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Changes to Marine Trophic Networks Caused by Fishing

Andrés F. Navia[1,2], Enric Cortés[3], Ferenc Jordán[4],
Víctor H. Cruz-Escalona[2] and Paola A. Mejía-Falla[1]
[1]*Fundación Colombiana Para la Investigación y Conservación de Tiburones y Rayas SQUALUS*
[2]*Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional*
[3]*NOAA, National Marine Fisheries Service, Panama City Laboratory*
[4]*The Microsoft Research – University of Trento COSBI, Trento*
[1]*Colombia*
[2]*México*
[3]*USA*
[4]*Italy*

1. Introduction

Multiple anthropogenic sources, such as contamination, habitat degradation, eutrophication, and, more recently, fishing, have steadily been impacting marine ecosystems for at least the past two centuries, generating probably irreversible structural and functional changes (Estes et al., 2011; Lotze & Milewski, 2004). In particular, increasing fishing pressure during the past 50 years and habitat degradation have had a wide range of impacts on ecosystems worldwide, which are reflected in changes in abundance, spatial distribution, productivity, and structure of exploited communities (Blaber et al., 2000; Hall, 1999; Jackson et al., 2001; Lotze et al., 2006; Myers & Worm, 2005). These impacts on community structure and function have been widely documented and quantified in many marine ecosystems (Haedrich & Barnes, 1997; Jennings & Kaiser, 1998; Pauly et al., 1998; Sala et al., 2004; Worm et al., 2006; Yemane et al., 2005).

Some authors have suggested that, although changes in species composition are an important indicator to identify perturbed ecosystems, a holistic knowledge allowing identification of structural and functional effects could emerge from the study of communities as networks interconnected by trophic interactions (Bascompte et al., 2005; Dunne et al., 2002). Owing to the relatively stable characteristics of trophic networks, these interactions can provide information on species relationships within a community and how human activities could be degrading ecosystems (Dell et al., 2005).

Recent publications that have assessed the relationship between fishing and possible alterations of direct and indirect trophic relationships within impacted ecosystems have detected strong ecological effects, such as trophic cascades and changes in ecosystem control equilibrium, either top-down or bottom-up (Barausse et al., 2009; Baum & Worm, 2009;

Ferretti et al., 2010). Thus, these publications have generated particular interest on top predators given their role as regulators of intermediate predator populations, or mesopredators, and further proposed that removal of top predators can result in changes in intraguild relationships that affect biodiversity and the equilibrium of the ecosystems under study (Baum & Worm, 2009; Ritchie & Johnson, 2009).

Extensive work has also been conducted on the relationship between species loss and secondary extinctions generated by predator-prey interactions (Dunne & Williams, 2009, Dunne et al., 2002, 2004), finding in many cases that the increase in the capacity of response of trophic networks is related to the increase in diversity (expressed as species richness) and the number of interactions among these species in the network (connectance).

Owing to the variety of approaches used to study trophic networks and the large number of topics studied in these systems, we conduct a review of the effects detected in trophic networks that have been proposed to originate in the fisheries impacting different ecosystems throughout the world's oceans. This review consists of three main themes: 1) effects of fishing on the structure of trophic networks, 2) effects of fishing on the function of trophic networks, and 3) effects of fishing on interspecific trophic relationships (direct and indirect effects). With the aim of exploring the effect of fishing on a trophic network, we conclude by presenting a topological analysis of a network by simulating fishery removals and assessing the effect of parameters considered to be important in network structure, but not addressed in sufficient detail in previous work.

2. Effects of fishing on trophic networks

Human-induced changes to marine ecosystems have been taking place for centuries, but have only reached global dimensions in the past few decades. Thus, there are three effects with major connotations generated by humans: 1) changes in nutrient cycles and climate which affect ecosystem structure from the bottom up, 2) fishing activity which could affect ecosystems, mainly from the top down, and 3) habitat alteration and contamination which affect ecosystems at all trophic levels.

This chapter focuses on the fact that human beings have used marine resources throughout history, from subsistence fishing activities to large-scale fisheries in almost all the oceans in the planet. With the often unrestrained increase in fishing activity, some have sounded the alarm on the possible effects of this practice on populations and the world's marine ecosystems (Jackson et al., 2001; Lotze & Worm, 2009). Since fisheries have both direct and indirect effects on the ecosystem, wherein commercial and non-commercial species establish feeding interactions, it is very likely that impacts from human activities, which are exerted on individuals, propagate to populations and finally emerge at the community level (Sandström et al., 2005).

Most studies have focused on the effects of fishing on the population dynamics of species, most often charismatic species or those with high commercial value (e.g. Lotze & Worm, 2009; Lotze et al., 2011). In terms of communities, many studies have tried to assess the effects of anthropogenic activities on functional groups or entire ecosystems, documenting various types of responses (e.g. Jackson et al., 2001; Pandolfi et al., 2003), but even then the consequences of these activities on the structure and functioning of ecosystems remain unclear (Lotze et al., 2011).

2.1 Effects of fishing on the structure of trophic networks

2.1.1 Structural attributes of trophic networks

Trophic networks display structural attributes that appear to be constant, or at least regular, throughout the planet's latitudinal range. These regularities have been linked to the stability of networks and their capacity to respond to different types of environmental stressors (Bascompte et al., 2005; Dunne et al., 2004; Solé & Montoya, 2001). These structural attributes are based mainly on the number of interactions between predators and prey, proportional abundance of predators, intermediate species, and basal species, and the number of species at different trophic levels.

Despite these being the most basic structural properties of trophic networks, very few studies on the effects of fishing have addressed them. In that respect, Lotze et al. (2011) found significant changes in the constant proportions that must exist among top predators (T), intermediate species (I) and basal species (B), known as "species scaling laws" (Briand & Cohen, 1984). Additionally, based on other structural indicators of trophic networks (link density, connectance, cannibalism), Lotze and collaborators concluded that the trophic network in the Adriatic Sea has been subjected to overfishing of high trophic levels, leading to its structural simplification, progressively becoming less connected and complex. This type of structural changes directly affects the capacity of the network to respond to species loss (robustness) and increases the likelihood of secondary extinctions, even with low values of species reductions, leading the network to structural collapse more easily (Dunne et al., 2004).

2.1.2 Structural simplification

In the study by Lotze et al. (2011), the trophic network was significantly simplified and the loss of slightly less than 50% of the original richness of the network would result in its total collapse. Although very few studies explicitly mention structural simplification of networks as a result of fishing (Coll et al., 2008a, 2009a, 2009b), or changes in "species scaling laws", they can be inferred in studies reporting changes in the distribution of biomass among different trophic levels through time. This phenomenon has been observed in a large number of studies that use mass balance trophic models as analytical tools (e.g. Albouy et al., 2010; Barausse et al., 2009; Coll et al., 2008a, 2008b, 2009a, 2009b; Hinke et al., 2004; Jones et al., 2009; Savenkoff et al., 2007a, 2007b).

Using this approach, Coll et al. (2008a, 2009a, 2009b) found significant differences in the composition of a trophic network subjected to different fishing levels through time. Their results showed a change in the biomass proportions (equivalent to species scaling laws) among trophic levels between the ecosystem without fishing pressure and the three scenarios with increasing fishing pressure. Coll and collaborators studied the Mediterranean Sea ecosystem, which has been subjected to increasing fishing pressure for over two millennia and displays, according to these authors, a high level of degradation in trophic network structures and thus a dangerous simplification. These authors also found that highly impacted environments, not only in terms of intensity but also of time, show stronger overexploitation effects at high trophic levels, larger network simplification, and high reductions in productivity and biomass. As a result of this drastic structural simplification, Mediterranean ecosystems showed less robustness to secondary extinctions than other less impacted ecosystems (Coll et al., 2009a, 2009b).

All these indicators of structural simplification of trophic networks have a very important implication, which is the possible reduction in functional redundancy, part of the biological insurance of ecosystems (Montoya et al., 2001). Thus, fishing pressure creates two highly dangerous scenarios for the stability of trophic networks: removing a functional level in the network, or transforming a species previously belonging to a feeding guild and sharing its ecological function with other species, into a key species, which upon being impacted would seriously challenge the stability of the whole ecosystem. Attempts to measure the effect of fishing on community structure based on indices that describe community attributes (equitability, richness, Hill indices, and others) have shown limited success (Piet & Jennings, 2005) because cause-effect relationships as well as the direction of the fishing effect on these indices are unclear (Bianchi et al., 2000; Rice, 2000). Other indicators have also been explored as evidence of fishing effects on populations, communities, and ecosystems (Friedlander & DeMartini, 2002; Fulton et al., 2005). These authors proposed that some community and ecosystem-based indicators could be useful in management actions, but that some, especially those based on network analysis and ecological models (e.g. ascendency), have low reliability because they depend on information that is difficult to collect, model formulation, and level of knowledge on the modeled systems.

2.1.3 Fishing down versus fishing through marine food webs

Pauly et al. (1998) proposed an important fishing effect related to the structure and composition of trophic networks called *fishing down marine food webs*. It postulates that selective catches of top predators have modified the composition of fishery landings and reduced their mean trophic level (MTL). Given the interpretation given to this phenomenon, whereby fishing has substantially modified trophic networks, from being dominated by large predators of high trophic level to small species of lower trophic levels, fishing down marine food webs was initially considered an effect of dire consequences. It was documented both at a global (Pauly et al., 1998) and regional (Pauly & Palomares, 2005; Pinnegar et al., 2002, 2003) scale, as well as at a local scale in countries such as Thailand (Christensen, 1998), Canada (Lotze & Milewski, 2004; Pauly et al., 2001), China (Pang & Pauly, 2001, as cited in Pauly, 2010), Portugal (Baeta et al., 2009), Iceland (Valtysson & Pauly, 2003), Namibia (Willemse & Pauly, 2004) Senegal (Laurans et al., 2004), USA (Steneck et al., 2004), Mexico (Sala et al., 2004), Spain (Sánchez & Olaso, 2004), Chile (Arancibia & Neira, 2005), Greece (Stergiou, 2005), Uruguay and Argentina (Jaureguizar & Milessi, 2008), India (Bhathal & Pauly, 2008), and Brazil (Frieire & Pauly, 2010).

However, several criticisms emerged to the general interpretation of this mechanism by Pauly and collaborators, the first one by Caddy et al. (1998). These authors argued that the degree of taxonomic resolution used for the analysis affected the trophic level assigned to species, that the trophic level of catches does not necessarily reflect the trophic level of the ecosystem, that the statistical data used (from FAO) were influenced by aquaculture production, and finally that eutrophication of coastal ecosystems has increased the abundance of lower trophic level organisms. Pauly (2010) countered each of these criticisms and we encourage the reader to judge how well they were addressed. Essington et al. (2006) in turn proposed that fishing down marine food webs is a phenomenon specific to North Atlantic fisheries caused by the sequential collapse and replacement of the fisheries in the region, and that the decline in mean trophic level of the catches in many other areas of the

world is caused by increased harvesting of low trophic levels in marine networks (sequential addition of new fisheries), even when catches of high trophic level species remain constant or increase. This pattern of sequential addition to the fisheries of low trophic level species was termed *fishing through the food web*. The controversy thus arose of whether the drastic effect on the structure and mean trophic level of the landings was or not reflective of a real effect of fishing on marine trophic networks. Essington et al. (2006) argued that results based on catch or landing records do not necessarily reflect the composition and state of ecosystems because the indicators are biased by the interests of fisheries operating in each region.

In that regard, Litzow and Urban (2009) reported that the historical periods of decrease in the trophic levels of catches in Alaska obeyed to fishing through the food web and not fishing down the food web, adding as an argument that declines in the trophic level of catches are caused in many cases by temporary additions of fisheries targeting low trophic level species (e.g. crustaceans). Litzow and Urban (2009) concluded that it is clear that commercial exploitation has had profound effects on marine ecosystems in Alaska, but that due to the complexity of connections in marine trophic networks it is difficult to understand these effects. In terms of the ecological interpretation of fishing through the food web, Essington et al. (2006) noted that although they found increases in the catches of high trophic level species, this does not mean that these stocks are healthy and that their findings should not be used to make population inferences since they worked with species categories grouped by trophic level.

2.1.4 Mean Trophic Level (MTL) as an indicator of ecosystem health

Although the MTL of catches is the indicator most frequently used to assess the status of marine ecosystems, it has been widely questioned (Branch et al., 2010; Essington et al., 2006; Powers & Monk, 2010) because it is influenced by economic interests in the different fisheries. Branch et al. (2010) reported that the computation of catch MTL does not adequately correlate with ecosystem MTL and thus this index does not properly measure the magnitude of fishing effects or the rate at which ecosystems are being altered by fishing. Owing to the weaknesses of the catch MTL, it is unlikely that this indicator alone reliably shows any structural effects on trophic networks, let alone any effects of fishing on their complexity and stability. Another argument against this indicator is that in ecosystems where fisheries simultaneously harvest species at different trophic levels (multispecific fisheries), changes in the MTL become masked and the index remains more or less stable with time, potentially giving the impression of a sustainable fishery through time (Pérez-España et al., 2006).

An example of the above was reported for Colombia's Pacific Ocean coast where direct monitoring of shrimp fishery landings between 1995 and 2007 revealed that the MTL of elasmobranch fishes decreased from 3.60 to 3.55 (Mejía-Falla & Navia, 2010), suggesting that the fishery has not impacted these species considerably. However, using only the MTL value is not sufficient because the authors recorded the loss of shark species at trophic level 4 from the catches (*Carcharhinus* spp. and *Sphyrna* spp.) and an increase in the proportion of species at lower trophic levels. Thus, we suggest that indices based on the MTL of catches alone are insufficient to identify structural changes in trophic networks and to detect possible consequences of these changes on network function.

2.1.5 Topological analysis as a tool to detect the effect of fishing on trophic networks

Nearly all studies dealing with the structure of trophic networks mentioned thus far have focused on assessing the effects of fishing on specific characteristics of the network structure (i.e. proportion of species, trophic level, scaling laws), but almost none has attempted to evaluate the effect of fishing on the global structure of networks and how that structure responds to fishing pressure. Only Gaichas and Francis (2008) assessed the structural configuration of the Gulf of Alaska trophic web, finding that that network has small-world attributes and scale-free network properties, and concluding that fishery management actions should focus on highly connected species, which are those that maintain the structural integrity of the network. However, these authors did not carry out simulations supporting their choice of the most adequate management measures proposed for this trophic network.

2.2 Effects of fishing on the function of trophic networks

Fishing does not only affect network structure. Different levels of fishing pressure can generate multiple effects on the function of species and their interactions. These effects are much more difficult to detect and assess than structural effects and often cause the largest changes in ecosystems because they link the different types of ecosystem control spreading across trophic networks. These mechanisms are referred to as *top-down*, *bottom-up*, and *wasp-waist* (Cury et al., 2003; Pace et al., 1999).

Since fisheries have mostly targeted large species, which exert predatory functions within trophic networks, the most well-known effects to date are those based on the decrease in abundance of those species. A growing body of literature has reported a strong relationship between fishing and decreases in abundance of populations of top predators, with depletions reported to reach such critical levels as 90% of virgin. These reductions have been documented in coastal, benthic, demersal, and pelagic environments and are associated with different fisheries (Baum et al., 2003; Ferretti et al., 2008; Shepherd & Myers, 2005). The decrease in top predator abundance has allegedly led to community restructuring, with their composition (richness and abundance) now being dominated by medium-sized species with lower trophic levels (Ellis et al., 2005; Lotze et al., 2011; Myers et al., 2007). Estes et al. (2011) recently referred to the loss of top predators as "humankind's most pervasive influence on nature".

2.2.1 Trophic cascades and mesopredator release

The decrease in abundance of the large predators, and the associated reduction in top-down ecosystem control mediated through predation or "risk effect", can contribute to the increase in populations of intermediate predators (*mesopredators*)— marine mammals, sharks, rays, and turtles—, thus inducing the formation of trophic cascades (Ferretti et al., 2010; Heithaus et al., 2008). Most published studies have focused on assessing how the decrease in abundance of one species can affect relationships in the trophic network. Hence, the most widely cited and studied effect of fishing on trophic networks is indeed the trophic cascade (e.g. Baum & Worm, 2009; Essington, 2010; Estes et al., 2010; Sandin et al., 2010). This phenomenon has been documented in different marine environments (e.g. Albouy et al., 2010; Andersen & Pedersen, 2010; Casini et al., 2008; Daskalov, 2002; Daskalov et al.,

2007; Estes et al., 1998; Frank et al., 2005; Heithaus et al., 2008; Myers et al., 2007; Pace et al., 1999; Ritchie & Johnson, 2009; Scheffer et al., 2005), and in general all studies describe how a reduction of a large predator population and the ensuing increase in abundance of some of its prey (e.g. seabirds, turtles, reef sharks, and seals) lead to a rapid decline in abundance of species at lower trophic levels and even basal species.

These studies suggest that overfishing can initiate and maintain both structural and functional changes, whose indirect effects can result in a complete reorganization of the network. Frank et al. (2005) even suggested that the trophic cascade effect results from the virtual elimination of the structuring function of large predators in marine ecosystems. In that vein, Bascompte et al. (2005) proposed that trophic cascades reduce the percentage of omnivory and increase the vulnerability of trophic networks to different types of perturbations.

Most of these studies on trophic cascades gave rise to the concept of mesopredator, which has been basically used to refer to medium-sized predator species, which as a result of overfishing of top predators, are increasing in abundance in many marine environments around the world (Beentjes et al., 2002; Levin et al., 2006; Okey et al., 2004; Stevens et al., 2000) and even collapsing populations of their main prey (Myers et al., 2007). More specifically, mesopredator population increases have been mainly recorded in cold and temperate water and low diversity environments such as the western North Atlantic (Choi et al., 2004; Frank et al., 2005), eastern North Atlantic (Blanchard et al., 2005), North Sea (Daan et al., 2005), Baltic Sea (Österblom et al., 2007), and subtropical waters of the North Pacific (Polovina et al., 2009), and we are only aware of a few studies reporting this effect in tropical trophic networks, most of which were carried out in reef ecosystems (Dulvy et al., 2004a, 2004b; Heck et al., 2000; Huges, 1994; McClanahan, 1997, 2000; Ward & Myers, 2005). Sandin et al. (2010) concluded that results of research in tropical coastal ecosystems provide good evidence of "prey release", but only limited support for trophic cascades.

2.2.2 Functional redundancy and ecosystem control

In contrast to the ideas just exposed, Cox et al. (2002) reported that although North Pacific fisheries substantially decreased predator abundance, evidence for the onset of trophic cascades is very limited. Similarly, it has been documented that decreases in abundance of large predators, especially sharks, do not necessarily trigger a mesopredator effect, and that the results and magnitude of this phenomenon could be related to the ecological richness and redundancy of the ecosystem in question (Carlson, 2007; Kitchell et al., 2002; Navia et al., 2010).

Andersen and Pedersen (2010) proposed that fishing can potentially activate trophic cascades, normally buffered both upwards and downwards in trophic networks. They proposed that although the effects of fishing on large predators can be observed even at the plankton level, their intensity is low. They also suggested that when a fishery acts on the different trophic levels of a network, it eliminates the variability characteristic of trophic cascades. Frank et al. (2007) suggested that species diversity and temperature influence potential effects of trophic cascades because high-diversity, warm-water environments have high functional redundancy and if one species is reduced, another could occupy its niche and thus prevent or buffer the trophic cascade. These authors even proposed that while low-

diversity, cold-water environments could succumb to top-down ecosystem control effects and their recovery would be very difficult (if at all possible), warmer water environments could oscillate between top-down and bottom-up ecosystem controls according to the level of fishing and shifting temperature regimes.

In general, the fact that most studies reporting top-down control effects and hence trophic cascades are based on cold-water, high-latitude environments (e.g. Estes et al., 2010; Frank et al., 2005, 2007) has to do with these ecosystems exhibiting several characteristics important for these phenomena to be observed in the first place: they are ecosystems of little complexity and low species richness, which translates into low levels of omnivory in the trophic network. These low-diversity marine ecosystems are generally strongly interconnected and highly dependent on trophic interactions that develop within their networks (e.g. Barents Sea between Norway and Russia), which makes them more vulnerable to fishing (Gislason, 2003).

In contrast, ecosystems in tropical latitudes seem to be a little more resistant to the effects of harvesting since time series studies on composition, diversity, and volume of catches show much weaker effects than those recorded in cold and temperate ecosystems (Harris & Poiner, 1991; Sainsbury, 1991; Sainsbury et al., 1997). For example, Hinke et al. (2004) modeled the effects of different oceanic fisheries on trophic networks in the Pacific Ocean finding that a population decline of scombrids of the genus *Auxis* led to increases in biomass of other species of similar trophic level and function. They attributed these population increases to the reduction of predation by tunas due to fishing, but ignored that the population reduction of *Auxis* spp. is precisely what allowed for increased prey availability for species in the same feeding guild, thus facilitating their increase in abundance.

Thus, owing to the importance in their capacity to respond, ecosystems must maintain functional redundancy and the fraction of omnivory to the extent possible since reductions in these characteristics are indicators of fragility and destabilization of the network (Bascompte et al., 2005). Ecosystems subjected to high levels of fishing pressure have already been found to show lower omnivory indices (Morissette et al., 2009). It has also been documented that, in addition to functional redundancy, the identity of predators could play an important role in regulating the lowest trophic levels in the food chain. This is because when the abundance of forage fish (i.e. engraulids and clupeids) declines as a result of fishing, populations of forage invertebrates would not be able to control the abundance of algae thus causing changes in the composition of the trophic network (O'Connor & Brunno, 2007).

Although wasp-waist ecosystem control has been proposed for ecosystems where species at an intermediate trophic level exert control on the flow of energy in the network (Cury et al., 2000; Micheli, 1999), very few studies have assessed the structural significance of this control. Because this control mechanism is based on a single or a few species in very high abundance but also commercially important, one can predict that these ecosystems may become even more vulnerable than those regulated by top-down and bottom-up mechanisms. Jordán et al. (2005) suggested that model ecosystems under wasp-waist are very sensitive to effects on key species because of two main reasons. First, because interactions between wasp-waist species (i.e. anchovies and sardines) are stronger than those between other species pairs because even if these two species do not have direct

interactions between them, they share a large number of predators and prey. This allows for the change in abundance in one of them to spread indirect effects such as "apparent competition" or "exploitation competition" (Menge, 1995). Second, because wasp-waist species have higher population self-regulatory values than those of other species, which according to ecological theory could cause cyclical and chaotic dynamics (Hassell et al., 1976) and unpredictable oscillations in nature (Bakun & Broad, 2003).

2.2.3 Ecopath with Ecosim as a tool to detect the effect of fishing on trophic networks

Mass-balance models have been widely used to explore potential effects of fishing on the structure and function of trophic networks or important species or functional groups in those networks. This tool yields results on the energy and biomass balance of ecosystems as well as parameters or indicators needed to interpret the possible effects that fishing can generate on those ecosystems through time. Most analyses conducted with these models aimed at studying the effects of fishing on trophic networks reviewed in this chapter can be grouped into three categories that analyze different properties of the network: overexploitation of trophic levels, simplification of network structure, and imbalances in biomass and energy fluxes, the latter being the most widely studied.

Nearly all studies based on mass-balance models have shown fishing effects on the structure and function of trophic networks, with imbalances in the proportions of biomass among trophic levels being those most frequently found. More specifically, generalized effects are reductions in biomass of top predators and an increase in the proportion of species at intermediate trophic levels and basal species, suggesting that fishing is shifting ecosystem structure from large species with low abundance and slow developmental cycles to small species with high abundance and faster developmental cycles (Albouy et al., 2010; Arias-González et al., 2004; Barausse et al., 2009; Chen et al., 2008; Coll et al., 2007, 2008a, 2009a, 2009b, 2010; Duan et al., 2009; Lotze et al., 2011; Savenkoff et al., 2007a, 2007b). This generalized effect is reducing the naturally occurring competition among the original species in the network and facilitating the onset of indirect effects that generate competition among species that did not strongly interact before. Similar findings were obtained in southeast Australia with the Atlantis marine ecosystem model (Griffith et al., 2011).

Given the reduction in network complexity and abundance of high trophic level species, transfer efficiency of energy in ecosystems has increased through time. This has been identified as one of the main indicators of functional changes in trophic networks because this transfer indicates how efficient the flow of energy is from one trophic level to the next. Thus, an increase in this indicator suggests that energetic changes at low and intermediate levels can reach the upper portions of the network more quickly, making the ecosystem more vulnerable to the dynamics of basal species and thus more sensitive to environmental change. Many documents have reported an increase in the value of energy transfer of ecosystems subject to fishing (Chen et al., 2008; Coll et al., 2009a, 2009b; Duan et al., 2009; Lotze et al., 2011), and some of them suggested that when fishing stops the effect is reversed, that is, the upward energy transfer of the network decreases (Coll et al., 2009a). This happens because fisheries generally focus on high trophic level species with low levels of yield and biomass flow. Additionally, high connectivity values suggest that if an energy transfer pathway is altered, another will compensate for the loss so that total biomass changes at a given trophic level are minimal; thus, if the biomass of a particular prey

declines, predators will shift to alternate prey (Link et al., 2009). Overholtz and Link (2009) proposed that if systems are dominated by processes from the medium and low trophic levels, they will not become affected by changes in energy fluxes at high trophic levels and will further be protected by the high connectivity of the network components.

Imbalances in energy fluxes caused by the effects of fishing on trophic networks have also been measured with other indices. For example, increasing fishing pressure through time has caused reductions in the "fishing-in-balance index", which is helpful to analyze energy transfer within ecosystems, suggesting that changes in biomass considerably alter energy transfer from the lowest to the highest trophic levels (Pauly & Watson, 2005). These changes in biomass also decrease fluxes between different network components, leading to a reduction in the total yield of the system with increasing fishing pressure (Duan et al., 2009).

Since ascendency is an indicator of ecosystem maturity and a higher value indicates higher resilience to anthropogenic effects on the network, one would expect pristine ecosystems to have high values of ascendency. This relationship between less perturbed trophic networks and a higher value of maturity has been reported for some ecosystems (Morissette et al., 2009), and it has even been documented that the ascendency values of an ecosystem varied during two different time scales, with higher values occurring when fishing pressure was lower (Duan et al., 2009).

Based on results of different mass-balance models, most of which modeled the effects of different levels of fishing pressure in historical or simulated scenarios, the general tendency is that ecosystems reduce their maturity and complexity in direct relation to time and fishing effort. Morissette et al. (2009) explored whether fishing intensity could lead to significant variations in the structure and dynamics of two contrasting ecosystems (one pristine and one exhausted) finding that pristine ecosystems have ecosystem indicators (e.g. system omnivory index, ascendency) that suggest higher resilience and capacity of recovery to potential modifications in the trophic network. Libralato et al. (2010) explored the differences between the trophic networks of a marine protected area and an exploited area and ratified that the environments devoid of fishing pressure show more complex trophic networks that maintain the proportions of species scaling laws and structural and functional properties, and are thus more resistant to different types of environmental or human pressure.

In addition to the dependency of mass-balance models on the quality of information available, Coll and Libralato (2011) highlighted another important limitation of this approach in terms of their capacity of prediction of ecosystem changes resulting from fishing effort: the absence of models describing truly pristine ecosystems to use as benchmarks for those that are highly impacted. This problem is particularly notorious in the Mediterranean Sea where many studies describing the effects of fishing on ecosystem structures have been carried out, yet not enough information is available on how Mediterranean trophic networks are structured in the absence or at low levels of fishing. This limitation does not only apply to models developed with mass-balance analyses, but also to all models built using information based on harvesting activities in the study areas.

However, as proposed by Essington (2007), ecosystem models in tandem with a reflective analysis incorporating uncertainty could serve as the starting point for management actions, and therefore it is important to incorporate this type of analysis to generate models in the future. Some studies have already made a first attempt at improving this deficiency (Ciavatta et al., 2009; Coll et al., 2008a).

2.3 Effects of fishing on interspecific trophic relationships

2.3.1 Direct and indirect effects

High species diversity has been linked to the stability of trophic networks through the complex interactions that arise among network components, which in turn create multiple spreading pathways of effects through alternate routes that buffer the magnitude of changes (spreading through indirect effects). However, the presence of an indirect effect does not always contribute to network stability.

Results from a large number of studies on fishing effects indicate that the changes in structure and biomass to which trophic networks are subjected to through time trigger indirect effects that can be "visualized" by the establishment of new interactions among network components. These new interactions can be mediated by direct relationships (e.g. predation) or by indirect relationships (e.g. competition) and form the basis of a "new organizational state of the network". If these effects are relatively strong, the network will slowly enter a new organizational state that will be very difficult to leave. These progressive changes have been called *phase shifts* (Scheffer, 2010) and can occur at different scales, from an inversion in the predator-prey relationship that does not affect other species to periodic species replacements to alternate ecosystem states. These changes have already been reported in some marine ecosystems with different degrees of intensity (Barkai & McQuaid, 1988; Cury & Shannon, 2004; Frank et al., 2005; Jackson et al., 2001; Österblom et al., 2007; Scheffer & Carpenter, 2003; Scheffer et al., 2001; Vasas et al., 2007).

Specifically, some authors have reported that in addition to trophic cascades, indirect effects such as *exploitation competition* (Menge, 1995) have been detected in some trophic networks as a result of fishing (Chen et al., 2008; Coll et al., 2007; Duan et al., 2009) and that they could be reflecting phase shifts in these ecosystems. Exploitation competition is an effect that can spread rapidly as a result of a reduction in the abundance of top predators and that has received little attention heretofore. For example, Barausse et al. (2009) suggested that intense fishing pressure in the northern Adriatic Sea reduced fish stocks to such an extent that many of them, without having gone extinct, do not seem to have an impact on the mortality rates of their prey. It is thus possible that different competitors take advantage of this trophic void to increase their feeding rates on new prey items. An example of this was reported by Worm et al. (2005), who proposed that the high degree of diet overlap between whales and adult pelagic fish enabled the onset of exploitation competition between these two groups after the decrease in whale populations between 1950 and 1970 caused by fishing, with a shift from an ecosystem dominated by marine mammals to one dominated by pelagic fish.

2.3.2 Structural changes and phase shifts

A frequently detected effect in this review was the structural change of trophic networks, generally shifting from the dominance of large piscivorous fish to that of small-bodied forage fish, or also leading to the replacement of top predators. However, these are not the only possible or documented changes in alternate stable states or phase shifts in an ecosystem (Scheffer, 2010). For example, Savenkoff et al. (2007a, 2007b) identified, in addition to a change in network dominance, a change in predator structure because the reduction in large pelagic fish abundance allowed for marine mammals to be the only top predators in the system. Along the same lines, a decrease in mean size of the catch has been found in different ecosystems as well as a reduction in mean weight of species and

specimens caught (Zwanenburg, 2000). Levin et al. (2006) documented that between 1980 and 2001 catches of some fish species in the North Pacific increased in volume, but the mean weight of fish caught decreased between 56% and 67%, depending on the species. These authors attributed the changes in mean size of the catch and composition of the fish assemblage to fishing, noting that the species that now dominate the ecosystem have trophic levels and life history strategies very different from those of the species they replaced. Extreme examples of fishing-driven fluctuations in marine ecosystems are kelp forests in the Gulf of Maine, which have undergone three different stable states, from fish to urchins and from urchins to crabs (Bourque et al., 2007), and Nova Scotia coastal reefs, which have fluctuated between kelp forests and urchin barrens three times since 1965 (Steneck et al., 2002).

All these changes will be reflected in prey availability and trophic functions within an ecosystem, enabling the development of new interactions or modifying the strength of current interactions. The relationship between the presence or abundance of species and the strength of interactions has been identified as a force that facilitates the change of state at low trophic levels (Moréh et al., 2009). Some tropical ecosystems, especially coral reefs, have also undergone structural changes in composition, displaying phase shifts or alternate stable states (Hughes et al., 2003; Pandolfi et al., 2003; Sandin et al., 2008), switching from high coral cover, high rates of coral recruitment and low cover of competitive fleshy algae (McClanahan, 1997; Sandin et al., 2008) to ecosystems with low densities of fish biomass, high densities of echinoderms and high cover of fleshy algae (e.g. Dulvy et al., 2004a, 2004b; Pinnegar & Polunin, 2004).

Perhaps one of the most worrisome problems, if not the most important of all associated with the changes just described, is that, together with structural changes, the diet of some species has also been found to be altered, with a switch from diets dominated by fish to diets dominated by invertebrates. These changes cause the alteration of interaction forces between predators and prey and the establishment of a series of new predator-prey relationships and thus direct and indirect effects that could ultimately contribute, as proposed by Mangel and Levin (2005), to fishing modifying ecosystems so profoundly that it would lead them to alternate states where it would be virtually impossible for the species that have significantly decreased in abundance to recover. A possible example is the hypothesis by Springer et al. (2003) to explain the shift from a state dominated by sea otters to an urchin dominated phase in southwest Alaska. They proposed that the post-War World II whaling industry reduced prey availability for killer whales, leading to an expansion of their diet to include pinnipeds and sea otters, which in turn reduced the sea otter population and facilitated a population increase of sea urchins.

2.3.3 Trophic cycles

Population declines of some species could enhance the importance of the so-called trophic network cycles, which would play a central role in the pathways taken by networks under different levels of fishing pressure. Thus, phase shifts lead to the juvenile stages of top predators being more vulnerable to predation and competition than the adult stages of their prey (e.g. Köster & Möllmann, 2000). These changes between developmental stages and predation in fishes have already been well documented (de Ross & Persson, 2002; Worm & Myers, 2003). This phenomenon in turn leads to reduced recruitment rates of top predators, even to such low levels to impair stock recovery after fishing ends. Some authors have

proposed that it was the cause for why cod stocks in the North Atlantic and Baltic Sea have not recovered more than 15 years after fishing ceased.

2.3.4 Keystone species and fisheries

Another way in which fisheries have caused changes in interspecific trophic relationships with various ecosystem effects is when they have acted directly or indirectly on the keystone species of an ecosystem resulting in the creation of new trophic or even spatial (habitat modification) organizations. The latter case has been reported in some reef ecosystems where fishing removed predators and competitors of echinoderms (i.e. sea urchins, crown of thorns starfish), spreading indirect effects of reduction in algal cover and reef erosion, allowing for new dominant species to become established and ultimately modifying the biotic structure of the reef (Dulvy et al., 2004a, 2004b; Hughes, 1994; McClanahan & Muthiga, 1988; McClanahan et al., 1996, 2002; Pinnegar & Polunin, 2004). McClanahan et al. (2007) reported that almost 40 years after fishing stopped, the biomass of reef fishes in Kenya has recovered and is close to virgin levels, which in turn has increased predation levels on sea urchins in marine protected areas, leading to the recovery of coral cover and benthos heterogeneity.

In the coasts of Alaska and Canada, sea otters and some fish species act as keystone species predating on sea urchins and regulating their effect on the abundance of kelp forests, which support a large number of species in these regions. Thus, strong fishery impacts on sea urchin predators intensified grazing and the deterioration of kelp forests, leading to marked changes in the fauna of that ecosystem (Duggins et al., 1989; Estes & Duggins, 1985; Reisewitz et al., 2005; Tegner & Dayton, 2000).

Below we present a map showing the geographical distribution of the different effects of fishing on trophic networks presented throughout this chapter and covering all literature cited (Figure 1). It is expected that the number of ecosystems affected by fishing will grow considerably as new studies on the effect of fishing on trophic webs are completed.

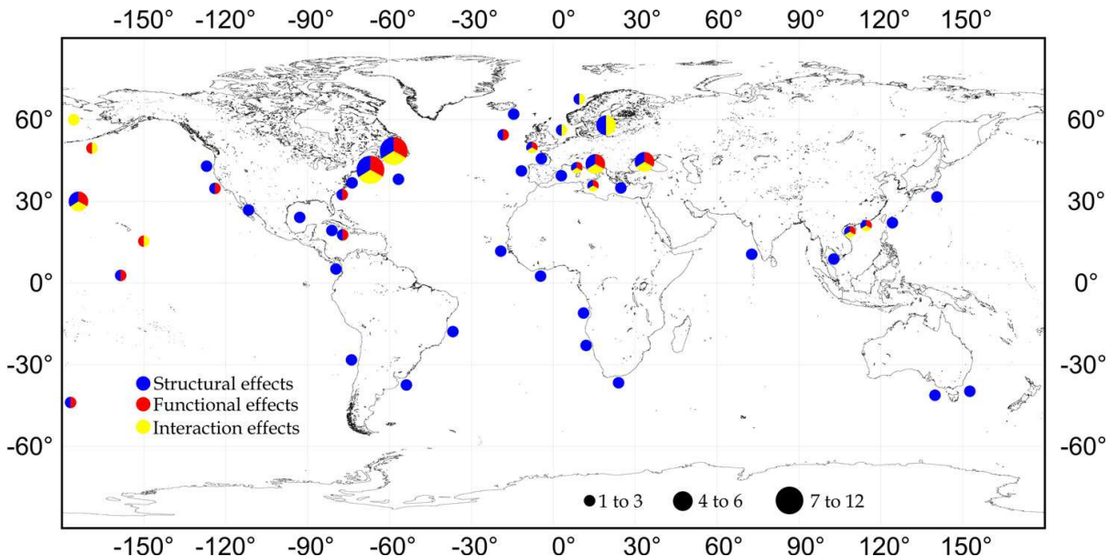


Fig. 1. Geographical distribution of studies reporting fishing effects on the structure, function, or interactions of trophic networks. The map is a simplification as these effects are often interrelated.

3. Case study

Although analyses of secondary extinction have been widely used as mechanisms to assess the resistance of trophic networks to species loss (Dunne et al., 2004; Solé & Montoya, 2001), we believe the assumption implicit in those analyses is a major simplification of the natural dynamics of trophic networks because a predator that loses one or more prey could adapt to use another available resource. In contrast, if the local extinction of a species does occur, it is very likely that the network becomes fragmented to some extent and, depending on the connectivity and topological importance of the species removed, the network could be led to a new organizational state.

Thus, assuming that the way in which species in a network organize and interact is important for network stability, it has been proposed that the consequences of *small-world* and *scale-free* structural patterns may be of great importance in recognizing the sensitivity to perturbations in biological networks (Montoya & Solé, 2002). It has also been demonstrated that a regular network can be transformed into a small-world network if a small proportion of nodes are reconnected to some randomly chosen nodes.

The small-world structural pattern, which is based on grouping of nodes, has shown to be useful to provide quick answers to different perturbations in some theoretical trophic networks, suggesting that this structural arrangement can be of benefit for network resilience. Solé and Montoya (2001) and Montoya and Solé (2002) determined that trophic networks with a small-world structural arrangement were more resistant to secondary species extinctions than those with random structure.

With the evidence presented throughout this chapter, we suggest that trophic networks are becoming simplified, some ecosystems are undergoing state changes, and in many others the proportions of species have been altered, all of which implies that large-scale structural patterns of trophic networks (e.g. scale-free, small-world) are being affected.

The Gulf of Tortugas in the Colombian Pacific Ocean has been subject to intense fishing since 1960. Although the target of these fisheries is shallow-water shrimp, a large number of fish and invertebrate species are also caught as bycatch. Several studies of the feeding habits of these species have been conducted in the area, facilitating the description and understanding of the community food web (Navia et al., 2010). However, the effect of fishing on that network has not yet been assessed. Thus, taking into account the structural consequences of fishing on networks, we designed an exercise to assess whether the trophic network of the Gulf of Tortugas displays a small-world structure, and if so, test the hypothesis that sustained fishing pressure can modify network structure, taking it from a small-world arrangement to a random one (Figure 2).

The first step was to assess whether the structure of the Gulf of Tortugas network meets the requirement of scale-free node distribution, and therefore can display a small-world arrangement. To that end we conducted two analyses. First, we computed a frequency distribution of the number of connections by node (node degree) of the original network (250 nodes and 579 interactions), and second, we calculated a frequency distribution (in log scale) of the node degree of a network with random structure, built with the same

number of nodes (250) and interactions (579) as the original network. Results were as follows:

1. Frequency distribution of the node degree of the original network: this analysis showed a power distribution of connections by node, i.e., the network displays many nodes with very few connections and very few nodes with a large number of connections. This type of distribution is characteristic of networks structured in a small-world arrangement and is known as a scale-free distribution (Figure 3a).
2. Frequency distribution of the node degree of the random network: this analysis, which was generated with the computer program Pajek (http://pajek.imfm.si), showed a Poisson frequency distribution, which is expected in trophic networks that adhere to a random structure (Montoya & Solé, 2002) (Figure 3b).

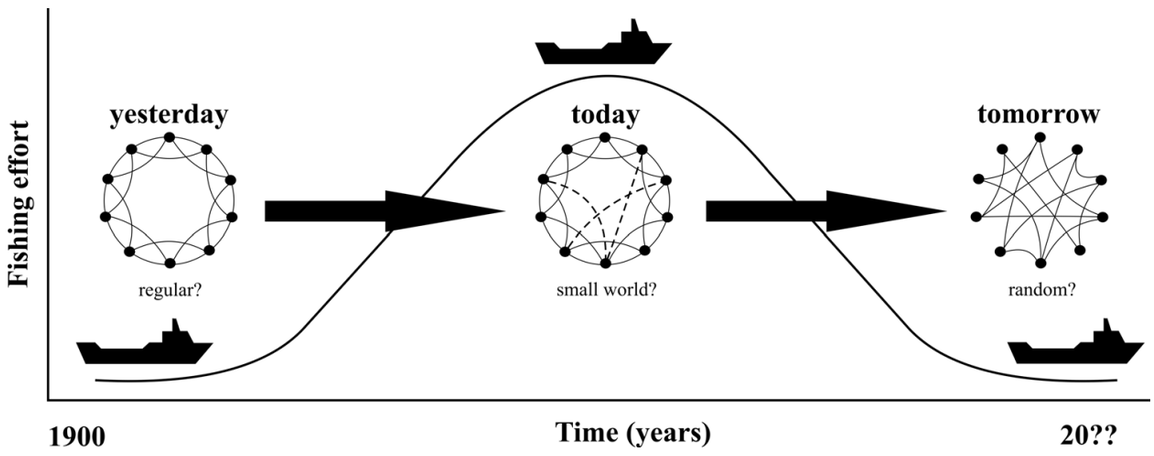


Fig. 2. Schematic representation of the hypothesis of the effect of fishing on the structure of trophic networks.

Based on these results, the fundamental principle for the trophic network under study to have a small-world structure is met, i.e., that the node degree follows a scale-free distribution. Next, to test our question of whether fishing effects can modify or at least induce changes in the structure of a trophic network, switching from a small-world to a random structure (or at least show a tendency), we chose two important structural features of networks: the *clustering coefficient* (CC) and the average *path length* (PL). The first index is helpful to determine the extent to which some groups of species are more connected internally than with other groups; the second index measures the average number of steps along the shortest paths to connect all possible node pairs in the network and is useful as a measure of the efficiency of information transport or mass transport in a network. Thus, a trophic network maintains its small-world structural arrangement if the CC of the observed network is greater than that of a random network of the same characteristics (nodes and interactions). Both small-world and random networks have low values of PL.

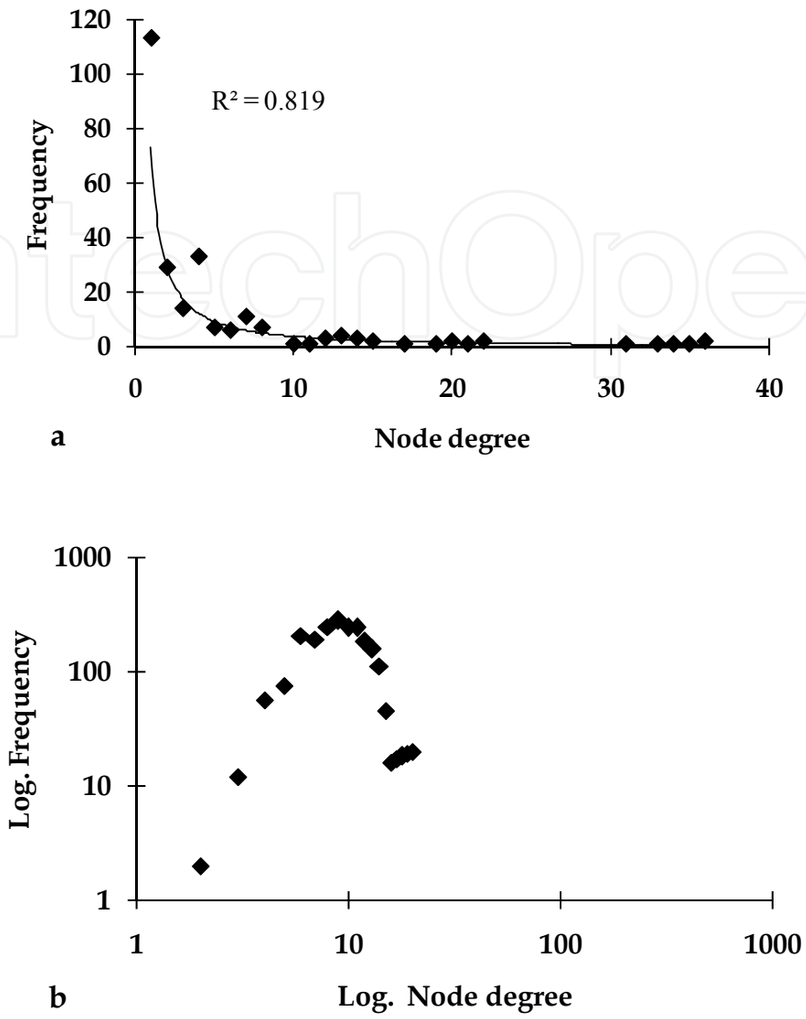


Fig. 3. Frequency distribution of the node degree of the trophic network in the Gulf of Tortugas. a) original network, b) random network generated with the same number of nodes and interactions as the original network.

These indices were selected because they have an ecological support that strengthens potential results. More specifically, CC is a measure that may indicate the degree of functional similarity of a trophic network, and therefore could be an indirect reflection of the functional redundancy in the network; trophic networks with high values of CC will be more interconnected and therefore greater functional redundancy is to be expected. On the other hand, PL is an indicator of the quantity of indirect interactions that can be established within a trophic network and therefore, of the buffering capacity of the network to a given effect. Changes in these indices, indicating the transition from a small-world to a random network, will imply that the new network will have a very short average path length and thus, since there is not much distance between species, an effect will rapidly spread throughout the network without finding many possible paths (indirect effects) for it to be

buffered. Additionally, random networks do not have significant values of CC, which suggests that species with diet similarities have decreased and that functional redundancy perhaps is no longer significantly present to serve as biological insurance for the network.

To develop this exercise we decided to assess the effect of two criteria for selecting species to be removed from the network and simulated the removal of those species as a result of fishing. The first criterion was fishery importance (commercial value of species) in the study area, and the second criterion was topological importance of the species in the trophic network.

Species of commercial importance:

These species were selected based on the presence of fishing fleets that have exerted historical pressure on these resources and their trading prices because, since they are the species of higher commercial value, their fisheries have been more intense than those of other species in the network. The species selected were:

- Shrimps
- Snappers
- Clupeiforms, in particular *Cetengraulis mysticetus* and *Ophistonema libertate*, which make up the so-called "carduma", which is the object of a targeted fishery.

Species of topological importance:

Network analysis provides a number of tools that can support quantitative community ecology. In particular, there exist techniques for quantifying the positional importance of species (system components) in food webs. Species that are of high importance in a trophic network can be in either central (like hubs) or unique positions. The latter can be interpreted as species having non-redundant neighborhoods. As a result, their extinction (or overfishing) has profound effects on the ecosystem. Here we present and use the *TO* index for quantifying *topological overlap*. *TO* is a mesoscale network index, considering also non-local neighborhood, but weighted by distance (i.e. not considering the whole network equally important). This is quite sound in ecology, as a suite of field and theoretical results support the importance of indirect interactions.

Several mesoscale indices have already been suggested in network science, most of them considering distance between nodes (e.g. closeness and betweenness centrality [Wasserman & Faust, 1994]). Some of these indices have been applied to ecological problems (Estrada, 2007; Jordán et al., 2007). Others have been slightly modified and adapted to ecology (see net status [Harary, 1961] and keystone index [Jordán et al., 1999]) or simply developed by ecologists (measuring apparent competition [Godfray et al., 1999; Müller et al. 1999]). We use a sophisticated version of the latter index, as it is quite general and suitable for quantifying redundancy of neighborhoods (uniqueness and replaceability of species).

The *topological importance* (*TI*) index (Jordán et al., 2009) makes it possible to analyze indirect interactions of various lengths separately (up to a 3-step-length). It assumes a network with undirected links where interspecific effects may spread in any direction without bias (we are interested in interaction webs, in the broadest sense, but considering only indirect chain

effects [Wootton, 1994]). The effect of species j on species i, when i may be reached from j in n steps, is defined as $a_{n,ij}$. When n=1 (*i.e.* the effect of j on i is direct): $a_{1,ij} = 1/D_i$, where D_i is the degree of node i (i.e. the number of its direct neighbors including both prey or predatory species). We assume that indirect chain effects are multiplicative and additive. When the effect of step n is considered, we define the effect received by species i from all N species in the same network (see Equation 1)

$$\Psi_{n,i} = \sum_{j=1}^{N} a_{n,ij} \tag{1}$$

which is equal to 1 (i.e. each species is affected by the same unit effect). Furthermore, we define the n-step effect originated from a species i (see Equation 2)

$$\sigma_{n,i} = \sum_{j=1}^{N} a_{n,ji} \tag{2}$$

which may vary among different species (i.e. effects originated from different species may be different). Here, we define the topological importance of species i, when effects up to n steps are considered (see Equation 3)

$$TI_i^n = \frac{\sum_{m=1}^{n} \sigma_{m,i}}{n} = \frac{\sum_{m=1}^{n} \sum_{j=1}^{N} a_{m,ji}}{n} \tag{3}$$

which is simply the sum of effects originated from species i up to n steps (one plus two plus three…up to n) averaged over by the maximum number of steps considered (n). With this index, it is possible to quantify the origins of effects influencing a particular species, i.e. the internal interaction structure of the network.

The $a_{n,ij}$-values for species j had been defined as its "trophic field" (Jordán, 2001). For long indirect effects, every species is connected to every other. It is reasonable to define a t threshold of $a_{n,ij}$-values separating strong interactive partners from weak interactors. Given a maximum length of indirect effects (n) and a threshold for interaction strength (t), every node may be characterized by its effective trophic range (Jordán et al., 2009). Since the sets of strong interactors of two, or more, nodes may overlap, it is important to quantify the positional uniqueness of graph nodes. The "trophic field overlap" (TO^{n}_{ij}) between nodes i and j is the number of strong interactors appearing in both i's and j's effective range. The sum of all TO-values between species i and others ($\Sigma TO^{n,t}_{ij}$ summed over all j with $i \neq j$) provides the summed trophic field overlap of species i ($TO^{n,t}_{i}$), and this may be normalized by dividing it with the maximum value ($TO^{n,t}_{max}$) for a given network ($relTO^{n,t}_{i} = TO^{n,t}_{i} \,/\, TO^{n,t}_{max}$). Note that all this is determined by t, n and the topology of the network. We define the "topological uniqueness" of species i as $TU^{n,t}_{i} = 1 - relTO^{n,t}_{i}$. Here, we used n=3 and t=0.001. This index may contribute to the problem of how to quantify species and role and redundancy in ecosystems (Bond, 1994; Luczkovich et al., 2003; Shannon & Cury, 2003).

Results of TU^3 showed that nodes 50 (*Carcharhinus leucas*), 218 (*Sphyrna lewini*), and 103 (*Galeocerdo cuvier*) had the greatest topological uniqueness (Figure 4) and were the most difficult to replace because there are no other species that can overlap their function.

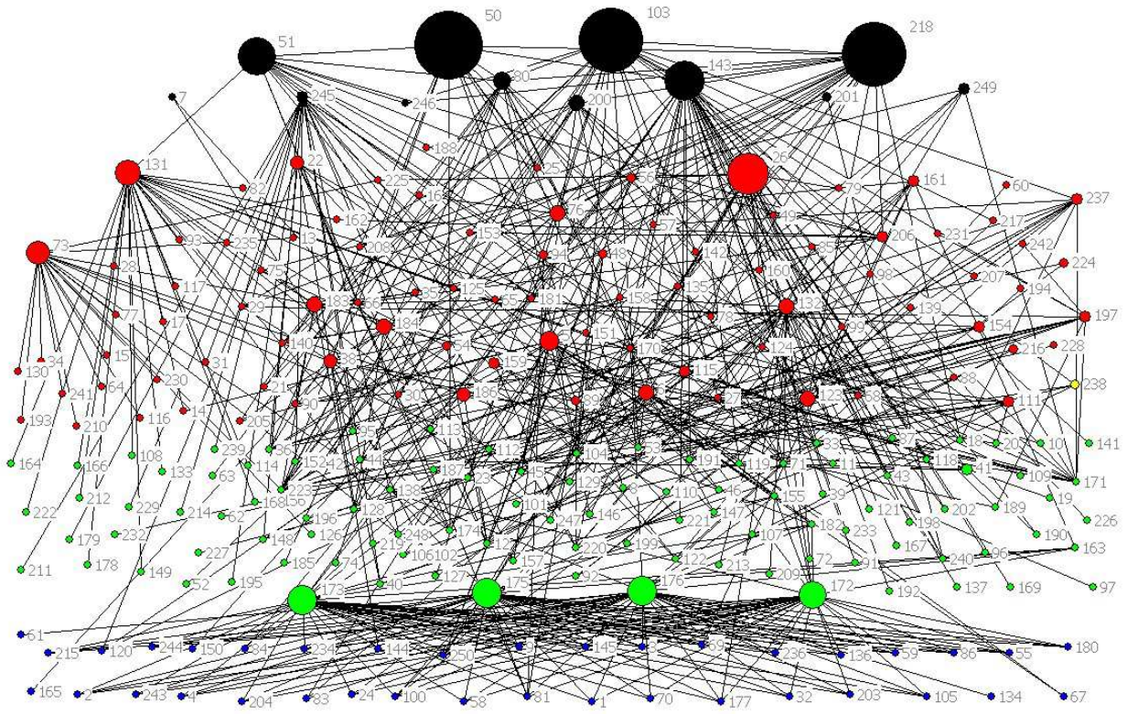


Fig. 4. Schematic image of the trophic network of the Gulf of Tortugas based on TU^3. The size of the nodes is directly proportional to topological uniqueness, indicating the low redundancy of their neighborhood. Black: elasmobranchs; red: teleosts; green: invertebrates; blue: zooplankton and phytoplankton.

To assess the effect of fishing on the structure of the trophic network of the Gulf of Tortugas, we compared values of CC and PL of the original network to those of the corresponding random network in different scenarios under the two criteria defined above (commercial importance and topological importance). The scenarios consisted of leaving the network unaltered and then sequentially removing the groups defined above to simulate the effect of fishing. The scenarios were as follows:

Species of commercial interest

Scenario 1. The trophic network was left unaltered (250 nodes, 579 interactions), without eliminating any nodes (initial network), and values of CC and PL calculated for this and the corresponding simulated network. Based on the analyses described at the beginning of this section (scale-free distribution) and the CC and PL results, we established that the Gulf of Tortugas network displays small-world structure.

Scenario 2. The nodes representing shrimps in the trophic networks were removed and values CC of PL calculated for this and the corresponding simulated network (232 nodes and 398 interactions).

Scenario 3. In addition to the shrimp nodes, nodes representing snappers were also removed and values of CC and PL calculated for this and the corresponding simulated network (229 nodes and 349 interactions).

Scenario 4. In addition to the previous removals, nodes representing the "carduma" category were also removed and values of CC and PL calculated for this and the corresponding simulated network (226 nodes and 329 interactions).

Species of topological importance (TU^3)

Scenario 1. The trophic network was left unaltered (250 nodes, 579 interactions), without eliminating any nodes (initial network), and values of CC and PL calculated for this and the corresponding simulated network. Based on the analyses described at the beginning of this section (scale-free distribution) and the CC and PL results, we established that the Gulf of Tortugas network displays small-world structure.

Scenario 2. The node with the greatest topological importance in the trophic network was removed (50, *Carcharhinus leucas*) and values of CC and PL calculated for this and the corresponding simulated network (249 nodes and 565 interactions).

Scenario 3. In addition to node 50, the second-most important node topologically was removed (218, *Sphyrna lewini*) and values of CC and PL calculated for this and the corresponding simulated network (248 nodes and 543 interactions).

Scenario 4. In addition to the removal of the previous nodes, node 103 (*Galeocerdo cuvier*), which was the third-most important topologically, was also removed and values of CC and PL calculated for this and the corresponding simulated network (247 nodes and 520 interactions).

Fisheries and species of commercial interest

In terms of the loss of high-value commercial species, one can see that the relationship between the CC of the observed and the random networks is not significantly modified, with the value of the observed network always being higher (Figure 5a). These results suggest that the loss of these species does not cause any detectable effects on the compartmentalization of the network or on the interactions that take place in those compartments. Not even the loss of shrimps (one of the groups with the highest centrality within the network) results in any indication of alterations in the CC pattern of the network. Since the CC values of the observed networks are higher than those of the corresponding random networks, the small-world organization in the trophic network of the Gulf of Tortugas is maintained, even with the loss of species of high commercial value.

In all scenarios explored, the observed trophic networks had, on average, shorter paths between the most distant nodes than those of the random networks (< 2) (Figure 5b), which is characteristic of trophic networks with a small-world structure (Williams et al., 2002), and has been found in other work using this type of analysis (e.g. Gaichas & Francis, 2008). This feature is important in terms of spreading effects within the network because indirect effects with an average length of 2 (e.g. apparent competition or keystone predation) tend to dissipate when the average is greater than 3 steps, and therefore reduce the capacity of buffering the spread of effects within the network.

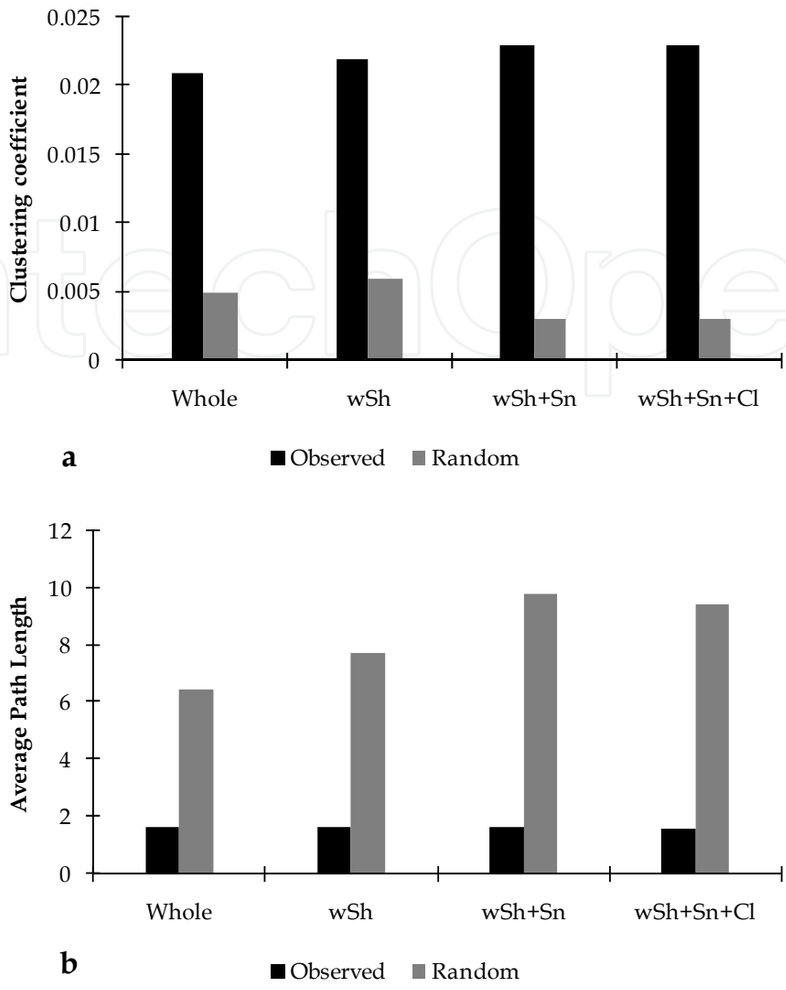


Fig. 5. Clustering coefficient (a) and average path length (b) values of the observed networks and their corresponding simulated networks in each scenario. These scenarios correspond to the removal of species with high commercial value. Whole: entire network; wSh: without shrimps; wSh+Sn: without shrimps or snappers; wSh+Sn+Cl: without shrimps, snappers or "carduma".

In terms of the relationship between the observed and random PL values, one can see that the loss of shrimps has the largest effect on the relationship because once snappers and clupeiforms are removed, PL values of the simulated networks increase relatively little. This could be due to the fact that shrimps are, among high-valued species, those with the highest centrality in the network and therefore their removal leads to a significant effect in the connectivity of the network.

Fisheries and species of topological importance

A rather different pattern from that previously described can be observed when removing species of high topological importance. The original trophic network also has higher CC values than the simulated network, but upon removal of nodes, CC values of the observed

networks decrease whereas those of the simulated networks tend to increase. This tendency is rather strong because when reaching scenario 4 (removal of nodes 50, 218, and 103), the CC value of the observed network becomes lower than that of the simulated network (Figure 6a). These results suggest that the small-world organization of the trophic network of the Gulf of Tortugas has been significantly altered, perhaps to the extent of losing it.

In terms of the relationship between the observed and random PL values for species of topological importance, one can see that the loss of these nodes does not affect the network since the PL values of both the observed and simulated networks remain relatively constant in the four scenarios (Figure 6b).

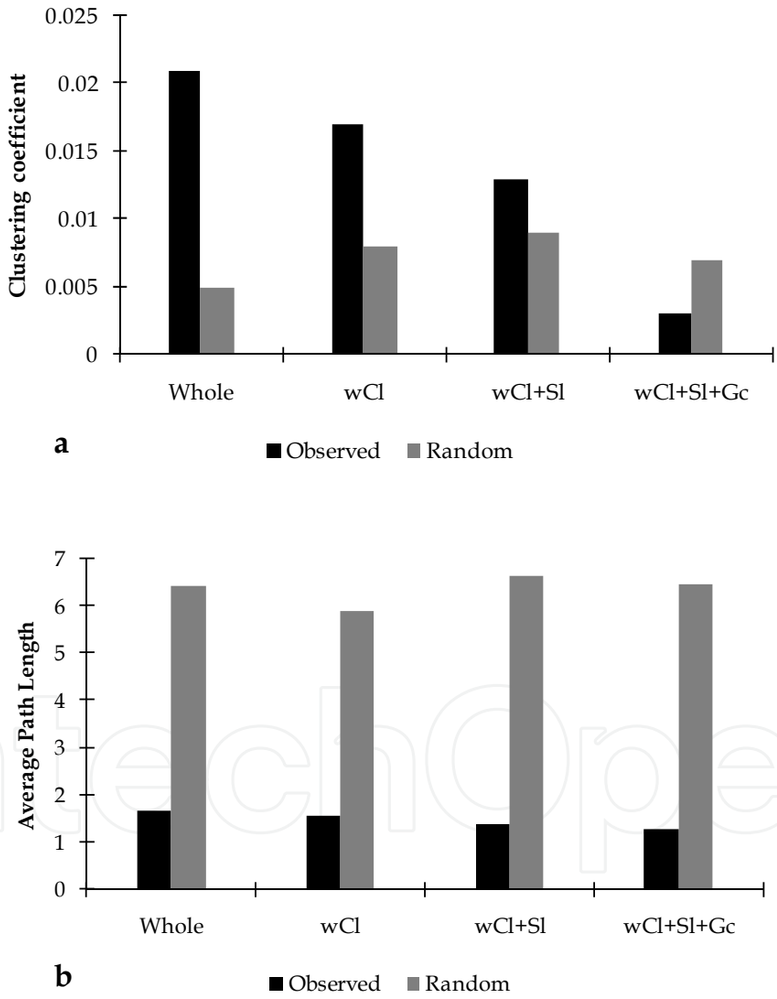


Fig. 6. Clustering coefficient (a) and average path length (b) values of the observed networks and their corresponding simulated networks in each scenario. These scenarios correspond to the removal of species with high topological importance. Whole: entire network; wCl: without *Carcharhinus leucas*; wCL+Sl: without *C. leucas* or *Sphyrna lewini*; wCL+Sl+Gc: without *C. leucas*, *S. lewini* or *Galeocerdo cuvier*.

Results of this exercise suggest that the trophic network of the Gulf of Tortugas in the Colombian Pacific Ocean display properties typical of a small-world structural arrangement and a scale-free interaction distribution. These results are thus relevant in terms of network stability and even fisheries management because it has been reported that these features are important for network stability. This seems consistent with the fact that removing the two groups with the highest connectivity in the network (shrimps and snappers) did not cause an effect indicative of a substantial alteration of the structural properties of this network. However, our results showed that trophic networks with a small-world organization are susceptible to the removal of species of high topological importance, especially those that have low positional redundancy within the network. In this case, three top predators are the species of highest topological importance in the network.

This exercise, which represents only a first attempt at assessing the effects of fishing on the structural features of a highly complex network, and the first at applying this type of approach to a purely tropical environment, must be supported with the exploration of additional scenarios to corroborate that the Gulf of Tortugas network is indeed highly resistant to the targeted removal of species with high connectivity and economic importance, but not to that of species of topological importance. Finally, based on these results, we highlight the importance of adopting fishery management measures involving not only species of high commercial value, but also those that play unique roles in the network by contributing disproportionately to the structure and stability of marine trophic networks.

4. Conclusions

Some have proposed that the solution to the current biomass reductions of some commercial species is a decrease in fishing mortality or even a complete cessation of fishing. As an example, Chen et al. (2008) proposed that adopting different strategies of reduction in fishing mortality in the Gulf of Beibu, China, would allow the biomass of most species in the network to increase by almost an order of magnitude, which seems like a simplistic proposal and ignores many important considerations of trophic network dynamics, which we present next.

Trophic networks are complex structures that establish high levels of interaction among their elements and therefore maintain dynamic processes that contribute to their stability. As reviewed throughout this chapter, fisheries can affect trophic networks from several perspectives: structural, functional, or in terms of the trophic interactions among species, and an effect generated by one of these aspects will likely affect the others.

Although we divided the effects in three themes for ease of understanding, they are all interrelated and become magnified as fishing pressure increases. For example, a trophic network that suffers a "simple" imbalance in the proportion between predators and prey could spread an indirect effect, which in turn could foster an interaction that was not previously significant. If the species involved are not adapted to adjust to this new dynamic, some of them may experience population declines that could spread another sequence of indirect effects like those mentioned, which could even modify some ecosystem functions. Thus, all these processes can add up and magnify to the point of producing a larger change in some of the species in the network and lead to the so-called phase shift. Alternatively, if the network is highly redundant, the effect may not be visible because it might dissipate throughout the network.

The problem with this hypothetical sequence of changes is that fishing pressure on trophic networks does not only affect the structural features of the network, but also promotes indirect effects that can force functional changes and lead to irreversible modifications. The magnitude of these changes is related to fishing intensity and the time it is exerted on the network.

The conclusion is therefore that under current levels of fishing pressure most trophic networks are headed towards experiencing phase shifts to a greater or lesser extent and in different time and intensity scales. For example, trophic networks in cold and temperate ecosystems and wasp-waist trophic networks have a higher likelihood of being impacted by fishing effects and cause phase shifts with little probability of return than those in tropical ecosystems. These changes have already been evidenced from trophic cascade effects reported in these ecosystems. Modifications of these trophic networks are so marked in some cases that, although fisheries have not operated for many years, predator populations have not returned to their initial states.

In the case of tropical ecosystems, the high diversity, connectance, and interactions among highly redundant species lead to fishing effects dissipating somewhat in the trophic web and thus being less apparent, yet still present. Another issue is that in tropical ecosystems, multispecific fisheries operate that extract species at all trophic levels, which could lead to imbalances in the structural and mass-balance properties not being easily observed, perhaps masking functional or interaction effects dangerous for network stability.

To know the real effects that fishing can generate on trophic networks it is first necessary to understand the forces that condition the interactions and dynamics among species, such as the capacity of species to switch to new prey types once the abundance of current prey is reduced, the effect of ontogenetic changes on the functional redundancy of species, and the importance of mutual predation on the population dynamics of species, among others.

5. Acknowledgments

AFN thanks IPN-CICIMAR and CONACYT, and PAMF thanks COLCIENCIAS for providing funding for their PhD degrees. VHCE thanks SNI, IPN-EDI, IPN-COFAA and SIP-IPN-20120949. This study was partially supported by COLCIENCIAS-SQUALUS (Grant RC No. 156-2010).

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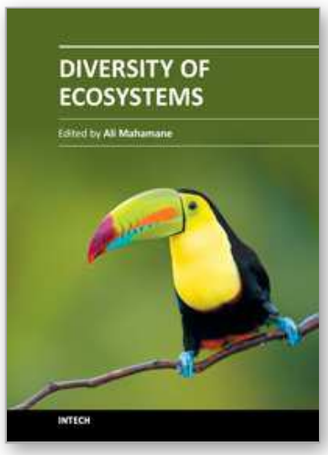
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Diversity of Ecosystems
Edited by Prof. Mahamane Ali

ISBN 978-953-51-0572-5
Hard cover, 484 pages
Publisher InTech
Published online 27, April, 2012
Published in print edition April, 2012

The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

How to reference
In order to correctly reference this scholarly work, feel free to copy and paste the following:

Andrés F. Navia, Enric Cortés, Ferenc Jordán, Víctor H. Cruz-Escalona and Paola A. Mejía-Falla (2012). Changes to Marine Trophic Networks Caused by Fishing, Diversity of Ecosystems, Prof. Mahamane Ali (Ed.), ISBN: 978-953-51-0572-5, InTech, Available from: http://www.intechopen.com/books/diversity-of-ecosystems/changes-to-marine-food-webs-caused-by-fishing

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Phone: +86-21-62489820
Fax: +86-21-62489821

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