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Approaching a functional measure of vulnerability in marine ecosystems

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ABSTRACT

Ecosystem vulnerability is a major concern for management purposes, especially when directed toward conservation and sustainable exploitation. We estimate the relative vulnerability of selected marine-ecosystems in the Gulf of Mexico through simulation experiments based on trophic models. The same perturbation pattern was applied to different functional groups at different trophic levels. Perturbation consisted of increasing biomass extraction for a single group up to 98% at a constant rate over 50 years. The ratio Ascendency to Capacity of Development, A/C, was estimated as a measure of ecosystem order. The maximum negative difference respect to the initial A/C represents the gain of entropy. The slope of the relationship between entropy gained and the trophic level provides an estimate of the relative vulnerability of the ecosystem. This was applied to five ecosystems in the Gulf of Mexico: Florida coral reef; Mexican coastal lagoon, Terminos Lagoon; and three continental shelves, the northern Gulf of Mexico, USA; Yucatan and the Campeche Sound, Mexico. The pattern of vulnerability among ecosystems is related to ecosystem complexity. The coral reef exhibited a lower slope, corresponding to higher vulnerability, which is related to higher connectivity, production efficiency, and net ecosystem production. Increasingly higher slopes, corresponding to lower vulnerability, followed a gradient from the coral reef to the continental shelves to the least vulnerable system, the coastal lagoon. Middle trophic levels contribute to higher vulnerability. This interpretation is supported by the concept of energy flows within trophic networks. The relevance of these findings for management is discussed.

1. Introduction

Ecosystem vulnerability is a major concern for human society for a variety of reasons. Particularly critical is the need to cope with variability and uncertainty in the use and management of natural resources. Several approaches to estimating and addressing vulnerability can be found in the literature, including studies that warn of certain species' extinction vulnerability (Dulvy et al., 2003; Graham et al., 2011), identify vulnerable marine areas (Zacharias and Gregr, 2005), propose strategies to cope with climate change (Luers et al., 2003; Eriksen et al., 2005; Romieu et al., 2010), or provide methodological approaches to evaluate risks or formulate management policies (Helpern et al., 2007; De Lange et al., 2010; Teck et al., 2010).

The concept of vulnerability may be defined differently in any of these areas of research, and these variable definitions are associated with the particular problems to be addressed. Here, we are concerned with the vulnerability of marine-ecosystems represented by trophic models and with exploring the internal processes in these systems. For this purpose, we define vulnerability as the sensitivity of an ecosystem to stresses, perturbations or damage that may alter the dynamic ecological balance. Sensitivity is related to the effect of such perturbations, which is a function of ecosystem organization and functioning. Our measure of vulnerability is based on the thermodynamic concept of entropy.

The exploitation of natural living resources in an ecosystem (e.g., fishing) results in the removal of biomass, thus altering ecosystem function and organization. Although exploitation creates some level of stress, if the perturbation does not affect the natural renewal rate of the exploited species, then the species and the ecosystem will respond by recovering the lost biomass and restoring their energy flows to maintain their dynamic balance; this process is known as resilience, which is strongly related to the concept of sustainability (Ulanowicz, 2011a; Ulanowicz et al., 2009; Turner et al., 2003). The self-organization process represents the natural dynamics through which an ecosystem maintains order. If the perturbation alters the natural renewal rate, then the biomass

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of the exploited species cannot be recovered at the state previous to the perturbation, and the energy flows in the trophic web cannot be restored and the system enter in a self-organization process. Even if the ecosystem's self-organization processes act to promote recovery, the result will be an unbalanced state, generating entropy. Under this framework, sustainability is a dynamic process that maintains a balance between order and entropy (Ulanowicz, 2009, 2011b), and vulnerability is related to increasing entropy.

Our purpose is to explore the dynamics behind the order-entropy balance to address the following questions: how does a system react to a stressor based on its organization and function? How can we measure internal processes to evaluate vulnerability, especially in exploited ecosystems? Understanding internal ecosystem processes related to vulnerability is critical to formally estimate the probability of success of management decisions.

Ecosystem functioning refers to attributes related to energy flows and to the way in which an ecosystem uses and distributes energy (Ulanowicz, 1986); being a measure of the activity of the system, or its metabolism (Mageau et al., 1995). In general terms, numerous authors have argued that ecosystem-based management must focus on preserving ecosystem health, that is, on preserving an ecosystem's function, organization and resilience (Costanza, 1992, 2012; Costanza and Mageau, 1999; Mageau et al., 1998; Ulanowicz, 1980), understanding organization as a measure of the number and diversity of interactions between the components of an ecosystem, and resilience, as the ability of a system to maintain its structure and pattern of behavior in presence of stress (Mageau et al., 1995). This goal could be referred to as maintaining ecosystem order, or the dynamic balance between order and entropy, assuming entropy to be a measure or indicator of ecosystem degradation.

Ulanowicz (1986) provided a theoretical framework to describe ecosystem properties based on energy flows in trophic networks; and following Ulanowicz (2009) the ratio A/C (Ascendency, A, over Capacity of Development, C) provides a measure of ecosystem order. Ascendency is described by

$$A = \sum_{ij} T_{ij} \log \left(\frac{T_{ij} T_{\bullet\bullet}}{T_{i,\bullet} T_{\bullet j}} \right)$$

where i,j represent the prey (resources) and predator (consumer), respectively; T represents the energy flows; and $\bullet$ is the sum of the energy flows of the prey or predators, with $T_{i,\bullet}$ being the flows from one prey species to all of its predators $T_{\bullet j}$ being the total consumption of a predator species summed over all of its prey, and $T_{\bullet\bullet}$ being the total flow occurring in the system.

The Capacity of Development of the ecosystem is a measure of the maximum ascendency that the ecosystem can reach and is represented by

$$C = \sum_{ij} T_{ij} \log \left(\frac{T_{ij}}{T_{\bullet\bullet}} \right)$$

Ascendency represents the organized power of the system, and the magnitude of the energy (power) flowing within the ecosystem toward particular ends. Ascendency also depicts the density of links in the system implying the ability of self-organization to direct itself to the mature and fully developed stage The Development Capacity is the upper limits of the Ascendency and represents the whole capacity of information within the system boundary and indicates the complexity of the system's activities (Ulanowicz, 1986; Chen et al., 2010).

In our context, if we consider A/C to be a measure of ecosystem order, then $1 - A/C$ is a measure of ecosystem entropy. In terms of ecosystem dynamics, a system can maintain order if it has enough energy in reserve to deal with perturbations. When this energy is exhausted, the ecosystem will lose some order; in a thermodynamic sense, entropy will rise. The energy in reserve is called the Overhead (Ulanowicz, 1986) and is represented by the difference $C - A$. Our goal is to estimate the ecosystem entropy (or loss of order) generated by perturbing certain functional groups and to characterize ecosystem-vulnerability patterns for its potential use in a management framework.

2. Materials and methods

To estimate changes in the ascendency and the capacity of development of a given ecosystem, a simulation experiment was designed using trophic models constructed with the suite of programs Ecopath with Ecosim (Pauly et al., 2000; Christensen and Walters, 2004). The experiment consisted of perturbing selected functional groups at different trophic levels (Table 1) in an ecosystem model and measuring the ecosystem response to these perturbations in terms of A and C. The perturbations consisted of gradually extracting biomass from 0% to 98% of the initial biomass at a constant rate over a 50-year period. The functional groups to be perturbed were selected covering the whole range of trophic levels and taking care that groups between ecosystems were as similar as possible and from comparable trophic levels. For demonstration purposes, we assumed that the current ecosystem model can be used as baseline against which to compare ecosystem attributes after being disturbed, in which order and entropy were balanced. Several functional groups were selected within each ecosystem (Table 1), but only one group was perturbed at a time.

The perturbation (P) of a functional group was applied according to the relationship

$$P = \left[\frac{I}{(I+M)} \right] [1 - \exp\text{-}(I+M)]$$

where I is the instantaneous impact rate and M is the instantaneous natural mortality rate, both on an annual basis, and P expresses the proportion of the biomass extracted for a given impact rate.

The simulation outputs consisted of estimates of the ecosystem ascendency and capacity of development for each perturbed functional group based on the yearly perturbation rate. These estimates were used to calculate order (A/C) and entropy ($1 - A/C$). Additionally, a negative deviation of the order from its initial state ($A/C_{sim} < A/C_{ini}$) was assumed to represent a gain in entropy and consequently a trend toward ecosystem deterioration. The results for different functional groups within each ecosystem were analyzed and compared to those from other ecosystems.

As test cases, we used trophic models of five ecosystems within the Gulf of Mexico: the northern Gulf (Browder, 1993) and a Florida coral reef (Venier and Pauly, 1997), both in the United States; and the Yucatan continental shelf (Arreguín-Sánchez, 2000), the Campeche Sound (Zetina-Rejón and Arreguín-Sánchez, 2003) and Terminos Lagoon (Manickchand-Heileman et al., 1998), all in Mexico.

For correlations we used the reduced major axis (RMA) linear regression (Hofman et al., 1986; Leduc, 1987; Smith, 2009), in which the fitting process assumes both variables are measured with error, in contrast with the conventional linear egression analysis where only the dependent variable is assumed to be measured with error (Fig. 1).

3. Results

For each ecosystem, we selected functional groups at different trophic levels to be perturbed (Table 1). The perturbation rate, representing the proportion of biomass extracted, was applied to each functional group using the Ecosim model (Walters et al., 1997), and the results were expressed in terms of changes in the ascendency, capacity and order (A/C) of the ecosystem. For example, Fig. 2