developed using input from other scientists, federal and state agencies experts and managers, non-governmental environmental organizations, private industry stakeholders and the public. The resulting qualitative end-to-end model was used for identifying key system components and processes (Fulton, 2010). In the next step, we treat the CEM as a digraph in the mathematical sense and assign positive and negative signs to each connection (arc) which allows a quantitative assessment through its adjacency matrix (Roberts, 1979; Harris et al., 2008). In the third step appropriate edge weightings (representing the influence of one ecosystem component on the other) were developed for each arc, which turns the digraph into a network (West, 2001) and the qualitative model into a quantitative one. We call this the network approach, since the directions of interactions on the graph are specified, as are their quantitative weights (Dale and Fortin, 2010). The weighted adjacency matrix of this network can then be used to determine how well our network models the reef system of the SE Florida shelf. Once the network represents the processes on the reef adequately enough, the model makes it possible to trace changes made to the “Driver” (the processes affecting the ecosystem) to quantifiable changes in “State” variables (the components of the ecosystem). Thus, scenario analysis becomes possible with a minimum of mathematical and computational complexity.

Our CEM is based on the EBM-DPSER (Drivers, Pressures, States, Ecosystem Services, Response) approach which is a modification of the DPSIR (Kelble et al., 2013) and includes humans in every element of the framework. “Responses” (R) can be initiated by both changes in “State” (S) as well as changes in “Ecosystem Services” (Ault et al., 2012). The weighted adjacency matrix based on the EBM-DPSER graph was populated using literature data and/or observations, where available. We then demonstrate the use of the model for two potential management scenarios.

2. Methods

The study site is one of the USA’s shallow coral reef complexes spanning from Dry Tortugas to Martin County, Florida, a threatened tropical coastal and marine environment adjacent to an urban human population of ∼6 million residents (Banks et al., 2008) and therefore of special management relevance. To develop the CEM, we used the EBM-DPSER (Drivers–Pressures–State–Ecosystem Services–Response) framework (Kelble et al., 2013); a slightly modified form of the DPSIR framework developed by the European Environmental Agency (EEA, 2001). “Drivers” (D) exert “Pressures” (P) on the environment and, as a consequence, the “State” (S) of the environment changes. This impacts the “Ecosystem Services” (E) provided to the human community. Changes in “State” (S) or “Ecosystem Services” (E) may lead to societal “Responses” (R) that feed back to the “Drivers” (D), “Pressures” (P) and “State” (S) (Kelble et al., 2013).

The EBM-DPSER model (Fig. 1) was developed within the Marine and Estuarine Goal Setting for South Florida project (MARES) for Southeast Florida coral reefs (Nuttle and Fletcher, 2013). The model was developed considering regional, social, political, cultural, economic and public health factors next to ecological variables. The goal of MARES was to reach a science-based consensus about the defining characteristics and fundamental regulating processes of a South Florida coastal marine ecosystem that is both sustainable and capable of providing the diverse ecosystem services beneficial to society. The graphical output of the EBM-DPSER model consists of boxes representing the different elements of the model and arrows showing the influences between these elements. The analogy to the vertices and arcs in a digraph in a mathematical sense is obvious (Højsgaard et al., 2012; Harris et al., 2008; Lauritzen, 1996; Roberts, 1979). One goal of this CEM is to define which elements of the ecosystem are affected by changes in management. While EBM-DPSER models lend themselves very well to the identification of these elements, determination of actual levels of change is aided by quantification of the model. This step was undertaken by weighting the links between the elements of the digraph creating a network and its expression as the underlying weighted adjacency matrix (Dale and Fortin, 2010; Roberts, 1979). This allows quantitative statements aimed at finding fundamental regulating processes of the ecosystem and comparing different management options.

The extension of the EBM-DPSER-type model to a network followed three steps: conversion of the model, validation, and production of different scenarios using the model.

2.1. Conversion

In a digraph, every link (arc) between the elements (vertices) is directed and can be weighted (given a numerical value) or signed (given a ± weight), which allows a quantitative assessment through

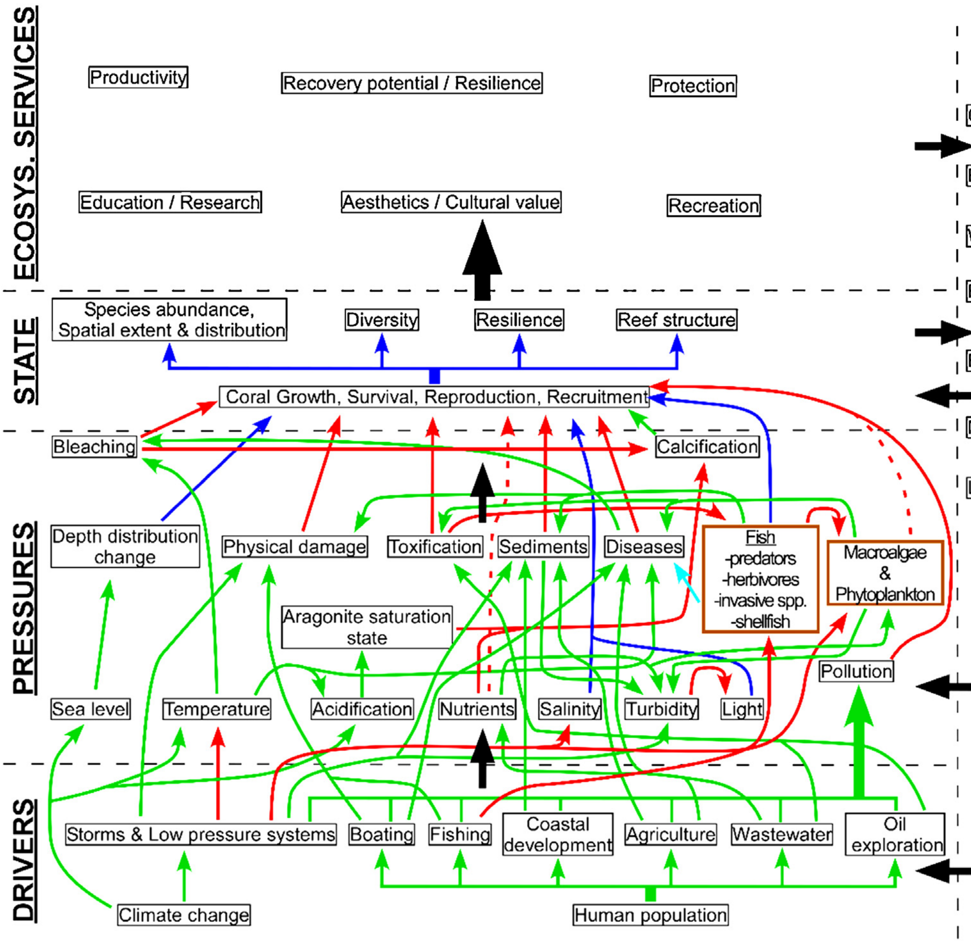
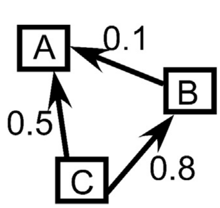


Fig. 1. DPSER model of the Coral reef and Hardbottom for the Southeast Florida Shelf. Green arrows represent positive relationships (increase in vertex 1 leads to increase in vertex 2), red arrows represent negative relationships. Relationships drawn with dark blue arrows are of unknown sign and the relationship in turquoise is debatable. Fish and Macroalgae are in brown boxes since they represent state elements of other CEMs in the MARES project but are here part of the pressures since these CEMs are focusing on Coral reef and Hardbottom. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

its adjacency matrix (Roberts, 1979). Weighted digraphs can also be referred to as networks. A weighted adjacency matrix (*WA*) is the linear algebraic representation of the network, where each position a_{ij} is weighted 1 (or a multiple/fraction thereof) if a connection exists between the components, 0 if none exists (Fig. 2).



Network

		To		
		A	B	C
From	A	0	0	0
	B	0.1	0	0
	C	0.5	0.8	0

Weighted adjacency Matrix

Fig. 2. A network and its weighted adjacency matrix.

The adjacency matrix can be used to explore connectedness, walks, distances, and vertex degree (which expresses how many other vertices it influences due to the number of its incident edges). Since the graphs used in this paper are directed, the matrix is not symmetric. To obtain a matrix, vertices and their weights on the digraph have to be measurable. While the elements of the EBM-DPSER referring to "Ecosystem Services" and "Responses" are difficult to measure, its "Drivers", "Pressures" and "Ecosystem States" can be quantified with relative ease. Only the latter were included and our model therefore is only valid for them. Two adjacency matrices, which can be exploited for different management-relevant information, can be generated. These are an adjacency matrix (*A* matrix) consisting of ones and zeros (1 where connections exist, 0 where there are none) based on the digraph, and a weighted adjacency matrix (*WA*-matrix), which is based on the network and defines the interaction strength among the various vertices (i.e. the influence of vertices on each other via the spanning edges).

In a first step, a sign (±) was giving to every arc in the EBM-DPSER model. During this process, two vertices (Oil Exploration & Pollution) and eight arcs were excluded from the EBM-DPSER model since there either was no literature found that dealt with this process, the process was already incorporated into another arc, or the effect of it was very minor in SE Florida. They were therefore considered not to be of major relevance to the system.

Table 1
Complex relationship between macroalgae and coral cover (Bell and Elmetri, 1995; Connell et al., 1997; Done, 1992, 1997; Done et al., 1997; McCook, 1999).

		Eutrophication	
		Yes	No
Disturbance leading to coral cover decline	Yes	Coral cover decreases, macroalgae colonize free space	Coral cover decreases, corals recolonize free space
	No	Coral cover stays stable	Coral cover stays stable

The complexity of the competition between macroalgae and corals (Table 1) was not captured in the EBM-DPSER model, for this reason the vertices "Phase shift" and "Coral cover recovery" were introduced to the digraph. The vertex "Phase shift" is influenced by the nutrient level, modeling the influence of eutrophication on the macroalgae–coral interaction (see Fig. 3, year 1 steps 3 and 4). A high value in the vertex "Phase shift" leads to macroalgae overgrowing all area lost by corals and macroalgae the previous year while macroalgae will not overgrow the area lost if "Phase shift" is low, leaving the space free to be recolonized by corals. This was modeled by the two arcs leaving "Phase shift". Coral recolonization depends on multiple other factors next to eutrophication, therefore the vertex Coral cover recovery was introduced into the model. The vertex "Coral cover" recovery has a high value if no factors inhibit coral recolonization, leading to a 1.79% increase in "Coral cover" in the *WA* matrix. This growth rate was based on Connell et al. (1997); coral cover without human disturbance recovered by 1.79% of total bottom area per year after a disturbance. The introduction of these vertices concluded the conversion from the EBM-DPSER model to a digraph with an underlining adjacency matrix.

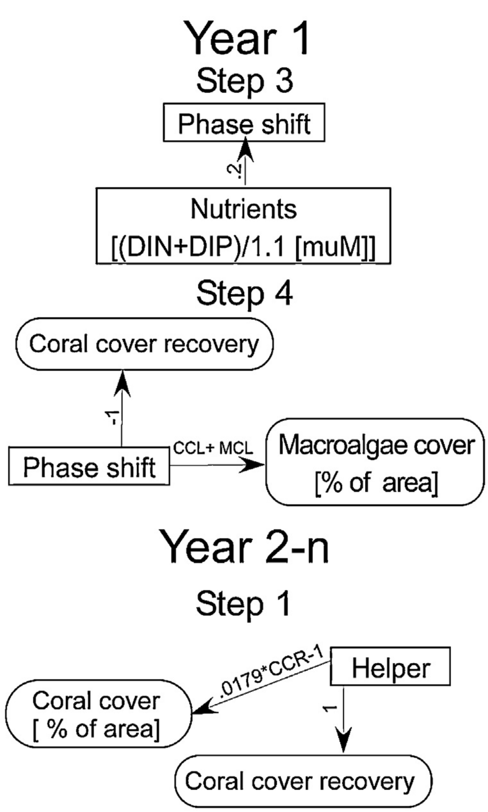


Fig. 3. Modeling of the complex relationship between coral cover and macroalgae cover. Dependent on the nutrient level either macroalgae or corals recruit to the freed space by coral and algae mortality. This is modeled by the vertex Nutrients influencing the introduced vertex Phase shift: the higher the nutrients level the higher the value for Phase shift. In the next model step, two arcs originate from Phase shift, one toward Coral cover recovery and one toward Macroalgae cover. The higher the level of Phase shift the lower the value for Coral cover recovery and the higher the increase in Macroalgae cover. In the first step of next years model run, Coral cover is increased dependent on the value of Coral cover recovery of the year before through the arc (Helper, Coral cover). Additionally, the arc (Helper, Coral cover recovery) gives the vertex Coral cover recovery a starting value of 1 for this new model cycle. Table 4 explains the acronyms used in this figure.

Interactions (edges) between ecosystem components (vertices) are of interest, so walks (i.e. sequence of interactions,) and their distances (i.e. lengths, like eccentricity, the greatest distance of a given node to any other) may help to identify parts of the network that are of particular importance/interest. The weighted adjacency matrix can be altered to represent the influence of vertices on others, as if defining "wins" in a tournament (coded 1; Roberts, 1979). A win represents a change in the value of an adjacent vertex based on the pulse. For example, "population" may increase "pollution", a win for "population", and "pollution" may decrease "Coral cover", a win for "pollution" but also, over distance 2, for "population". Matrix *S* (Harris et al., 2008) identifies influential vertices that may dominate the network and be key drivers:

$$S_k = A + A^2 + A^3 + \cdots + A^k, \quad (1)$$

where *A* is the adjacency matrix.

Row-sums of *S* show walks of distance *k* from any vertex, which is number of vertices influenced. Vertices influencing many others (i.e. many walks at any distance) may be key to the system and can be quickly found by Eq. (1). Alternatively, walks with short distance may have very strong effects, based on edge weights, but this must be evaluated with the weighted matrix (see below). Many algorithms (like spanning trees, path and centrality analyses, etc.; Estrada and Bodin, 2008; Urban et al., 2009; Moilanen, 2011) are available for definition of vertex influence, but Eq. (1) is easily implemented and suffices for present needs. All operations were executed on the *A* matrix, which represents the original flow and connectivity of the conceptional diagram. Furthermore the number of vertices and arcs in the largest possible out-trees from the vertices Climate change and Waste water were counted. An out-tree is an oriented tree in which all vertices are reachable from a single vertex, the largest possible out-tree consists of all vertices which are reachable from a single vertex. The out-trees for both the vertices Climate change and Waste water were drawn and then the number of vertices and arcs present in them were noted.

In contrast to the purely conceptual model and above evaluation, an appropriate time step is needed for forecasting and scenario-development, which was considered one year. Forecasts are achieved by multiplying a vector **v** of input ecosystem states by matrix **WA**. This changes states in **v** by the processes assumed to act at **A**'s vertices and results in a vector of modified ecosystem states. By adding an input vector **i** to the input state vector **v**, a pulse (or change) can be introduced at any chosen state:

$$\mathbf{WA} * (\mathbf{i} + \mathbf{v}(\text{input})) = \mathbf{v}(\text{output}) \quad (2)$$

However, a single multiplication of the input vector with the weighted adjacency matrix did not lead to a response in all output states, rather, only after six multiplications had the initial input (pulse) traveled through the model with the desired effects. If one model run (i.e. one multiplication) had been considered a single year, 6 such years would have been needed until the effects of all "Drivers" had effects on all output states (Fig. 4). However, they are known to affect the state of the reef within the same year. Therefore

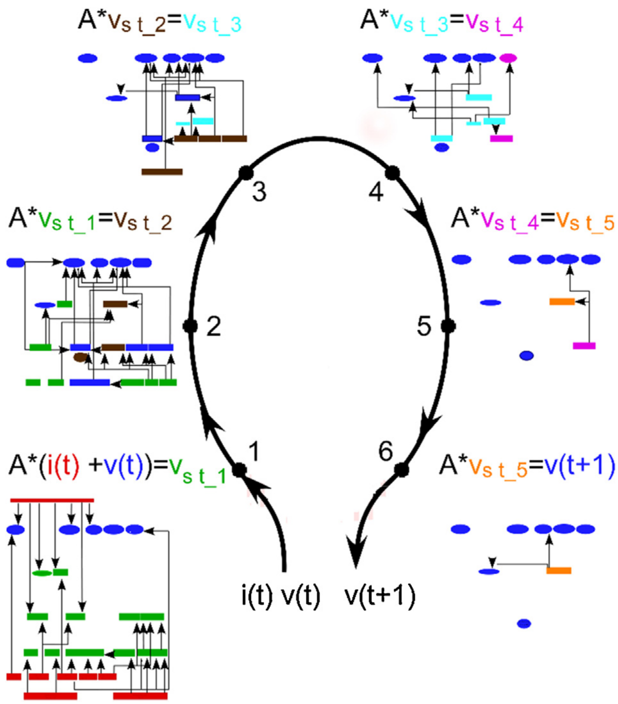


Fig. 4. The six multiplication steps of a model cycle (1 year). Each step is illustrated showing the arcs that inflict a change in the output and the vertices with non-zero values in this step. The colors of the vertices correspond to them having non-zero values in the same colored vectors. Blue colored vertices have non-zero values in both vectors of the displayed step. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

six multiplication steps were needed to represent a single cycle (i.e. model year). This led to following sequence of calculations:

$$\begin{aligned} &\mathbf{WA} * (\mathbf{i}(t) + \mathbf{v}(t)) = \mathbf{v}_{s\,t\_1} \\ &\mathbf{WA} * \mathbf{v}_{s\,t\_1\ldots t\_4} = \mathbf{v}_{s\,t\_2\ldots t\_5} \\ &\mathbf{WA} * \mathbf{v}_{s\,t\_5} = \mathbf{v}_{(t+1)} \\ &\mathbf{WA} * (\mathbf{i}(t+1) + \mathbf{v}(t+1)) = \mathbf{v}_{s\,t+1\_1} \end{aligned} \tag{3}$$

where **WA** is the weighted adjacency matrix, **i** is the input (pulse) vector and **v** is the state vector.

A difference exists between the logical causality of ecosystem processes acting on each other, and the reach and speed of the interaction. For this reason, four logical causalities issues arose after weighting the digraph. Firstly, to see changes in the state variables over time, the values of the state vector $\mathbf{v}(t)$ had to be added to the effect the input pulse had on the state variables. This was done by adding loops with the weight of 1 to all vertices representing state variables (purple vertices in Fig. 8). Secondly, since matrix multiplication calls for all cells to be multiplied at each step, the three loops in the digraph (Fish and Shellfish, Reef Framework, Diseases) lead to six fish reproduction and reef framework growth events per year, one for each multiplication step, as well as diseases being carried over 6 times per year instead of once. To guard against this, the vertex "Helper" was introduced. The vertex "Helper" was always assigned a value of 1 in the input vector $\mathbf{i}(t)$ and otherwise had a value of 0 due to its indegree of 0. Replacing the above mentioned loops with a vertex from Helper eliminated repeated multiplication by itself. To obtain the exact same value as a single multiplication using the original loop, the weight of the arc ("Helper → Fish and Shellfish") includes the value assigned to Fish and Shellfish in the current state vector $\mathbf{v}(t)$.

Original multiplication:

$$F_{s\,t\_n} = (HF * F_{s\,t\_n-1}) \tag{4}$$

New multiplication:

$$F_{s\ t\_n} = (HF * F_{s\,t\_n-1}) * H_{s\,t\_n-1} \tag{5}$$

$F_{s\,t\_n}$ = value assigned to "Fish and Shellfish" in the output vector $\mathbf{v}(t)_{s\,t\_n}$.
$F_{s\,t\_n-1}$ = value assigned to "Fish and Shellfish" in the input vector $\mathbf{v}(t)_{s\,t\_n-1}$.
HF = weight of the arc ("Fish and Shellfish → Fish and Shellfish").
($HF^* F_{s\,t\_n-1}$) = weight of the arc ("Helper → Fish and Shellfish").
$H_{s\,t\_n-1}$ = value assigned to "Helper" in the input vector ($\mathbf{i}(t)+\mathbf{v}(t)$) or $\mathbf{v}(t)_{s\,t\_n-1}$: $(\mathbf{i}(t)+\mathbf{v}(t)) \to H_{s\,t\_n-1} = 1$, all other time steps $H_{s\,t\_n-1} = 0$.

To determine the amount of diseases carried over to the next model year, the vertex Total diseases was introduced, to add up all the values of vertex Diseases during one model run (6 multiplications). At the end of each model run, the value assigned to Total diseases in the state vector $\mathbf{v}(t+1)$ was multiplied with a random number between 0 and 1.7 to determine the amount of diseased corals that could carry the disease to the next year. This number (DCO in Figs. 5 and 8) was used as the weight of the arc ("Helper → Disease") to model the still diseased corals and as part of the weight of the arc ("Helper → Bleaching") to model that a fraction of these still diseased corals may bleach due to being diseased and weakened (Fig. 5).

Thirdly, the loop between Diseases and Bleaching did not reflect the process we wanted to model correctly. With this loop in place, a part of the bleached corals would have become diseased and vice versa in the 2nd multiplication step. In the 3rd step some of the bleached corals which became diseased in step two would have become bleached. The same would happen in the 4th, 5th and 6th step. Therefore some corals would have become bleached once due to elevated sea temperatures, then become diseased and bleached two more times because they were diseased (steps 3 and 5) and diseased 2 more times because they were bleached (steps 4 and 6) – all in the same year. This is not realistic. For this reason the arc ("Diseases → Bleaching") was substituted with the arc ("Helper → Bleaching") which caused an increase in bleaching (and loss) dependent on the amount of corals diseased at the beginning of the model cycle (Fig. 5). The arc ("Bleaching → Diseases") was kept in the model, increasing diseases after a bleaching event.

Lastly, the arc (Coral cover recovery, Coral cover) would lead to a change in the vertex Coral cover during four of the six multiplication steps. The vertex Coral cover recovery was introduced to add up the influences of bleaching, calcification impairment and eutrophication on coral recolonization and increase the vertex Coral cover accordingly once a year. The arc (Coral cover recovery, Coral cover) does not reflect the process to be modeled when 6 multiplication steps are present. For this reason, the arcs (Helper, Coral cover recovery) and (Helper, Coral cover) were introduced (Fig. 3, year $2-n$, step 1). The arc (Helper, Coral cover recovery) was given a weight of 1, allowing the vertex Coral cover recovery the initial value of 1 at the beginning of every cycle/year, representing maximal coral recolonization potential. The arc (Coral cover recovery, Coral cover recovery) was assigned the weight 1, to make sure the value of Coral cover recovery remained 1 until influenced by the vertices Phase shift, Bleaching or Calcification impairment. This also enabled it to keep the value obtained from the different arcs acting on it until the end of the cycle. To model the increased in Coral cover, the arc (Helper, Coral cover) was assigned the weight 0.0179 × Coral cover recovery$_{-1}$ increasing Coral cover by 0.0179 times the value of Coral cover recovery at the end of the last cycle/year.

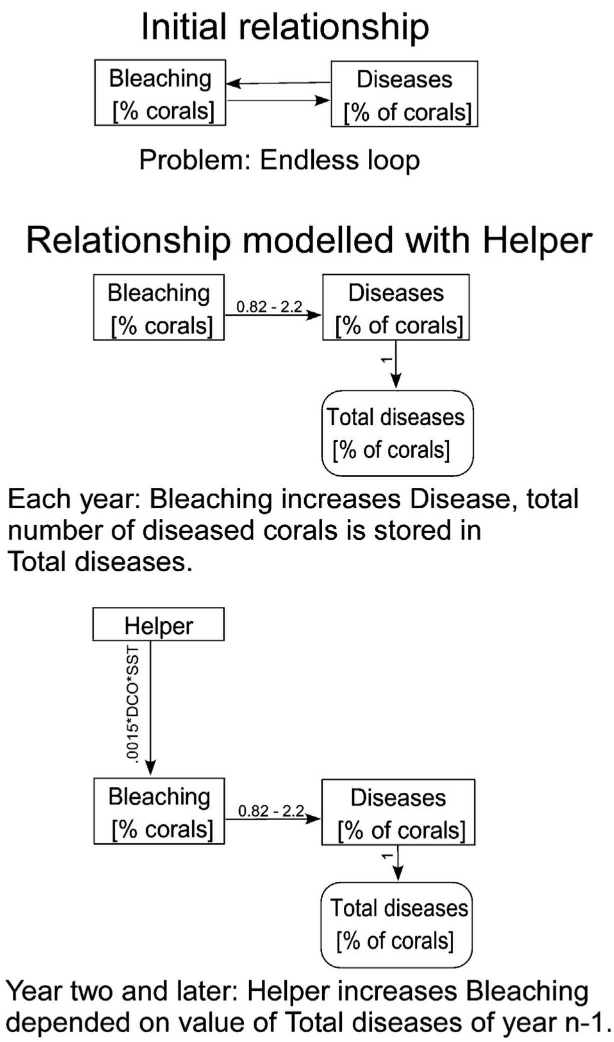


Fig. 5. Relationship between Bleaching and Diseases. This figure shows how the introduction of the vertex Helper was used to avoid the loop between the vertices Bleaching and Diseases. Without this introduction, the loop between these vertices would have led to a steady increase in Bleaching and Diseases during each multiplication step instead of each of the vertices influencing each other just once during a model cycle. Table 4 explains the acronyms used in this figure.

The changes made during the conversion from a digraph to a network were necessary to model the logical causality of ecosystem processes correctly. Nonetheless, it is clear that ex/inclusion of arcs shortens/lengthens paths and reduces/increases connections, for this reason the *WA* matrix cannot be used to determine connectivity and path lengths.

Weights for arcs in *WA*-matrix (i.e. the interaction strength of different components in the ecosystem) were derived from literature or by analysis of local data. Several approaches that utilize a range of approaches to capture interactions were used to determine the weights (Fulton, 2010). The weight of an arc from vertex x to y represents the influence of vertex x on vertex y. For each arc, literature was searched for direct quantitative relationships describing these influences. Results from prediction models, observations, in situ and lab experiments were utilized. Once quantifiable relationships were found, they were adapted to be expressed in the form of

$$\text{vertex}\,y = \text{weight of arc}\,(y, x) * \text{vertex}\,x \tag{6}$$

For some arcs, several quantitative relationships were found, leading to different results regarding the strength of the arc in question. This indicates variable influence of the initial vertex on the terminal vertex. In such cases, a range of values instead of a single value was used as weight and the model was run twice for scenario analysis, employing the upper and lower extremes of influences.

Not every arc could be quantified from literature, to determine these weights, local data for both initial and terminal vertices were used. If x was the only vertex dominating y, the data was plotted against each other, assigning each value of vertex x the corresponding value of vertex y of the same year. The weight of the arc was then found through regression analysis of the plotted data leading to

$$\text{vertex}\,y = \text{weight of arc}\,(y, x) * \text{vertex}\,x \tag{7}$$

If more than one vertex influenced vertex y, literature was used to determine the relative influence of each on the recipient vertex y. The proportion of change in vertex y caused by the individual vertices was then plotted against the data for the corresponding vertices as described above:

$$\begin{aligned}\text{vertex}\,y = {} & \text{weight of arc}(y, x) * \text{vertex}\,x \\ & + \text{weight of arc}(w,\ y) * \text{vertex}\,w + \cdots \end{aligned} \tag{8}$$

For some arcs neither direct quantitative relationships nor local data were available to determine their weights. One way of weighting these arcs was to pair qualitative statements with local data. For example, a table of coral species-specific response to turbidity levels from Erftemeijer et al. (2012) was used to determine the effect of turbidity on diversity. By comparison to coral composition data from the Florida Keys (Callahan et al., 2007), the number of species in each tolerance group was determined. The qualitative statements about effects on the coral species was then translated into mortality rates for coral species using the assumption that one third of the species which experience mass mortality suffer extinction at that site. For arcs influencing the vertex Sedimentation, direct quantitative relationships and local data were also not available. To find weights for these arcs, sedimentation and turbidity data from the Basin Hills dredging project (Griffin, 1974) were used to determine how sedimentation levels correspond to turbidity levels. With the help of this relationship, a weight for the arcs with vertex Sedimentation as terminal could be found by determining the weight of the arc with the same initial vertex and the vertex Turbidity as terminal:

$$\text{weight of arc(Sedimentation}, x) = 1.4 * \text{weight of arc(Turbidity}, x) \tag{9}$$

Unlike other vertices in the model, elevated sea surface temperatures (High SST) and storms do not occur every year. For this reason they were added to the initial input vector of the model together with the drivers. Probabilities of storm occurrence or a certain level of Degree Heating Weeks (DHW) were determined using literature. A random number between 0 and 1 was generated to determine the number of Degree Heating Weeks and whether or not a storm occurred. There is a 0.106 probability of a hurricane hitting Florida. Therefore, for random numbers $\leq$0.106, a storm was introduced. Climate change both increases the occurrence of elevated sea surface temperatures and the intensity of storms. Thus, probabilities of occurrence of the DHW levels were adjusted every year with climate change, increasing the probabilities of high DHW and lowering the probabilities of low DHW. Strength of introduced storms was determined by generating random number between 54 and 148 knots and multiplied by (1 + 0.002 * years with climate change); based on predicted increase in hurricane intensity of 16%

Table 2
Sources and time periods for data used to validate the digraph model. No data was available to validate the output for the following vertices: Coastal construction, Sea level rise, Waste water, Physical damage, Sedimentation, Calcification impairment, Reef framework.

Vertex	Category	Data availability	Source
Population	Driver	1980–2010	U.S. Census Bureau http://quickfacts.census.gov/qfd/states/12000lk.html
Commercial Vessels	Driver	2002–2011	Broward County Port Everglades Department http://www.porteverglades.net/about-us/statistics/ Miami Dade County http://www.miamidade.gov/portofmiami/business-portstatistics.asp Port of Palm Beach District http://www.portofpalmbeach.com/administration/tonnage/
Recreational Boating	Driver	1965–2006	FFWCC
Fishing	Driver	1981–2009	NOAA Fisheries http://www.st.nmfs.noaa.gov/st1/recreational/queries/catch/time_series.html
Agricultural Runoff	Driver	1987, 1992, 1997, 2002, 2007	USDA http://www.agcensus.usda.gov/Publications/Historical_Publications/index.php
Storms	Driver	1980–2009	NOAA http://www.nhc.noaa.gov
High SST	Pressure	1985–2011	NOAA http://www.osdpd.noaa.gov/ml/ocean/cb/vs_graph_sombrero_cur.html http://coralreefwatch.noaa.gov/satellite/archive/sst_series_sombero_path.html
Acidification	Pressure	1935–1996	Helmle et al. (2011)
Salinity, Turbidity, Nutrients, Phytoplankton	Pressures	1995–2010	FFWCC http://ocean.floridamarine.org/fknms_wqpp/pages/gis_data.html
Diseases, Diversity, Macroalgae Cover	Pressure, States	1997–2006	Callahan et al. (2007)
Bleaching	Pressure	1973–2007	Wilkinson and Souter (2008)
Coral cover	State	1979–2006	NOAA http://www.nodc.noaa.gov/archive/arc0001/0001394/1.1/data/0-data/ Callahan et al. (2007)
Fish and Shellfish	State	1979–1998	NOAA http://www.nodc.noaa.gov/archive/arc0001/0001394/1.1/data/0-data

between 2004 and 2084, an increase of 0.2% per year (Holland, 1997).

Many processes lead to a fractional decrease in the according terminal vertex, e.g. an increase in Salinity by 36‰ to 37‰ lead to a 10% decrease in coral cover instead of a certain fixed area of coral cover loss. To incorporate this, the weight of the arc was determined by multiplying the fractional component of the weight (0.1 for the example above) with the value of the terminal vertex at that moment, which can be found in the vector $\mathbf{v}(t)$ for the first time step and in the vector $\mathbf{v}_{s\,t\_n-1}$ for the following time steps (n = time step) (Table 4, Eq. (3)).

Two additional arcs present in the EBM-DPSER model were removed from the network either because the R^2 value of the relationship found was too low or no linear relationship could be found. Both those arcs originated from the vertex Human population. The removal of these arcs and the earlier removal of the arc ("Human Population → Coastal Construction") turned the vertices Fishing, Commercial Vessels and Coastal Construction into sources, i.e. they had indegree zero (no arc terminating in them). Therefore they were added to the initial input vector $\mathbf{i}(t)$ which already contained values for Climate change and Human population. Without this modification, uncertainty of quantitative output of the network would have increased due to uncertain weights being assigned to arcs in the bottom of the model, increasing the uncertainties for most vertices of the model. The drawback of this modification is that the network does not represent the fact that humans are the ultimate cause of fishing, commercial vessels and coastal construction. But since these pressures were added to the input vector $\mathbf{i}(t)$, their quantitative impact on the system was still correctly represented and results of the processes shown in the EBM-DPSER model were still obtained.

The units of the vertices were based on commonly used units of measurements. Due to some weights being derived from regression analysis with trend lines not intercepting (0, 0), some vertices were measured by adding a set value to the actual value measured in the natural system. For example, negative effects of high salinity levels on coral cover emerge after salinity levels surpass 36‰. For this reason the vertex Salinity is measured in ‰ subtracting 36‰ from the actual salinity level, which gives it a value of 0‰ for a salinity level of 36‰. These additions were noted in the units of the vertices in Fig. 8, e.g. [promille −36] for Salinity. Other processes modeled were found to be non-linear. To incorporate them into the *WA*-matrix, which can only deal with linear processes, one of the vertices was transformed in order to obtain a linear relationship, requiring transformation of the unit of measurement for this vertex. To produce a numerical and graphical output for the model scenarios, the transformations and added values explained above were undone resulting in an output in commonly used units of measurement. Some vertices refer to "Processes" rather than "States", therefore no commonly used unit of measurement was available. Calcification impairment captures coral growth inhibition, measured as percentage of reduced coral skeleton growth (1 = total coral growth inhibition, 0 = maximum growth). Phase Shift refers to a change from a coral to algae dominance and assigns area lost by coral cover to algal overgrowth or recolonization by corals. A value of 1 resulted in 100% overgrowth by algae with no coral recolonization, a value of 0 suggested that no algae can settle giving corals the opportunity to colonize a maximum of 1.79% of the total bottom area (Connell et al., 1997). Area recolonized by corals depended on the value of vertex Coral cover recovery, which refers to the ability of existing corals and recruits to colonize new areas (0 = no colonization, 1 = coral cover increases by 1.79% of the total bottom area).

Each arc was weighted to represent the equation

$$\text{vertex}\,y = \text{weight of arc}(y, x) * \text{vertex}\,x \qquad (10)$$

Therefore the unit of each arc is the unit of the terminal vertex (vertex y) divided by the unit of the initial vertex (vertex x). This terminates the conversion from the EBM-DPSER model to a network.

Table 3
Model input for the scenarios Waste water and Climate change.

Scenario	Initial model including driver	Changes made to model to exclude driver
Waste water	Weight of arc (Population, Waste water) = 0.00752	Weight of arc (Population, Waste water) = 0
Climate change	Vertex Climate change = 1 Vertex Storms = wind speed increases by 0.075–0.2% per year Vertex High SST = Probabilities according to Table 4	Vertex Climate change = 0 Vertex Storms = wind speed does not increase over years Vertex High SST = Probabilities of DHW 0–2 = 0.777, DHW 2–4 = 0.223, DHW ≥4 = 0

2.2. Validation

The conceptual EBM-DPSER model was constructed as part of the MARES project (Kelble et al., 2013) with input from other scientists, federal and state agencies experts and managers, non-governmental environmental organization, private industry stakeholders and the public. Operational validation of the quantitative model was performed by comparing model runs covering the period from 1981 to 2008 with historic reef data from the Florida Keys obtained from online data bases (Table 2). Eq. (5) shows one model run, which was used in the validation process to model 1 year. To be able to compare the model runs with historic reef data, units used in the model were transformed to standard units as explained above. After unit transformation, a graphical output for every vertex was produced. First, the historical reef data was plotted as black crosses for each year if it was available for the vertex (Fig. 6A). Then the model was run using the limits with higher negative impacts of the weights with ranges. After each model year the values of $\mathbf{v}(t)$ were plotted in the graph of the according vertex. These values were then connected by a line (Fig. 6B). The model was run for a second time using the other limits of the weights with ranges. Like with the first model run, the values of $\mathbf{y}(t)$ were plotted in the graph of the according vertex. The area between the plotted line of the first model run and the second model run was filled with color (Fig. 6C). Validation was determined subjectively by visual goodness of fit between the red area and the black crosses, using time series as visualization techniques (Rykiel, 1996). We did not perform a quantification of model fit due to the model output being a range rather than a single value for many vertices and historic data not being available for every single year. Where needed, the model parameters were adjusted to better reflect the data without contradicting the underlying scientific knowledge about the process.

2.3. Developing scenarios

Different scenarios were developed to determine effects of changing regulatory processes. To evaluate the influence of a "Driver", the model was run with different values for this "Driver" for the time period from 1980 until 2008 (Table 3). To model a scenario without climate change, the value of the input vector $\mathbf{i}(t)$ corresponding to the vertex Climate change was 0 instead of 1. To keep things simple, it was assumed that the probabilities of occurrence for high sea surface temperatures did not change between 1979 and 2008. Therefore the occurrence probabilities found for 1979 by Hoegh-Guldberg (1999) were used for the entire modeling period (Table 3). A second scenario was developed to

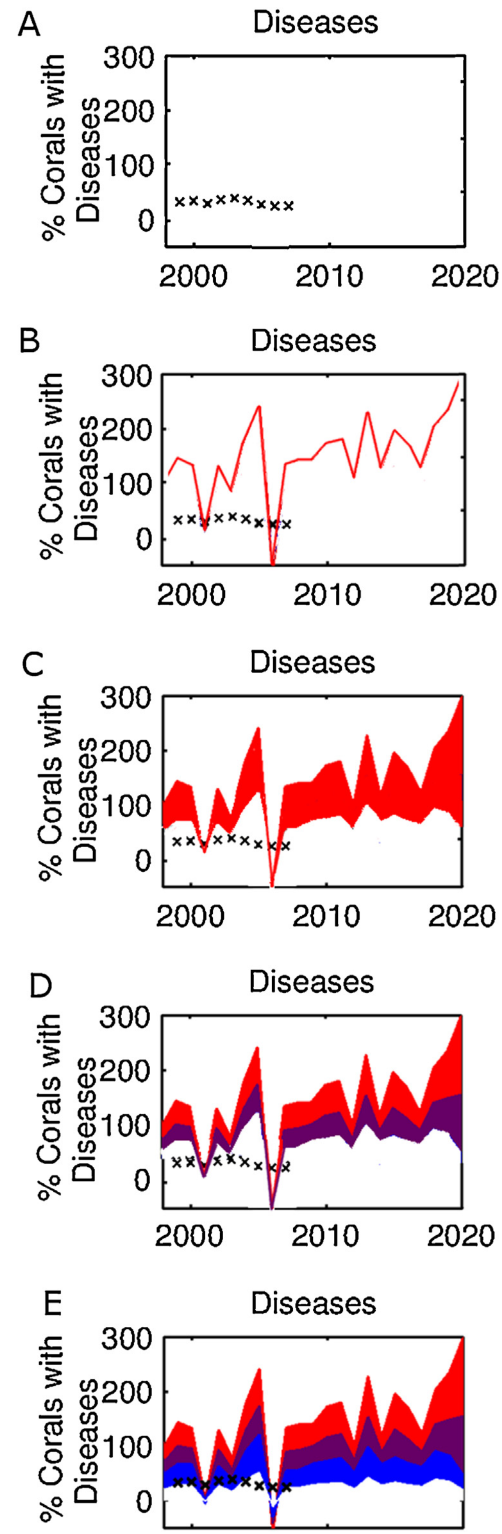


Fig. 6. Step by step method of producing the plots used for model validation (step A–C) and scenario analysis (step A–E). Black crosses: historic reef data. Red line: model output using limits with higher negative impacts of the weights with ranges. Red area: range of possible model output values for the network. Blue area: range of possible model output values for the network excluding a certain driver/pressure. Purple area: Overlap between red and blue area. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

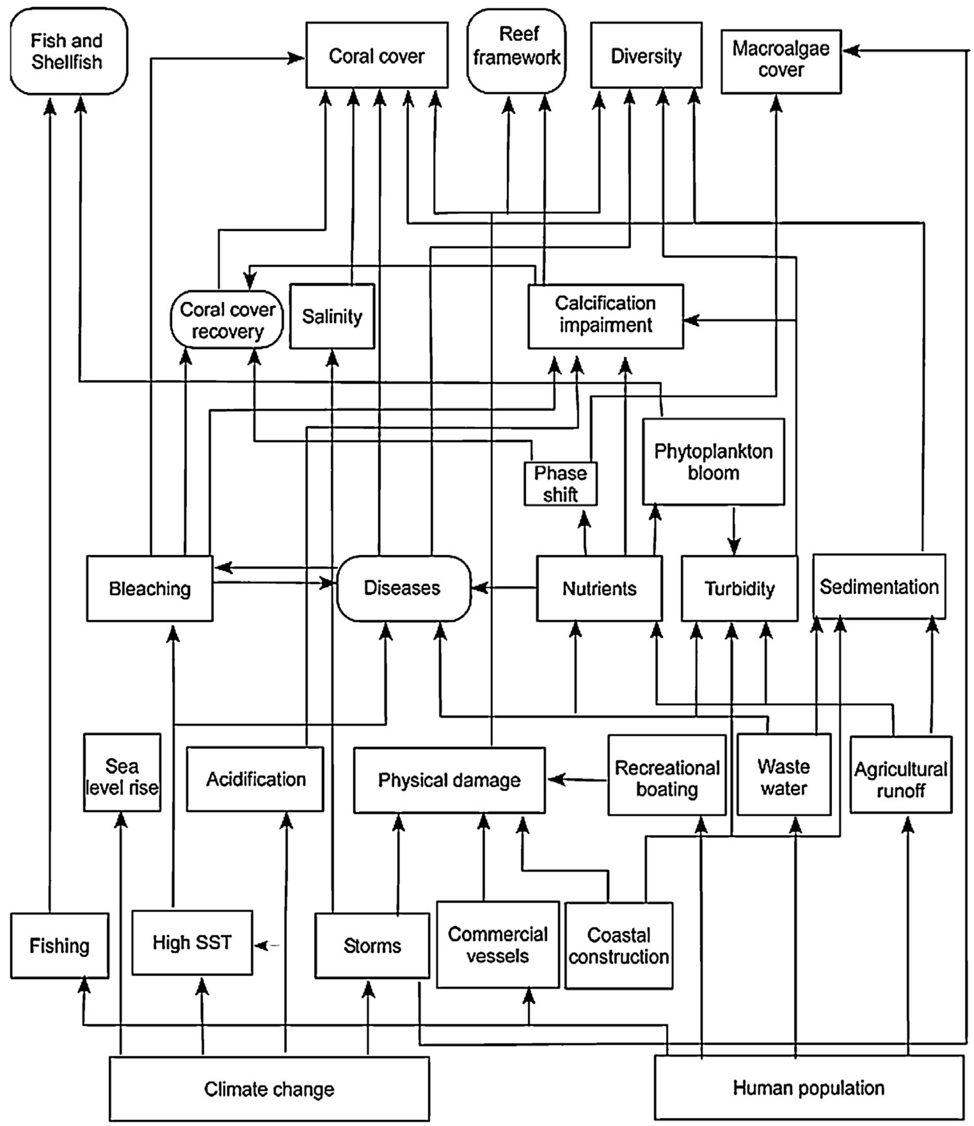


Fig. 7. Digraph developed based on a DPSER/DPSIR-type model of the SE Florida shallow marine ecosystem. Vertices which have an arc with the weight 1 coming back to themselves (loop) are displayed as rounded boxes.

look at the impact of waste water. This is of interest because the quality of waste water treatment in the Florida Keys is debatable (CH2MHILL, 2000) and therefore the construction of advanced waste water treatment plants is a possible action to protect the reefs. Nutrient and bacteria loads could be reduced. Since human fecal bacteria have been shown to cause White Pox (Sutherland et al., 2011) and may be derived from sewage, consequently, disease frequency could be reduced (Fig. 9). The scenario without

Table 4
Probabilities of occurrence of DHWs used in the digraph model. The probabilities of occurrence of DHWs for years after 1998 is determined by "*DHW in 1998*"+(*year-1998*)*"*Change per year after 1998*". For years before 1998 it is calculated by "*DHW in 1998*" – (*1998-year*)*"*Change per year 1979–1998*", when the calculations lead to a value below zero it was replaced by zero. The probabilities of occurrence of DHW ≥2, ≥4 and ≥6.8 in 2020 were derived from Hoegh-Guldberg's (1999) predictions. The probabilities of occurrence of DHW ≥8, ≥12.4 of 1998 were multiplied with 13.5 to derive a value for their probabilities of occurrence in 2020 since both DHW ≥4 and ≥6.8 increase with this factor. The change per year after 1998 was calculated by assuming a linear increase from the probabilities of occurrence of DHWs in 1998 and the predicted probabilities of occurrences of DHWs in 2020. To model the increase of the probabilities of certain DHWs occurring between 1979 and 1998, the assumption was made that the DHW categories ≥2 and ≥6.8 increased with the same rate as DHW ≥4 and that DHW ≥8 and ≥12.4 increase by 0.002 respectively 0.001.

Degree Heating Weeks	Florida Keys in 1998 [probability]	2020[a] [probability]	Change per year after 1998[b] [probability]	1979[a] [probability]	Change per year 1979–1998 [probability]
≥2	0.296	1	+0.032	0.223	+0.004
≥4	0.073	1	+0.042	0	+0.004
≥6.8	0.037	0.5	+0.021	0 (until 1988)	+0.004
≥8	0.011	0.15	+0.006	0 (until 1993)	+0.002
≥12.4	0.002	0.03	+0.001	0 (until 1996)	+0.001

[a] According to Hoegh-Guldberg's predictions.
[b] If climate change is present.

waste water was constructed by omitting the arc (Human Population → Waste water) from the model, creating a scenario where no waste water was produced.

The same method and equation as in the validation process was used to generate a graphical output for the scenarios. The historical data is represented with black crosses and the output for the two model runs (upper and lower limits of ranges) with the driver was plotted in red (Fig. 6C). The model was then run without the driver and the output for these two model runs was plotted in blue (Fig. 6D and E). If there was an overlap between the blue and the red area, that area was colored in purple (Fig. 6D). The purple area therefore corresponds to both the scenario with the driver and the scenario without the driver.

2.4. Uncertainty

Uncertainty is a key issue in integrated assessment (IA) modeling (Rotmans and van Asselt, 2001). Our model resembles IA in the intention to capture a set of cause–effect relations, which leads to the model being faced with a wide variety of uncertainties originating from different sources as well as their accumulation (Rotmans and van Asselt, 2001). Most of the uncertainty in our model is due to lack of data (22 arcs), variability (13 arcs) and simplification (11 arcs). Other sources of uncertainty are unsure future relationships (4 arcs), randomness of nature (2 arcs), linearization of a nonlinear process (3 arcs), probability (2 arcs), approximation (2 arcs), use of nonlocal data (1 arc) and aggregation (1 arc). Table A in supplement materials lists the uncertainties present for each arc and also gives them a weight to show how strong the uncertainty is compared to others in the model, providing the reader with a tool to interpret the results with more or less caution. Uncertainty was reduced by providing a range instead of a single value as weight for seven of the arcs displaying a wide range of responses to a process. The model was then run using the limit with the highest negative impact on the terminal vertex of this range for all these arcs first and in a second run the other limit was utilized. The outputs of these two runs were then combined into a range as seen in Figs. 9 and 10. Furthermore, randomness was introduced into the model by incorporating probabilities into the occurrence of High SST and Storms. Removal of some arcs from the digraph (explained above) decreased uncertainty, especially since these arcs were part of the first step in the model, which would have caused uncertainty to accumulate over several steps.

A rigorous validation process decreased uncertainty by comparing model output with local data. Uncertainty of model output is higher for elements where local data was not available, since no process-validation was possible. Furthermore, the model output consists of a range of possible outcome values instead of a single value (as seen in Figs. 9 and 10), based on the ranges provided for certain weights. The users will therefore be able to judge the uncertainty of the model output by the width of that range.

3. Results

The digraph and the fully developed network are shown in Figs. 7 and 8, the abbreviations used in the model are explained in Table 5. The *A*-matrix is simply underlying adjacency matrix of the digraph while the *WA*-matrix is the weighted adjacency matrix corresponding to the network.

The *A*-matrix was evaluated as a dominance-directed graph, where every pair of vertices is jointed by exactly one directed arc. Number of walks over k distance was evaluated over 6 steps, because each *WA* matrix was multiplied six times per year. Due to the high number of walks emanating from many vertices, the number of longer-distance walks (up to $k = 6$) was high, indicating a highly connected network. “Human Population”, “High SST”, “Bleaching” and “Waste water” were the vertices with highest walks up to distance 6, which suggest them to be influential (Table 6). “Human Population” is a primary driver, “High SST”, “Bleaching”, and “Diseases” are a problem complex linked to climate change, while “Waste water”, “Nutrients” and “Agricultural runoff”, all with high scores, represent opportunities for potential management strategy. We considered these vertices important, if only for the many connections, and used them as targets for manipulation in scenario models. The results are not surprising in a densely populated area with fertilizer-intensive agriculture but it demonstrates that the goals of including humans into the fabric of ecosystem functioning has apparently been achieved in a plausible way. It also suggests that waste-water treatment should be a prime management goal, since changes in human population will be difficult to achieve. Thus, the evaluation of the adjacency

Table 5
Explanations of acronyms in the network diagram (Fig. 3).

Acronym	Meaning
CC	Value of the vertex Coral Cover in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: % of area
CCL	Value of the vertex Coral Cover in vector $\mathbf{v}(t-1)$ minus value of the vertex Coral Cover in $\mathbf{v}(t)$. This corresponds to Coral cover loss from the last year/cycle. Unit: % of area
CCR-1	Value of the vertex Coral Cover Recovery in vector $\mathbf{v}(t)$. This corresponds to the value of this vertex in the end of the last cycle. Unit: –
DCO	0–1.7 × TD-1
DIV	Value of the vertex Diversity in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: # species
F	Value of the vertex Fish and Shellfish in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: No. of Fish per 176.715 m^2
HF	0.43 + (−0.9 to +0.1 × CCL) + (−0.9 to −0.3 × RFL)
MC	Value of the vertex Macroalgae cover in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: % of area
MCL	Value of the vertex Macroalgae cover in vector $\mathbf{v}(t-1)$ minus value of the vertex Macroalgae cover in $\mathbf{v}(t)$. This corresponds to Macroalgae cover loss from the last year/cycle. Unit: % of area
P → AR	Weight of arc (Human population, Agricultural runoff) Unit: 10^5 acr/humans/sq mi
P → WW	Weight of arc (Human population, Waste water) Unit: 10^{10} l/year/humans/sq mi
RFL	Value of the vertex Reef framework in vector $\mathbf{v}(t-1)$ minus value of the vertex Reef framework in $\mathbf{v}(t)$. This corresponds to Reef framework loss at the end of the last cycle
SST	Value of vertex High SST in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: $10^{0.034\mathrm{DHW}+0.71}$
TD	Value of vertex Total diseases in vector $(\mathbf{i}(t)+\mathbf{v}(t))$ for step one and $\mathbf{v}_{s\,t,n-1}$ for step 2–6 (n = step). This corresponds to the value of this vertex at the end of the last step. Unit: % of corals
TD-1	Value of the vertex Total diseases in vector $\mathbf{v}(t)$. This corresponds to the value of this vertex in the end of the last cycle. Unit: % of corals
y.w/CC	Amount of years with climate change modeled so far. Unit: year
Cla con.	Chlorophyll a concentration
DHW	Degree Heating week
DIN	Dissolved inorganic nitrogen
DIP	Dissolved inorganic phosphorous
Red. growth	Reduced growth

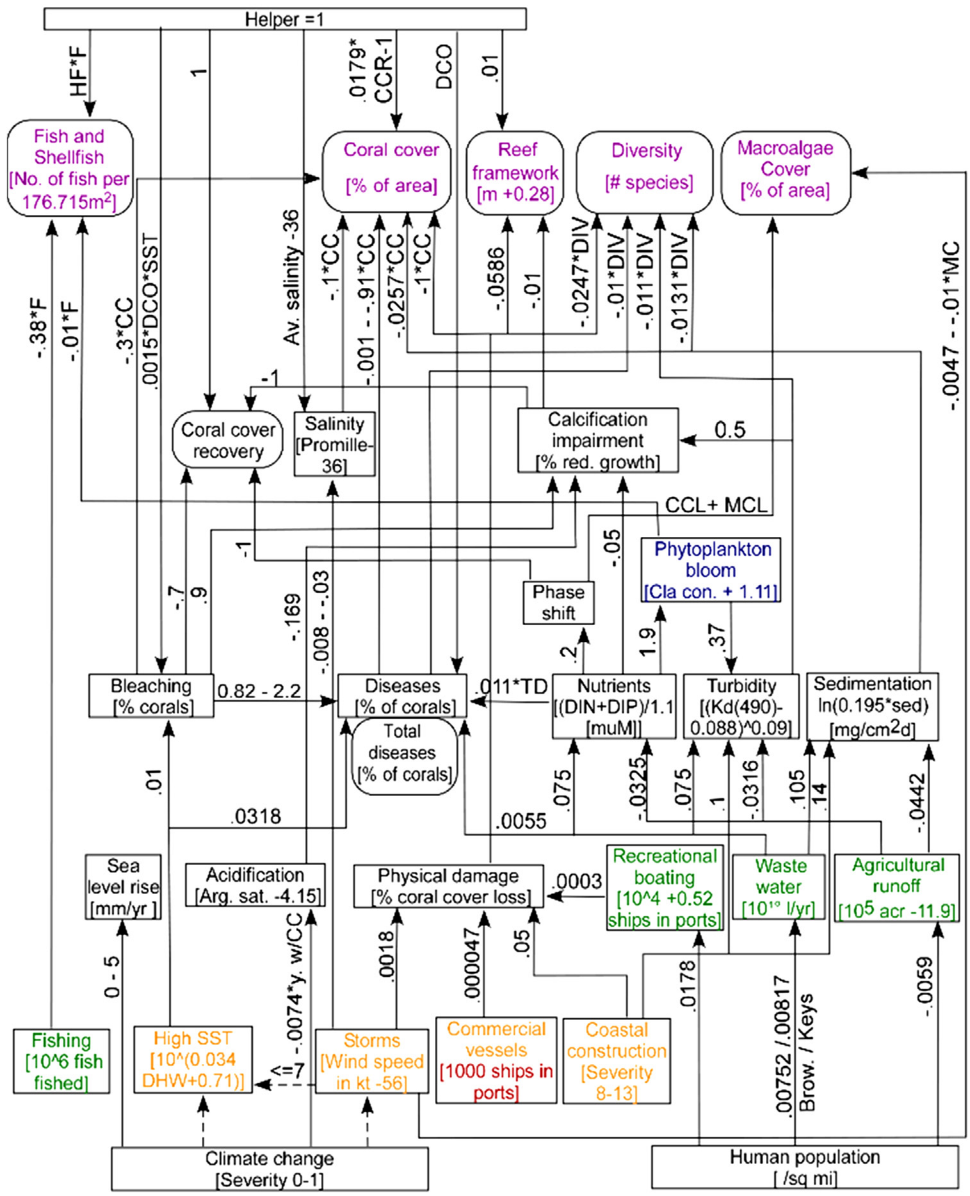


Fig. 8. Network developed based on a DPSER/DPSIR-type model of the SE Florida shallow marine ecosystem. Vertices which have an arc with the weight 1 coming back to themselves (loop) are displayed as rounded boxes. Purple vertices are state variables and yellow vertices show pressures that do not occur every year. The red vertex applies only to Broward County, the blue vertex only to the Florida Keys and the green ones only to Broward and the Florida Keys. Table 4 explains the acronyms used in this figure. The dashed lines without weights represent relationships were values are induced randomly according to their occurrence probability. When a storm is present, the value for High SST will be below 7, this is indicated by ≤7 on the arc between these two vertices. The units of the weights are not shown in this graphic due to lack of space. Nevertheless, each arc has a unit assigned to them consisting of the unit of the terminal vertex divided by the unit of the initial vertex. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

matrix provided clear clues as to which scenarios should be closer investigated.

In order to develop scenarios, the *WA*-matrix was multiplied by an input vector and state vector as shown in Eqs. (2) and (3). A great number of scenarios could be evaluated, but since it is simply our goal to demonstrate the usefulness of the approach, we present only two plausible scenarios, guided by above analysis.

The first scenario assumes that no waste water entered the ocean between 1980 and 2008. This scenario suggests that introduction of advanced waste water treatment in the Florida Keys could potentially lead to higher diversity and reef framework growth and less macroalgae cover. It could also increase coral cover, fish/shellfish abundance, and eliminate phytoplankton blooms (Fig. 9).

In the second scenario, some plausible effects of climate change were examined. While the model output showed that climate change must be expected to have an effect on sea level rise, acidification, bleaching and diseases, its overall influence on coral cover, reef framework, and macroalgae was unexpectedly small. Also, no difference was seen for expected diversity on the reefs between the two model runs (Fig. 10). Nevertheless, climate change is a major future threat to coral reefs and the impacts of an increased frequency of mass coral bleaching events (Hoegh-Guldberg, 1999) and increased disease frequency are expected in future. Thus, another scenario investigated the impact of climate change between 1997 and 2020 (Fig. 11). Due to many unknown variables (population size, fishing pressure, waste water and agricultural run-off), effects of climate change were not followed all the way through to coral

Table 6
Outcomes of treatment as dominance-directed graph (application of Eq. (1)). Columns signify the number of "wins" (incidences when a change is forced by a vertex on the value of another adjacent one, wins are signed 1, the matrix used is therefore A) over a distance of at most k (k = 1–5, but could be higher). Values in each row are cumulative and the number of walks (i.e. vertices influence by the vertex in row i) at each distance is obtained by $N_k - N_{k-1}$.

	Distance 1	Distance 2	Distance 3	Distance 4	Distance 5	Distance 6
Human population	6	20	60	112	213	387
Bleaching	4	12	29	68	150	319
High SST	3	12	30	66	145	316
Waste water	4	16	36	71	143	302
Diseases	4	12	28	61	133	287
Nutrients	4	14	30	62	132	277
Coral cover recovery	2	8	24	56	120	254
Commercial vessels	2	11	26	67	120	222
Climate change	4	11	26	48	92	189
Agricultural run off	3	11	23	42	81	168
Calcification impairment	2	5	12	29	62	127
Phase shift	2	4	10	26	58	122
Turbidity	2	4	7	14	31	64
Acidification	1	3	6	13	30	63
Coastal construction	3	10	13	17	25	43
Phytoplankton bloom	2	5	8	12	20	38
Storms	3	7	8	9	10	11
Recreational boating	1	4	5	6	7	8
Physical damage	3	4	5	6	7	8
Fishing	1	2	3	4	5	6
Reef frame work	1	2	3	4	5	6
Fish and shellfish	1	2	3	4	5	6
Sediments	2	2	2	2	2	2
Salinity	1	1	1	1	1	1
Sea level rise	0	0	0	0	0	0
Coral cover	0	0	0	0	0	0
Macroalgae cover	0	0	0	0	0	0
Diversity	0	0	0	0	0	0

cover change. Instead the vertices High SST, Bleaching and Diseases were used to show a possible future trend for the impact of climate change. Fig. 11 suggests that until 2008, climate change only had a sporadic effect on the reef, with some years showing a difference between the scenarios and others not. After 2008, the effects of climate change can be seen almost every year.

4. Discussion

A mathematically very simple and easy to implement extension of a EBM-DPSER model proved useful to quantitatively examine several "what if" scenarios and therefore has the potential to extend what can be learned from a conceptual ecological model (CEM). The process shown here is really just a small step toward the implementation of a true systems model but it has assisted us in better appreciating the differential importance of different drivers and pressures. The unweighted adjacency matrix (consisting of ones and zeros) gives indications as to the influence of vertices and helps to rank drivers and pressures of ecosystem processes. We chose the vertices with the most walks at greater distances, and manipulated them to further evaluate how different management strategies might change model (and, if implemented, ecosystem) outcomes. The two scenarios developed here show that the quantitative impact of different regulation processes can vary profoundly even if the number of arcs and vertices in the largest possible out-tree of the vertices in the A-matrix in question are comparable (26 arcs and 13 vertices for waste water and 27 arcs and 14 vertices for climate change; an out-tree is an oriented tree in which all vertices are reachable from a single vertex, the largest possible out-tree consists of all vertices which are reachable from a single vertex). Waste water shows an effect on every state variable in the model while climate change causes a change in all except Fish and Shellfish. Without the mathematical extension, the influence of climate change and waste water might have been weighted equally since both influence a comparable amount of vertices. The network extension of the EBM-DPSER/DPSIR-type model therefore assists in the appreciation of variable importance of drivers and will be useful in determining which regulation processes are fundamental (in this example for the South Florida coastal marine ecosystem).

In our model, the vertex Waste water refers to waste water reaching the reef, therefore seepage of waste water into the ocean through groundwater (Futch et al., 2010; Lapointe et al., 1990; Paul et al., 1997, 2000). The results of the waste water scenario showed that a reduction of waste water could lead to higher diversity and reef framework growth and less macroalgae cover while increasing coral cover. Our model also suggest that it would eliminate phytoplankton blooms, leading to a higherfish/shellfish abundance by removing the phytoplankton species *Karenia brevis* which has been shown to have lethal and negative sub lethal effects on fish (Brand and Compton, 2007; Flewelling et al., 2005; Landsberg, 2002). In South Florida, phytoplankton blooms form mostly in the Southwest Florida shelf and are related to land-based sources of nitrogen, phosphorous and silicon entering the bay from river water. Blooms have been observed flowing through the passes between the Keys, which leads to them covering near shore reefs for varying periods of times (Diersing, 2009) and increasing *K. brevis* concentrations to 30,000–100,000 cells per liter. This concentration is not sufficient to kill fish (Landsberg, 2002; Flewelling et al., 2005) but the values come close to it and may affect the fish and marine life through accumulation of bevetoxin in their tissue. Bio magnification of this toxin could lead to rather high concentration of beventoxin at higher trophic levels, if *K. brevis* concentrations reach 1000 cells per liter or higher (Brand and Compton, 2007). Whether or not a reduction in phytoplankton blooms and the linked increase in fish abundance will occur when waste water ceases to reach the South Florida reefs is debatable since phytoplankton blooms are caused by nitrogen and phosphorous levels in the Southwest Florida shelf which is outside of our modeling area. Phytoplankton blooms have been directly caused by waste water in both the lower Florida Keys (Valiela et al., 1997) and Kaneohe Bay, Hawaii (Laws and Redalje, 1979; Smith et al., 1981). The extend of time phytoplankton blooms persist once they reach the reefs of the Florida

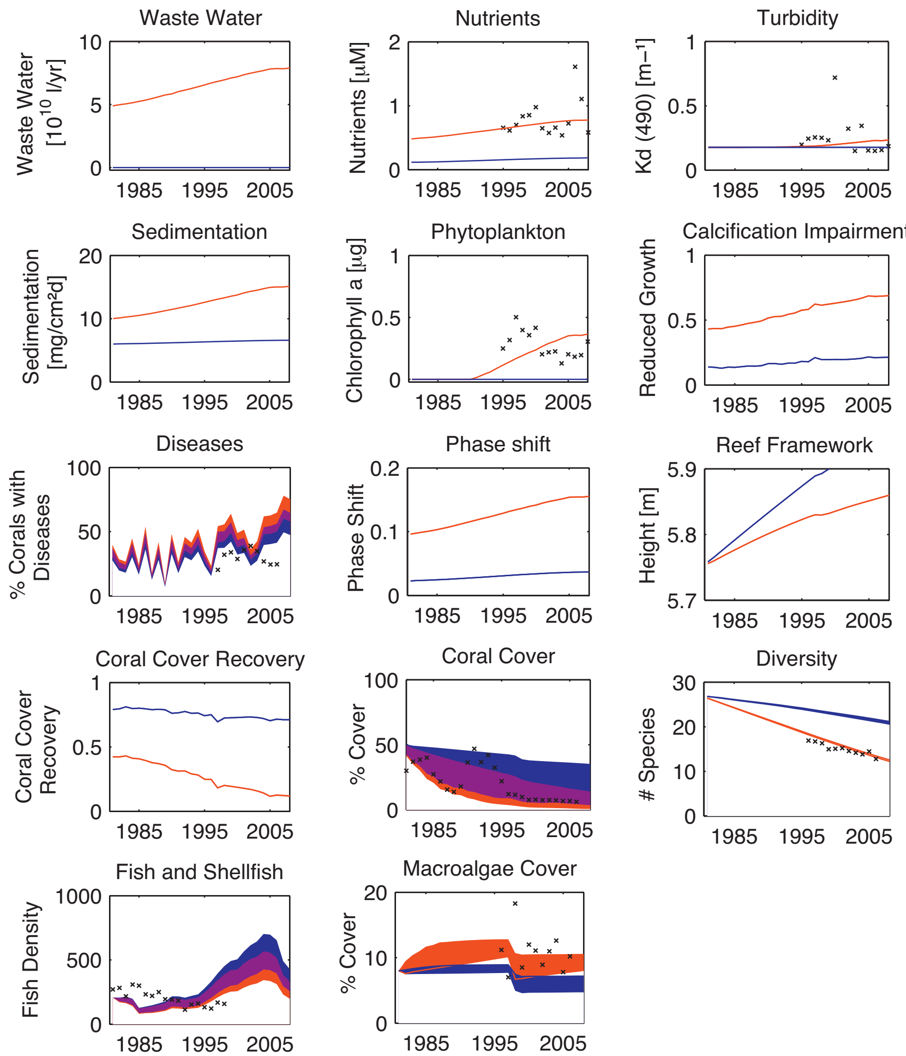


Fig. 9. Output for scenario 1: Waste water. These graphs show the output of the model for the years 1980–2008 with and without waste water. × represent the historic data, the data generated by the model with waste water is shown in red, the data generated by the model without waste water is shown in blue and the overlapping of the two scenarios is shown in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Keys varies profoundly (Diersing, 2009). It could therefore be possible that the amount of nutrients added to the reef by waste water influences the temporal extent of phytoplankton blooms on the reefs. However, if waste water influences phytoplankton blooms in the Florida Keys then just to a minor extent compared to other factors as nutrient loads in the Southwest Florida Shelf and ocean currents. The increase in fish biomass and decrease in phytoplankton blooms due to decrease in nutrients found in the model output is therefore an unlikely outcome.

The model output regarding nutrients is rather uncertain since it is sole based on discharges from agricultural and wastewater sources into Florida Bay measured between 1995 and 1997 (Corbett et al., 1999). No other data on the input of nutrients due to agriculture and waste water is available for this region. Wind-driven upwelling has been identified as another nutrient source on the reefs of the Florida Keys (Szmant and Forrester, 1996). Leichter et al. (2003) found that internal bores supply half to 10–20 times the annual input of nitrogen and phosphorus to near-shore waters than waster water and storm water. They concluded that internal tidal upwelling could lead to rapid algal growth. Lapointe et al. (2004) disagrees with the conclusions from Leichter et al. (2003) suggesting that the variability found in the temperature/NO_3 data reported by Leichter et al. (2003) indicate that mechanisms other than upwelling, for example offshore advection of enriched near shore waters and or submarine ground water discharge of DIN (Simmons, 1992), may contribute to a large part of the elevation of NO_3 and NH_4^+ concentrations on the shallow bank reef communities of the Florida Keys. *F*-ratio at Looe Key reef indicate that algae used more NH_4^+ derived from sewage pollution and/or Florida Bay outflows than NO_3 from deep, offshore upwelling to sustain their growth. For this reason Lapointe et al. (2004) concluded that upwelling has a minor effect on the nutrient load compared to land-based nutrient enrichment (sewage and agricultural). As these two studies show conflicting results on the origin of the nutrients found in the Florida Keys, more research is needed to confirm or reject the high impact of wastewater on the nutrients found by this model. Even though the acres of agricultural land decreased between 1980 and 2008 (FDACS, 2011), the input of nitrogen into the Florida Bay/Florida Keys region due to agricultural runoff reached a historical maximum in 1995/1996 (Lapointe et al., 2002). This could be due to changes in the hydrology of the Everglades. The nutrient levels caused by agricultural runoff are therefore only known for 1995 and 1997 and trends for the period before and after can only be guessed. Our model was adjusted to simulate the measured nutrient levels by increasing the nutrients due to agricultural runoff over time despite the area of agricultural land decreasing. More research and

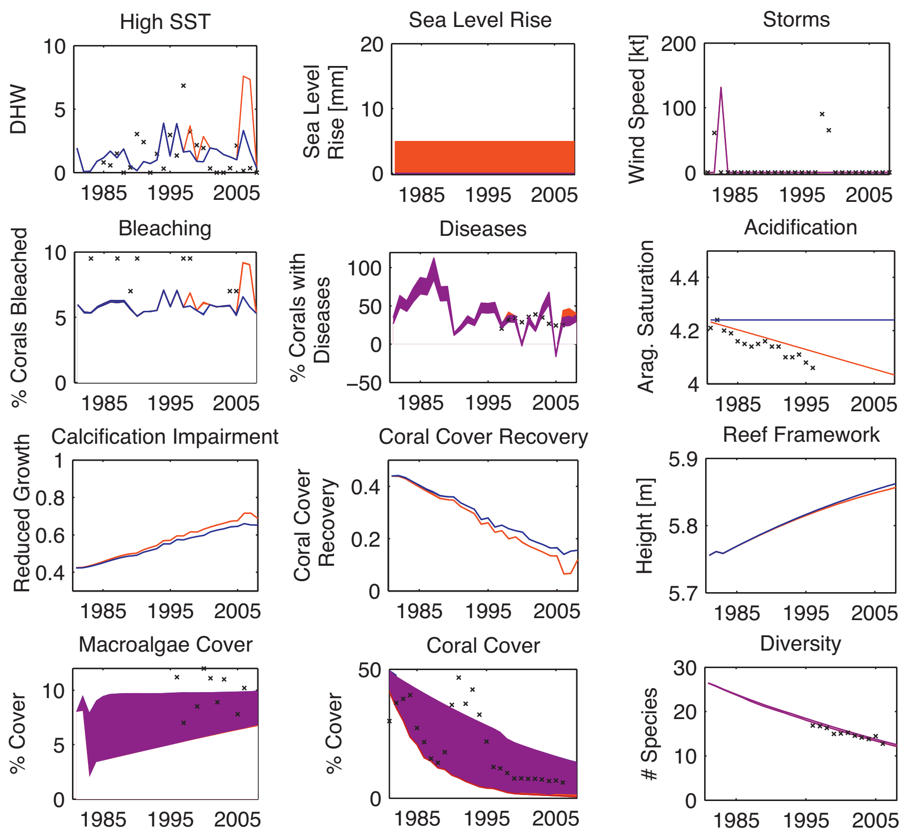


Fig. 10. Output for scenario 2: Climate change. These graphs show the output of the model for the years 1980–2008 with and without climate change. × represent the historic data, the data generated by the model with climate change is shown in red, the data generated by the model without climate change is shown in blue and the overlapping of the two scenarios is shown in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

monitoring is needed to measure the amount of nutrients caused by wastewater and agricultural runoff. This will determine how accurate the outcomes of this scenario are and determine the percentile impact of wastewater and agricultural runoff have on nutrient levels and phytoplankton blooms.

Taken together, this could lead to significant increases in recreational and educational value of the coral reef as well as its ability to protect the shore. Higher resilience and a small increase in productivity were additional positive results predicted by the model. Kelble et al. (2013) came to a similar result, when investigated the impacts of waste water in the Florida Keys using a EBM-DPSER model for the entire coastal marine ecosystem. They concluded that it would decrease the ecosystem services recreation, esthetics and existence, food and fisheries, waste treatment and biological interactions. Thus, provided that the parameterization of the model was correct, the results would suggest that better waste water treatment could be a highly efficient management option.

Surprisingly the influence of climate change on coral cover, reef framework, and macroalgae was unexpectedly small. This was likely a result of the already low coral cover and consequent low reef-building activity, and already high macroalgae cover. Furthermore the small effect seen on diversity can be traced to already depressed species diversity at this high-latitude, marginal reefal area. These sporadic effects found by the model are also seen in the measured DHW in the Florida Keys. The randomly generated DHW values for the scenario with climate change (mean: 1.8 stdev: 1.53) do not differ significantly from the DHW values measured (mean: 1.33, stdev: 1.58) (independent sample t-test: df = 46, $p = 0.30$). Coral bleaching events with widespread bleaching (>9.5% bleached corals) were observed more frequently in the Florida Keys than predicted by the model. These events occurred during years with DHW between 1.50 and 6.84. Widespread bleaching events therefore not only occur at high SST in the Florida Keys but also randomly at SST just over the long term average for the warmest month. The logarithmic relationship between the mean percentage of coral colonies affected by bleaching and regional SST anomalies found by McWilliams et al. (2005) used to weight the arc (High SST, Bleaching) is well suited to predict bleaching events triggered by high SST (e.g. 1997) but cannot explain the widespread bleaching that occurred in 1987, 1990 and 1998. The historic bleaching data used in this study was converted from qualitative statements (significant, widespread bleaching) to quantitative values (7% and 9.5% bleached corals), there is therefore a high uncertainty in these values, which could have led to this discrepancies. Nevertheless, the results from our model are in line with other studies which state that non-climatic stressors like diseases, overfishing and pollution played a more important role than coral bleaching in the live coral cover decline on Caribbean reefs prior to 2004 (Gardner et al., 2003; Hoegh-Guldberg, 1999; Reaser et al., 2000). The model predicts that the effect of climate change on the reef will intensify, with effects being present almost every year after 2008. Indeed, an usually cold winter in 2010 has since led to major coral mortality (Lirman et al., 2011). This future scenario is therefore in line with predictions that climate change will lead to an increased frequency of mass coral bleaching/mortality, by either high or low temperatures.

Even though the extension of the EBM-DPSER model to a network made it possible to look at 'what if' scenarios quantitatively, some limitations still apply to the model. End-to-end models are often uncertain due to their complication and complexity, therefore the absolute values of their output is not very reliable. Nonetheless they are suited to investigate patterns and the relative distribution of various drivers, thus making them good tools for system-level

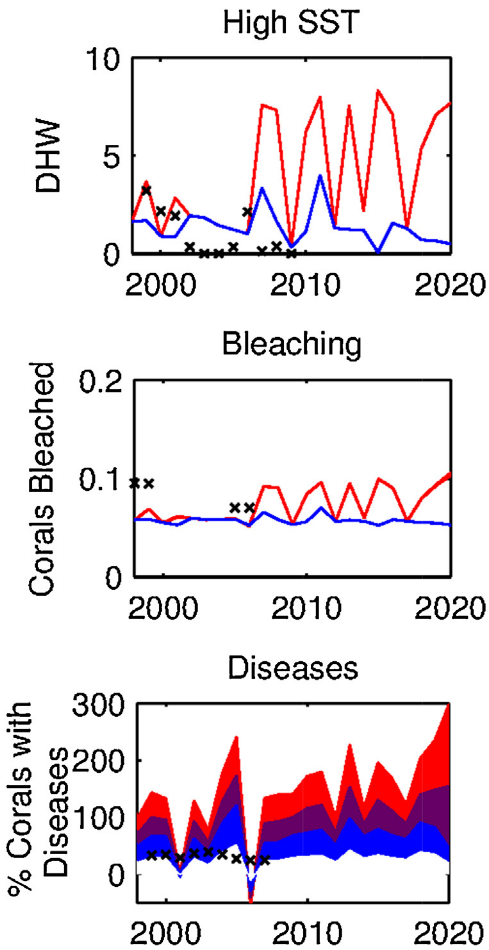


Fig. 11. Prediction of sea surface temperature, bleaching and diseases for 1997 until 2020. × represent the historic data, the data generated by the model with climate change is shown in red, the data generated by the model without climate change is shown in blue and the overlapping of the two scenarios is shown in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

'what if' management or impact scenarios (Fulton, 2010). The uncertainty of this model was increased by the simplifications and assumptions used during the modeling. Model validation dealt with many of these uncertainties, making the network a reasonably reliable source for patterns and relative distribution but as stated above the absolute values of the model output are less trustworthy. Furthermore, the deletion and addition of several arcs between the signed digraph and the network, make the network not suitable for visual interpretation of the model or analysis looking at path length and connectivity. Both these interpretations of the model can be performed using the signed digraph.

End-to-end models are valuable conceptual and strategic tools in adaptive resource management, giving insight into system functions, impact of human activities and the implication of combinations of management actions (Fulton et al., 2005, 2007; McDonald et al., 2006, 2008). The network created here is capable of giving managers these insights. It could be used as part of a management strategy evaluation framework like the simulation technique Management Strategy Evaluation (IWC, 1992). To find possible management options, the desired states of the "Ecosystem Services" elements in the EBM-DPSER/DPSIR-type model need to be translated into thresholds of the "State" variables. These thresholds are needed as targets for the management options and can be obtained through consultations, public participation, or by further ecological modeling (Rekolainen et al., 2003). The network developed here will generate general outcome patterns for these "State" variables for different management strategies. If absolute values for these "State" variable are needed to make a management decision, more detailed and complex sub models can be developed, which could then be used as target load models to calculate maximum values for the "Drivers" and "Pressures" that would not lead to exceedance of aforementioned thresholds (Rekolainen et al., 2003). Because of the interconnectedness of the system at hand, the development of such sub models would be a complex and time consuming task. Much thought should be given if absolute values for the thresholds are necessary or if relative thresholds, e.g. 20% increase from 1990 are sufficient. Our network model could be used to investigate such relative thresholds. Management options capable of meeting these thresholds can be determined through additional management and socio-economic models. These models will take into account the cost of the processes and the effect on different economic actors, therefore representing the "Response" category in the EBM-DPSER type model (Rekolainen et al., 2003).

Once the development of the management options is completed, future scenarios can be developed and modeled to determine how well they fit the set thresholds of the "State" variables. The different management options can be compared by using the model output, cost, acceptance and other factors influencing the processes. In our present case, inclusion of other factors additional to the model should be encouraged since at present the model does not take into account social, economic and cultural conflicts that surround the issue in focus (Svarstad et al., 2008). However, the relatively simple structure of the network makes such additions possible.

Besides the development of management options based on relative threshold targets, the quantitative output from the network extension and its scenario analysis are an effective way to communicate large amount of technical information (Alcamo et al., 1996). The trends and graphs produced by it can give stakeholder a fast grasp of the magnitude of impacts different "Drivers", "Pressures" and management options have. Quantitative output often has a stronger impact than qualitative information. For this reason the network has the potential to support EBM-DPSER type models to become even more powerful tools for communication with policy makers.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.04.012.

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