The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management

Andrés Felipe Navia [a,b,*], Víctor Hugo Cruz-Escalona [c], Alan Giraldo [b], Alberto Barausse [d]

[a] *Fundación colombiana para la investigación y conservación de tiburones y rayas, SQUALUS, Carrera 60A No. 11-39, Cali, Colombia*
[b] *Grupo de investigación en Ecología Animal, Sección de Zoología, Departamento de Biología, Universidad del Valle, A.A. 25360, Cali, Colombia*
[c] *Centro Interdisciplinario de Ciencias Marinas, Instituto Politecnico Nacional, Avenida Instituto Politecnico Nacional, P.O. Box 592, 23060 La Paz, BCS, Mexico*
[d] *Environmental Systems Analysis Lab (LASA), University of Padova, via Marzolo 9, 35131 Padova, Italy*

ARTICLE INFO

ABSTRACT

We reconstructed the structure of a tropical marine food web and then analyzed it to evaluate how the trophic network could respond to anthropogenic pressures such as the removal of species by fisheries. To reconstruct the presence/absence of predator-prey interactions, we assembled detailed quantitative information from the scientific literature on the stomach contents of 80 predator species (elasmobranchs, teleosts and invertebrates) collected in the Golfo de Tortugas (Colombia) between 1990 and 2009. We tested three conceptual models of network structure (random, small-world, and scale-free), characterized by different system properties and tolerance to perturbations, to evaluate which one better fitted the reconstructed food web. Our results suggest that this network has small-world structure and scale-free properties. An impact on one species may therefore spread to many species through short interaction chains; only a few nodes with high centrality values would support the network structure. However, contrary to current theory, our analysis revealed no clear relationships between species with high centrality and the large-scale structural patterns observed in the network (small-world and scale-free properties). This observation indicates that ecosystem-based fisheries management should prioritize not only high-centrality species (e.g., shrimps, which furthermore are species of high commercial value in the area), but should also consider species with unique structural properties such as those with little or no topological redundancy such as large sharks. For this reason, top predator conservation needs more attention than currently received in fisheries management.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Although the scientific literature repeatedly mentions the importance of biological diversity, neither its functional aspects nor the most adequate way to maintain it are known in detail (Terborgh, 1999). To understand the functional diversity of ecosystems, we need to know the roles that each species performs in the community (Jones and Lawton, 1995; Kareiva and Levin, 2003). Therefore, interspecific relations within the communities and the way that they affect community dynamics and stability have been a central topic of study regarding food webs (Pimm, 2002; De Ruiter et al., 2005), and underlie approaches for multi-specific management of ecosystems (May et al., 1979; Grant et al., 1997; Yodzis, 2000).

Numerous approaches for investigating the function and stability of communities have been carried out with mass-balance models of food webs (e.g., Vasconcellos et al., 1997; Christensen and Pauly, 2004; Arreguín-Sánchez et al., 2004a,b; Zetina-Rejón et al., 2004; Morales-Zarate et al., 2004; Rosas-Luis et al., 2008; Li et al., 2009), based on the evaluation of trophic interactions in the ecosystem and their relationship with fishing pressure; varied results have been obtained regarding the functional importance of the diverse components of the food web (Manichchand-Heileman et al., 1988; Fernández et al., 2001; Kitchell et al., 2002). These analyses used functional approaches to studying the effect of a predator on the population size of its prey, not focusing much on indirect effects such as trophic cascades, apparent competition, and keystone predation, all important forces that structure communities (Menge, 1995; Hughes and Roughgarden, 1998; Bascompte et al., 2005; Pawar, 2009; Vallina and Le Quéré, 2011).

* Corresponding author at: Fundación colombiana para la investigación y conservación de tiburones y rayas, SQUALUS, Carrera 60A No. 11-39, Cali, Colombia. Tel.: +57 23705589.
E-mail address: anavia@squalus.org (A.F. Navia).

The concept of "keystone species" became popular in ecology several decades ago (Mills et al., 1993; Libralato et al., 2006). Keystones can be defined as species which play an exceptionally-important role in structuring the organization of communities and in ecosystem functioning through their direct and indirect interactions with the other species. These interactions can be trophic or due to other types of processes (e.g., pollination, seed dispersion, physical habitat modification; Mills et al., 1993). A clear definition of what a keystone species is and of the effects of removing it from an ecosystem has important operational consequences, as non-redundant (Naeem, 1998) species with key ecological roles could be special targets of biodiversity conservation (Mills et al., 1993; Jordán et al., 2009). About hypothesized relationships between biodiversity and ecosystem functioning, Naeem (1998) proposes that the redundant species, those that perform similar ecological roles (Walker, 1992), are important to the reliability of the ecosystem, and that declining biodiversity means loss species redundancy in ecosystems.

The structural perspective provides a different option for the analysis of food webs (Wassermann and Faust, 1994; Bornholdt and Schuster, 2003; Newman et al., 2005), permitting the extraction of information necessary to identify the species that play important trophic roles in these communities. This approach has been widely applied to establish the relations among the diversity, complexity and stability of the food webs (Dunne et al., 2002a, 2004; Dunne and Williams, 2009), in addition to the structural importance of a species. The structural perspective considers both indices providing a global characterization of the food web, such as connectance (C; Martinez, 1992), and local indices like the distribution of trophic connections (Montoya and Solé, 2002). These indices reflect the web topology, but do not provide information on the specific position of the nodes or their most distant interactions (Holt and Lawton, 1994). Therefore, they can be complemented with intermediate-range or "mesoscale" indices, which are adequate if the investigation aims to understand the relations within a community (Jordán and Scheuring, 2002), and more so, if the goal is to quantify the relative importance of each species within a given system (Jordán et al., 2006).

According to graph theory, the frequency distribution of links (trophic interactions, in the case of a food web) within a web has deep structural implications, as it can highlight the presence of scale-free patterns associated with the web and indicate whether the properties of the web are independent of its size (Montoya and Solé, 2002). In theory, scale-free food webs are resistant to the loss of species with low centrality values, but are sensitive to the loss of species with the highest values. Further details of scale-free network theory can be found in Albert and Barabási (2002); examples of the application of this theory to food webs have been carried out by Solé and Montoya (2001), Montoya and Solé (2002), and Gaichas and Francis (2008). However, trophic interactions are flexible and the response of the community is much less predictable, so that properties of small world and scale-free networks should not be taken for granted.

Some theoretical approaches to graph complexity in nature have suggested that scale-free networks may present a "small-world" structural arrangement, a network in which most nodes are not neighbors of one another, but most nodes can be reached from every other node by a small number of steps. This architecture was initially described in technological networks (Watts and Strogatz, 1998), but has recently been documented in biological networks and, more specifically, in food webs (Montoya and Solé, 2002; Gaichas and Francis, 2008; Navia et al., 2012).

The consequences of the small-world and scale-free structural patterns can be highly important for recognizing sensitivity to disturbances in biological webs (Montoya and Solé, 2002). The small-world structural pattern (based on node clustering) has been associated to rapid responses to various disturbances in several theoretical food webs, suggesting that this arrangement may benefit web resilience. In this respect, Solé and Montoya (2001) and Montoya and Solé (2002) determined that food webs with small-world structural arrangements were more resistant to secondary extinction of species than networks with random structures. Accordingly, Gaichas and Francis (2008) proposed that, if the structure of a food web impacts the function of the communities in the web, then it may also bear important implications for fisheries management and the conservation of marine ecosystems.

The main objective of the current investigation was to describe and analyze the food web structure in the Golfo de Tortugas (GT) in the Colombian Pacific via graph theory and topological network analysis. We evaluated whether these tools could provide valuable advices about how this marine food web works, thus supporting multi-specific fisheries management in the area through the implementation of an ecosystem-based approach (Pikitch et al., 2004). Given the prediction that food webs with small-world structure are less robust to the loss of highly connected species than random webs, that shrimps have the highest node degree (D) in the GT (Navia et al., 2010, 2012), and that shrimp are of high economic value and are strongly affected by fishing pressure in the study zone (Rueda et al., 2011), we assessed whether the loss of shrimps and species with topological uniqueness impacted the structure of the GT web significantly.

2. Materials and methods

2.1. Data

The GT food web (Fig. 1) was reconstructed from a database of information obtained from the analyses of the stomach contents of fish and invertebrates captured in this zone between 1990 and 2009; these data were assembled from numerous publications (Appendix 1). Dietary information was unavailable for three top-predator shark species (*Galeocerdo cuvier*, *Carcharhinus leucas*, and *Carcharhinus limbatus*), and thus information from similar tropical ecosystems was used (Appendix 1). Quantitative information was obtained for 13,934 stomachs from 80 predator species (589 were empty). Most of the species included in this analysis are susceptible to capture with trawls, drift netting, and hook lines, and they are representative of the various environments and habitats in the study zone (e.g., bottom, pelagic, bentho-pelagic and neritic).

2.2. Building the trophic network

To construct the food web, information on stomach contents was compiled to the species taxonomic level when possible. When this information was not available, genus, families, or orders were used. Groups such as the Phytoplankton and Zooplankton, and categories such as the Teleostei, Pennaeidae, Brachyura, and Cephalopoda (Appendix 2) were maintained to include prey not identified to lower taxonomic levels but that contribute to the diets of some species and that play a role in the trophic functioning of the ecosystem.

From information on the diet of predators, a binary matrix of trophic interactions was constructed in which, for a given cell ij, "1" represents the presence of prey i in the diet of predator j and "0" represents the absence of this prey. The number of interactions per species was determined for all species (predators and prey) in the web. Hence, this analysis focuses on trophic interactions among species, but not on the strength of these interactions, and deals strictly with the topological properties of the GT web.