Ecosystems (2008) 11: 939–960
DOI: 10.1007/s10021-008-9171-y

ECOSYSTEMS

# Structural Degradation in Mediterranean Sea Food Webs: Testing Ecological Hypotheses Using Stochastic and Mass-Balance Modelling

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## ABSTRACT

Human-mediated disturbances such as fishing, habitat modification, and pollution have resulted in significant shifts in species composition and abundance in marine ecosystems which translate into degradation of food-web structure. Here, we used a comparative ecological modelling approach and data from two food webs (North-Central Adriatic and South Catalan Sea) and two time periods (mid-late 1970s and 1990s) in the Mediterranean Sea to evaluate how changes in species composition and biomass have affected food-web properties and the extent of ecosystem degradation. We assembled species lists and ecological information for both regions and time periods into stochastic structural and mass-balance food-web models, and compared the outcomes of 22 food-web properties. Our results show strong similarities in structural food-web properties between the North-Central Adriatic and South Catalan Seas indicating similar ecosystem structure and levels of ecological degradation between regions and time periods. In contrast, a comparison with other published marine food webs (Caribbean, Benguela, and US continental shelf) suggested that Mediterranean webs are in an advanced state of ecological degradation. This was reflected by lower trophic height, linkage density, connectance, omnivory, species involved in looping, trophic chain length and fraction of biomass at higher trophic levels, as well as higher generality and fraction of biomass at lower trophic levels. An analysis of robustness to simulated species extinction revealed lower robustness to species removals in Mediterranean webs and corroborated their advanced state of degradation. Importantly, the two modelling approaches used delivered comparable results suggesting that they both capture fundamental information about how food webs are structured.

**Key words:** food-web modelling; network analysis; ecosystem degradation; human impacts; robustness to species removal; Niche model; Ecopath model; Mediterranean Sea.

## INTRODUCTION

Degradation of marine ecosystems around the world through overexploitation, habitat destruction, pollution, invasion, and climate change has led to significant alterations in species composition

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Received 18 November 2007; accepted 30 June 2008; published online 13 August 2008

**Electronic supplementary material:** The online version of this article (doi:10.1007/s10021-008-9171-y) contains supplementary material, which is available to authorized users.

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and abundances (for example, Jackson and others 2001; Baum and others 2003; Lotze and Milewski 2004; Myers and Worm 2005; Lotze and others 2006) that have the potential to affect the structure and functioning of marine ecosystems and impair the maintenance of goods and services provided to humans (for example, Margalef 1968; Odum 1969, 1985; Pauly and others 1998; Steneck and Carlton 2001; Pauly and others 2002; Cury and others 2003; Lotze and others 2005; Jackson 2006; Worm and others 2006). Recent studies have suggested that although shifts in species compositions are an important way of identifying ecosystems that are degraded, a more holistic understanding which merges structural and functional effects may be gained by viewing a community as a network of feeding interactions (for example, Christensen and Pauly 1993; Dunne and others 2002; Bascompte and others 2005). These food-web networks provide a topological picture of the interactions of species in a community and can inform our understanding of ecological degradation as impacted food webs often display highly characteristic properties such as being short and fat, a lack of high trophic level predators, and a high proportion of basal species (Dell and others 2005).

The Mediterranean Sea may be one of the most degraded marine ecosystems worldwide as it has been inhabited and influenced by human civilizations for millennia (Margalef 1985; Hughes 1996; Lotze and others 2006). Today, its coast supports about 132 million inhabitants (AAVV 2008) and is considered the top tourist destination in the world. Currently, many species in the Mediterranean Sea are threatened by overexploitation of biological resources, direct habitat modification of sea and coastal areas, introduction of exotic species, pollution and climate change, and several marine species are presently listed as endangered (Bianchi and Morri 2000). Ecological changes that occurred in Mediterranean ecosystems over the past include proliferation of species and invasions (for example, Piccinetti and Piccinetti Mandrin 1984; Galil 2000; Daskalov and others 2007), change in species distribution due to climatic and environmental changes (for example, Lloret and others 2004; Sabates and others 2006; Santojanni and others 2006), harmful algal blooms and eutrophication (for example, Legovic and Justic 1997; Turley 1999; Kideys 2002). Evidence of fishing activity can be traced back to ancient times all over the Mediterranean Sea (for example, Cutting 1956; CIESM 2000; Florido 2004), and its coastal regions were already considered overexploited at the beginning of the nineteenth century (Margalef 1985) and show structural changes (Sala 2004). Today, the Catalan and Adriatic Sea shelf ecosystems are subjected to high levels of fishing impact (Coll and others 2006a, b, 2007), and several of their marine resources are highly exploited or overexploited (for example, Papaconstantinou and Farrugio 2000; Bass and others 2003; Bombace and Grati 2007; Tsounis and others 2007; Tudela 2004), while fishing is continuously developing towards deeper areas.

Common indicators of ecological degradation in marine ecosystems are the depletion of biomass at high trophic levels, the simplification of food webs, and shifts in biomass and productivity towards lower trophic levels. To determine whether these indicators apply to the North-Central Adriatic and the South Catalan Sea, we assembled feeding networks closely based on previous modelling work (Coll 2006; Coll and others 2006a, b, 2007, 2008) for the mid-late 1970s and mid-late 1990s. Although many of the detailed ecological changes in these ecosystems have been described in previous publications, we here focus on the overall changes in food-web structure and functioning. For this purpose, we used two different modelling approaches: a stochastic structural food-web model, the Niche model, which is an extension of the Cascade model and uses species richness ($S$) and connectance ($C = \text{Links/Species}^2$) as input parameters to construct a web (Williams and Martinez 2000), and a mass-balance model, Ecopath model, which integrates information on functional groups (or trophic groups), biomasses and flows (Pauly and others 2000; Christensen and Walters 2004). These two approaches are very different with respect to their configuration, input parameters and assumptions and thus should provide insight into more general and not model-specific results.

Our objectives were fourfold:

(1) To determine whether structural changes in the North-Central Adriatic Sea and the South Catalan Sea from the mid-late 1970s to the mid-late 1990s show increasing ecological degradation as indicated by (i) reduction in the mean and maximum trophic level, reductions in the fraction of top predators and increases in the fraction of basal species; (ii) simplification of the food web, with less complexity, decreased connectivity and shorter food-chain length; and (iii) changes in productivity and biomass allocation, with lower total biomass, lower biomass at high trophic levels and higher biomass at intermediate or low trophic levels, and higher turn-over rates;

(2) To compare food-web properties and the extent of ecological degradation of the North-Central Adriatic and the South Catalan Seas with other previously published marine food webs outside the Mediterranean Sea;
(3) To examine whether the North-Central Adriatic and South Catalan Seas were less robust to species loss than other marine food webs;
(4) To assess whether different food-web models (for example, structural versus mass-balance model, such as the Niche versus Ecopath model) provide qualitatively similar information about food-web structure and ecological degradation.

## METHODS

### Study Areas

The two study areas are located in the northwestern and central Mediterranean Sea (Figure 1). The South Catalan Sea comprises the continental shelf and upper slope associated with the Ebro River Delta, and has a depth range between 50 and 400 m. The South Catalan Sea is predominately oligotrophic with some nutrient enrichment occurring due to regional environmental events related to wind conditions, a temporal thermocline, a shelf-slope current, and river discharge (Estrada 1996). The North-Central Adriatic Sea area constitutes the widest continental shelf in the Mediterranean Sea (Pinardi and others in press) and has a depth range between 10 and 200 m. Owing to river runoff and oceanographic conditions, the region exhibits a decreasing trend of nutrient concentration and production from north to south and from west to east (Zavatarelli and others 1998). Both areas are important for the reproduction of small pelagic fish (Agostini and Bakun 2002) and are also strategic areas for marine vertebrate conservation (Groombridge 1990; Zotier and others 1999; Bearzi and others 2004). Important ecological changes occurring in both areas from the mid-late 1970s to the 1990s are changes in species abundance and composition due to exploitation (for example, Bas and others 2003, Santojanni and others 2003; Palomera and others 2007; Bombace and Grati 2007; Ferretti and others 2008), increasing jellyfish (for example, Piccinetti and Piccinetti Mandrin 1984; Benovic and Lucic 1996) and changes in species distribution and abundance due to climatic and environmental events (for example, Lloret and others 2004; Sabates and others 2006; Santojanni and others 2006).

### Food-Web Construction

Food webs were constructed for the North-Central Adriatic and the South Catalan Sea for the mid-late 1970s and mid-late 1990s closely based on previous modelling work (Coll 2006; Coll and others 2006a, b, 2007, 2008). Species lists, trophic information and biological parameters were obtained from available fishing and independent surveys (for example, scientific trawling, acoustics campaigns, visual census, core sampling, zooplankton monitoring) and available scientific literature (peer-review articles, and project final reports, research theses and data mainly from the *Institut de Ciències del Mar*, Barcelona, Spain ICM-CSIC, and the *Istituto di Scienze Marine, Sede di Ancona*, Italy ISMAR-CNR). Both food webs contain all main species identified in the ecosystems from lower to higher trophic positions regarding primary producers, benthic and pelagic invertebrates, fishes, marine mammals, birds, reptiles and also humans, including both commercial (for example, Norway lobster or European hake) and non-commercial (jellyfish and benthopelagic fish) species, and detritus, with a total of approximately 200 species. Functional feeding groups were used to group similar species according to ontogenetic stages and species with similar ecological and biological characteristics including feeding, habitat and mortality. A com-

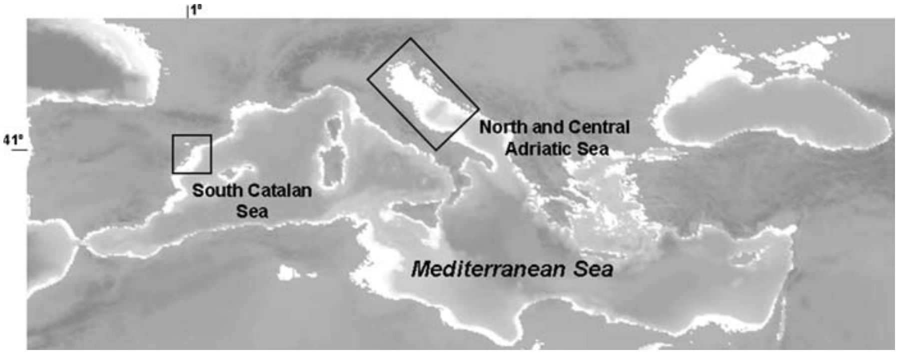

**Figure 1.** Location of the South Catalan Sea and North-Central Adriatic Sea study areas in the Mediterranean Sea.

**Table 1.** Functional Groups for the South Catalan Sea and North-Central Adriatic Sea Food-Web Models

| | Catalan Sea | Adriatic Sea |
|---|---|---|
| Functional groups | | |
| 1 | Phytoplankton | Phytoplankton |
| 2 | Micro- and mesozooplankton | Micro- and mesozooplankton |
| 3 | Macrozooplankton | Macrozooplankton |
| 4 | Jellyfish | Jellyfish |
| 5 | Suprabenthos | Suprabenthos |
| 6 | Polychaetes | Polychaetes |
| 7 | Shrimps | Commercial bivalves and gastropods |
| 8 | Crabs | Other benthic invertebrates |
| 9 | Norway lobster | Shrimps |
| 10 | Other benthic invertebrates | Norway lobster |
| 11 | Benthic cephalopods | Mantis shrimp |
| 12 | Benthopelagic cephalopods | Crabs |
| 13 | Red mullets | Benthic cephalopods |
| 14 | Conger eel | Benthopelagic cephalopods |
| 15 | Anglerfish | Adult hake |
| 16 | Flatfishes | Juvenile hake |
| 17 | Poor cod | Other gadiforms |
| 18 | Adult hake | Red mullets |
| 19 | Juvenile hake | Conger eel |
| 20 | Blue whiting | Anglerfish |
| 21 | Demersal fish (1) | Flatfish |
| 22 | Demersal fish (2) | Turbot and brill |
| 23 | Demersal fish (3) | Demersal sharks |
| 24 | Demersal sharks | Demersal skates |
| 25 | Benthopelagic fishes | Demersal fish (1) |
| 26 | European anchovy | Demersal fish (2) |
| 27 | European pilchard | Benthopelagic fishes |
| 28 | Other small pelagic fish | European anchovy |
| 29 | Horse mackerel | European pilchard |
| 30 | Mackerel | Other small pelagic fish |
| 31 | Atlantic bonito | Horse mackerel |
| 32 | Large pelagic fish | Macherel |
| 33 | Loggerhead turtles | Atlantic bonito |
| 34 | Audouins gull | Large pelagic fish |
| 35 | Other sea birds | Dolphins |
| 36 | Dolphins | Loggerhead turtles |
| 37 | Fin whale | Seabirds |
| 38 | Discards | Discards |
| 39 | Detritus | Detritus |
| Fishing fleets | | |
| 40 | Bottom trawl | Bottom trawl |
| 41 | Purse seine | Beam trawl |
| 42 | Long line | Purse seine |
| 43 | Tuna fleet | Longline |
| 44 | | Tuna fleet |

*Functional groups are described in Coll and others 2006b and 2007. Demersal fish groups are assemblages of demersal fish eating a mix of invertebrates and crustaceans (1), mainly invertebrates (2) and mainly fish (3).*

mon trophic structure was adopted to build standardized food webs to avoid biased results due to model construction (for example, Moloney and others 2005; Pinnegar and others 2005; Coll and others 2006a). This prevented problems when comparing food-web results (Fulton and others 2003). The ecosystem models contained 39 trophic groups including two detritus groups (natural detritus and discards from fishing) and fishing activities (Table 1). A total of 11 and 13 groups of invertebrate species were included in the Catalan and Adriatic model, respectively, whereas 20 groups represented fish species. Thus, all models are biased towards higher resolution of fish, and they show lower resolution for low-trophic level species due to less information available on stomach contents, biomass and abundance data. This is a common bias on food web studies (Fulton and others 2003; Romanuk and others 2006). The models from the different time periods reflect main ecological changes that occurred in the ecosystems during that time interval, including changes in species abundance and composition due to exploitation, invasion, eutrophication, increase of non-commercial species such as jellyfish, and climate and environmental changes (see description of study areas). Detailed explanations on data origin, ecological analyses to define trophic groups, construction of food webs and links by trophic groups are provided in Coll and others (2006a, b, 2007, 2008) and Coll (2006).

## Food-Web Properties

We used 22 food-web properties to characterize food-web structure (based on Odum 1969, 1985; Christensen 1995; Christensen and Pauly 1998; William and Martinez 2000; Dunne and others 2004; Christensen and Walters 2004). These food-web properties were grouped into three categories that describe ecological degradation related to (1) exploitation of higher trophic level species, (2) simplification of food-web structure, and (3) alterations in biomass and energy-flows (Table 2):

(1) Exploitation of high trophic level species was assessed by determining whether there were (a) significant decreases in five properties: the fraction of top predator taxa (%*T*), vulnerability (the number of predators, Vul), mean trophic level of the community (mTLco), mean short-weighted trophic level (SWTL) and maximum trophic level (maxTLi), (b) significant increases in two properties: the fraction of basal species (%*B*) and generality (number of prey, Gen), and (c) a non-linear effect on the fraction of intermediate predator taxa (%*I*). The fraction of intermediate predator taxa was expected to be higher in the historical webs due to indirect trophic effects and lower in the current webs due to processes related to ‘‘fishing down the food web’’ (*sensu* Pauly and others 1998).

(2) Simplification of food-web structure was assessed by determining whether there were (a) significant decreases in 6 properties: linkage density (*L*/*S*), connectance (*C* and *C*′) of the food web, the fraction of species involved in looping (%Loop), omnivory (%Omn and SOI), the mean number of links in every possible food chain or sequence of links connecting top to basal species (ChLen) and the mean trophic path length (Path and FPath) and (b) a significant increase in the fraction of cannibalism (%Can).

(3) Changes in productivity and biomass were assessed by determining whether there were (a) significant decreases in four properties: system biomass (Bt), the percentage of biomass of top predators (%BTP), the overall biomass/production ratio (*B*/*P*) and the total system throughput or the sum of all trophic flows within the system (TST) and (b) significant increases in three properties: the fraction of biomass in basal species (%BB), the fraction of overall flows to detritus over total flows (FD/TST), and the efficiency of energy transfer (TE) between trophic levels. (c) The fraction of biomass in intermediate predators (%BI) was expected to be higher in historical webs and lower in current webs.

Food-web properties were calculated using Niche and Ecopath models (Table 2). When the same property was calculated differently in the two model approaches used, both measures were included in the analysis. This was necessary for 4 properties: trophic level of the community (SWTL and mTLco), omnivory (%Omn and SOI), trophic path length (Path and Fpath) and connectance (*C* and *C*′) (Table 2). Five network properties that characterized trophic groups of food webs were calculated from Niche models to compare Mediterranean food webs at a finer level: connectivity (Co), vulnerability (Vul), generality (Gen), short-weighted trophic level (SWTL) and mean path length (Path).

## Niche Model

The Niche model is a stochastic food-web model (Williams and Martinez 2000; Dunne and others 2004; www.foodwebs.org) that standardizes empirical webs to take into account differences in species richness (*S*) (or diversity) and connectance (*C*) (or food-web complexity). When constructing the Niche model, empirical webs are compared with webs generated by the stochastic model that uses *S* and *C* as input parameters. Niche models were constructed following the methodology described in Williams and Martinez (2000) and Bersier and others (2002) and using FoodWebKB (www.foodwebs.org).

**Table 2.** Food-Web Properties Calculated from Niche and Ecopath Modelling Approaches

| Food-web properties | | Description | | Degradation state | Niche model | Ecopath model |
|---|---|---|---|---|---|---|
| (a) Overexploitation of high TL | | | | | | |
| 1 | Fraction of top predators | $\%T$ | Fraction of species with prey but no predators | Decrease | x | x |
| 2 | Fraction of intermediate predators | $\%I$ | Fraction of species with both prey and predators | Increase/ Decrease | x | x |
| 3 | Fraction of basal species | $\%B$ | Fraction of species with predators but no preys | Increase | x | x |
| 4 | Generality | Gen and GenSD | Number of prey items by species and standard deviation | Increase | x | |
| 5 | Vulnerability | Vul and VulSD | Number of predators by species and standard deviation | Decrease | x | |
| 6 | Mean trophic level of the community | SWTL | Short-weighted trophic level (SWTL) or the average of prey trophic level | | x | |
| | | mTLco | Mean trophic level taking into account biomass of preys and predators and diet composition (calculated from all TL and from TL $>1$) | Decrease | | x |
| 7 | Max trophic level | maxTLi | Maximum trophic level of the top predator in the food web | Decrease | x | x |
| (b) Simplification of food web | | | | | | |
| 8 | Linkage density | $L/S$ | All trophic link in the web ($L$) divided by $S$ (species or ecological groups) | Decrease | x | x |
| 9 | Connectance | $C$ | Proportion of actual trophic links to all possible links ($L/S^2$), 0 = no species preys on any species, 1 = every species preys on every other species including itself | Decrease | x | |
| | | $C'$ | Ratio of number of actual links to the number of possible links ($L/(S-1)^2$), where $S$ is the number of living groups | Decrease | | x |
| 10 | Fraction of omnivorism | %Omn | Fraction of species that feed directly on more than one trophic level and have food chains of different lengths | Decrease | x | |
| | | SOI | The average omnivory index of all consumers weighted by the logarithm of each consumer's food intake | Decrease | | x |
| 11 | Fraction of cannibalism | %Can | Fraction of species that feed directly on its own species | Increase | x | x |
| 12 | Fraction in loop | %Loop | Fraction of species involved in looping by appearing in a food chain twice | Decrease | x | |
| 13 | Mean short-weighted chain length | ChLen | Mean number of links in every possible food chain or sequence of links connecting top to basal species | Decrease | x | |

**Table 2.** continued

| Food-web properties | | Description | | Degradation state | Niche model | Ecopath model |
|---|---|---|---|---|---|---|
| 14 | Trophic path length | Path | Charactersitic path length or the mean shortest path length between species pairs | Decrease | x | |
| | | Fpath | Finn's path length or the average number of groups that an inflow or outflow passes through | Decrease | | x |
| (c) Changes in productivity and biomass | | | | | | |
| 15 | Overall biomass | Bt | Total biomass (calculated as t km$^{-2}$ from all Tl and from TL >I) | Decrease | | x |
| 16 | Biomass of top predators | %BTP | Percentage of biomass of species with prey but no predators | Decrease | | x |
| 17 | Biomass of intermediate predators | %BI | Percentage of biomass of species with both prey and predators | Increase/Decrease | | x |
| 18 | Biomass of basal species | %BB | Percentage of biomass of species with predators but no preys | Increase | | x |
| 19 | Overall biomass/production | *B*/*P* | Ratio between total biomass and total production | Decrease | | x |
| 20 | Total system throughput | TST | Sum of all trophic flows in the system (t km$^{-2} \cdot$ y$^{-1}$) | Decrease | | x |
| 21 | Fraction of flows to detritus | FD/TST | Ratio of sum of all trophic flows to detritus over TST | Increase | | x |
| 22 | Transfer efficiency | TE | Ratio of efficiency of energy transfer from lower to higher trophic levels | Increase | | x |

*The expected direction of change towards degradation is described.*

We performed 1,000 Monte Carlo simulations for each model allowing the calculation of a mean and standard deviation of each network property. Raw errors represented the difference between the empirical and the model mean and were normalized with the standard deviation of the property's simulated distribution. Normalized errors between −2 and 2 were accepted as good fits of the model to the empirical food-web data. Analyses were performed including and not-including fishing activity directly in model construction, and here we show the former results because they were both similar and consistent. Visualization of the food web was done using FoodWeb3D (R.J. Williams, Pacific Ecoinformatics and Computational Ecology Lab). An extensive review of limitations and capabilities of the Niche model can be found in Dunne (2005).

## Ecopath Model

Ecopath is a mass-balance food-web model (Pauly and others 2000; Christensen and Walters 2004; www.ecopath.org) that represents a snapshot of trophic flows and biomasses of an ecosystem and that has been widely applied to characterize the structure and functioning of marine ecosystems. It ensures mass balance by assuming that the production of each functional group (i) of the ecosystem equals predation mortality by all predators, exports from the system, biomass accumulation and other natural mortality, whereas consumption by each group equals production by (i), respiration by (i) and food that is unassimilated by (i). Parameterization requires biomass by functional group, production/biomass and consumption/biomass ratios, trophic information and other imports/exports of production from the system (catches, migration and biomass accumulation). The model is considered well balanced when realistic estimates of the key ecological missing parameters are obtained. Food webs from the North-Central Adriatic and the South Catalan Sea previously modelled with Ecopath and discussion on uncertainty of input parameters is provided in Coll (2006) and Coll and others (2006b, 2007) (Table 1). Comprehensive reviews of the limitations and capabilities of the Ecopath with Ecosim approach can be found in Christensen and Walters (2004), Fulton and Smith (2004) and Plagányi (2007).

## Comparison of Results and Statistical Analysis

An independent sample *t*-test was used to determine significant differences between the two Mediterranean ecosystems and the two time periods analyzed. Due to data limitations we could not compare differences in food-web properties within regions across time periods; thus properties from both regions and years were pooled to compare results between time periods, and properties from both time periods were pooled to compare results between regions.

Further differences between model results were explored with multivariate and factorial statistical analysis. Non-parametric ANOSIM and SIMPER procedures (PRIMER software, Plymouth Marine Laboratory) that are based on multi-dimensional scaling (MDS) of the Bray–Curtis dissimilarity index were used to analyze similarities between ecosystem models from different regions and time periods, and to quantify the relative contribution of each of the 22 network properties to differences among models calculated from either one or both modelling approaches. Data were log transformed ($\log(x + 1)$) prior to comparisons to focus attention on patterns within the whole community, and take into account contributions from properties with different scales. Spearman correlation coefficients were used to test relationships between properties.

Following the same methodology, results from the four Mediterranean models were compared with three other marine food webs described in the literature to contextualize the relative state of food-web degradation. Mediterranean Niche models were compared with the Southern Benguela upwelling, the Caribbean Sea and the North-eastern US continental shelf Niche models previously analyzed and presented by Dunne and others (2004). We re-calculated the Benguela and Caribbean Sea structural properties to include humans and detritus in model parameterization considering data provided in Field and others (1991), Yodziz (1998), Shannon and others (2003) and Anonymous (2004). Results from Mediterranean mass-balance models were compared with previous marine food-web models representing the Southern Benguela upwelling (Shannon and others 2003), the Caribbean Sea (Opitz 1996) and the South-eastern US continental shelf (Okey and Pugliese 2002).

## Extinction Analysis

To relate the degree of food-web degradation with the extinction risk of species and food-web robustness, we explored the potential effects of different types and magnitudes of species removals to trigger cascades of secondary extinctions. The structural robustness ($R_{50}$) of food webs to species removal was calculated as the fraction of species that had to be removed to result in total species loss of 50% or more of species (primary species removals and secondary extinctions) in the original food web as defined by Dunne and others (2002). A secondary extinction is defined when a non-basal species loses all of its prey and when a cannibalistic species loses all of its prey items except itself. We followed the methodology described by Dunne and others (2002) for the four Mediterranean models and compared these results with those for the Southern Benguela, Caribbean and NE US shelf (Dunne and others 2004). Species losses were simulated sequentially by removing species selected by the following criteria: (1) least connected species in the food web, (2) most connected species, and (3) species randomly chosen from 1,000 random removal sequences initiated for each food web. In addition, realistic natural extinctions were simulated by removing (4) the most commercial species (that is, the ones with highest catches in the mid-late 1970s and mid-late 1990s, Coll and others 2006b, 2007). When simulating loss of species, we excluded the basal species from the removal because this would have large food-web consequences not related with the hypothesis tested in this paper. The relationship between $R_{50}$ and the 22 network properties was explored using linear regressions for both Mediterranean and non-Mediterranean webs. The Bonferroni-corrected value of $P = 0.0125$ (0.05/4) was used to determine significance to account for multiple comparisons of properties at the same time.

# RESULTS

## Mediterranean Food-Web Properties

Most of the food-web properties calculated by the Niche model from the North-Central Adriatic Sea and the South Catalan Sea representing the mid-late 1970s and the mid-late 1990s had normalized errors between −2 and 2 when standardized by species richness ($S$) and connectance ($C$) and were thus accepted as good fits of empirical webs (Table 3). The exceptions were generality (Gen) and vulnerability (Vul) for all the 4 models, the fraction of top predator taxa (%$T$) for the Adriatic

**Table 3.** Niche Model Results for Food-Web Properties of the South Catalan Sea and North-Central Adriatic Sea (Mid-Late 1970s and Mid-Late 1990s) and Three Non-Mediterranean Systems

| | Catalan Sea 1970 | | | Catalan Sea 1990 | | | Adriatic Sea 1970 | | | Adriatic Sea 1990 | | | Southern Benguela | | | Caribbean Sea | | | US continental shelf | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** | **Data** | **Mean** | **SD** |
| (a) Overexploitation of high TL | | | | | | | | | | | | | | | | | | | | | |
| %*T* | 0.12 | 0.05 | 0.05 | 0.12 | 0.05 | 0.05 | 0.16 | 0.06 | 0.05 | 0.16 | **0.05*** | 0.05 | 0.03 | 0.05 | 0.05 | 0.02 | 0.03 | 0.04 | 0.04 | 0.02 | 0.03 |
| %*I* | 0.81 | 0.83 | 0.06 | 0.81 | 0.82 | 0.06 | 0.77 | 0.81 | 0.06 | 0.77 | 0.82 | 0.06 | 0.90 | 0.83 | 0.07 | 0.92 | 0.88 | 0.05 | 0.94 | 0.91 | 0.03 |
| %*B* | 0.07 | 0.12 | 0.04 | 0.07 | 0.12 | 0.04 | 0.07 | 0.13 | 0.04 | 0.07 | 0.13 | 0.04 | 0.07 | 0.12 | 0.04 | 0.06 | 0.09 | 0.03 | 0.02 | **0.06*** | 0.02 |
| GenSD | 0.78 | **0.99*** | 0.09 | 0.77 | **0.99*** | 0.09 | 0.78 | **1.01*** | 0.10 | 0.82 | **1.01*** | 0.10 | 0.84 | 0.93 | 0.09 | 0.89 | 0.93 | 0.07 | 0.91 | 0.92 | 0.06 |
| VulSD | 0.78 | **0.57*** | 0.10 | 0.78 | **0.57*** | 0.10 | 0.87 | **0.59*** | 0.10 | 0.87 | **0.58*** | 0.10 | 0.76 | **0.56*** | 0.10 | 0.59 | 0.54 | 0.08 | 0.72 | **0.53*** | 0.06 |
| SWTL | 3.15 | 3.14 | **0.57** | 3.11 | 3.11 | 0.53 | 3.12 | 3.03 | 0.47 | 3.19 | 3.09 | 0.54 | 3.20 | 3.24 | 0.91 | 2.93 | 3.59 | 2.37 | 3.07 | 3.91 | 0.92 |
| maxTLi | 5.12 | | | 5.07 | | | 5.26 | | | 5.50 | | | 5.14 | | | 5.43 | | | 5.16 | | |
| (b) Simplification of food web | | | | | | | | | | | | | | | | | | | | | |
| *L*/*S* | 7.77 | 7.78 | 0.22 | 7.74 | 7.75 | 0.22 | 7.32 | 7.32 | 0.22 | 7.36 | 7.37 | 0.21 | 7.03 | 7.04 | 0.19 | 11.45 | 11.45 | 0.33 | 18.31 | 18.31 | 0.51 |
| *C* | 0.18 | 0.18 | 0.01 | 0.18 | 0.18 | 0.01 | 0.17 | 0.17 | 0.00 | 0.17 | 0.17 | 0.00 | 0.23 | 0.23 | 0.01 | 0.22 | 0.22 | 0.01 | 0.23 | 0.23 | 0.01 |
| %Omn | 0.86 | 0.77 | 0.05 | 0.88 | 0.77 | 0.06 | 0.84 | 0.75 | 0.05 | 0.84 | 0.75 | 0.06 | 0.84 | 0.78 | 0.06 | 0.86 | 0.83 | 0.05 | 0.78 | **0.89*** | 0.03 |
| %Can | 0.28 | 0.22 | 0.06 | 0.26 | 0.21 | 0.06 | 0.27 | 0.20 | 0.06 | 0.27 | 0.20 | 0.06 | 0.16 | 0.29 | 0.07 | 0.41 | **0.29*** | 0.06 | 0.31 | 0.30 | 0.05 |
| %Loop | 0.40 | **0.19*** | 0.09 | 0.33 | 0.19 | 0.09 | 0.25 | 0.16 | 0.08 | 0.25 | 0.16 | 0.08 | 0.10 | 0.25 | 0.11 | 0.57 | **0.35*** | 0.10 | 0.36 | **0.46*** | 0.10 |
| ChLen | 2.47 | 2.24 | 0.26 | 2.47 | 2.24 | 0.24 | 2.50 | 2.22 | 0.23 | 2.48 | 2.25 | 0.28 | 2.58 | 2.26 | 0.32 | 2.20 | 2.31 | 0.27 | 2.63 | 2.36 | 0.27 |
| Path | 1.72 | 1.72 | 0.04 | 1.70 | 1.72 | 0.04 | 1.82 | 1.76 | 0.05 | 1.83 | 1.75 | 0.04 | 1.66 | 1.61 | 0.05 | 1.60 | 1.60 | 0.03 | 1.57 | 1.59 | 0.02 |

*Data: empirical food-web data, Mean: Niche model mean. *Normalized errors were not between −2 and 2 when standardized by S and C in Niche model. The empirical data are shown, as well as the mean and standard deviation (SD) of 1000 Monte-Carlo simulations*

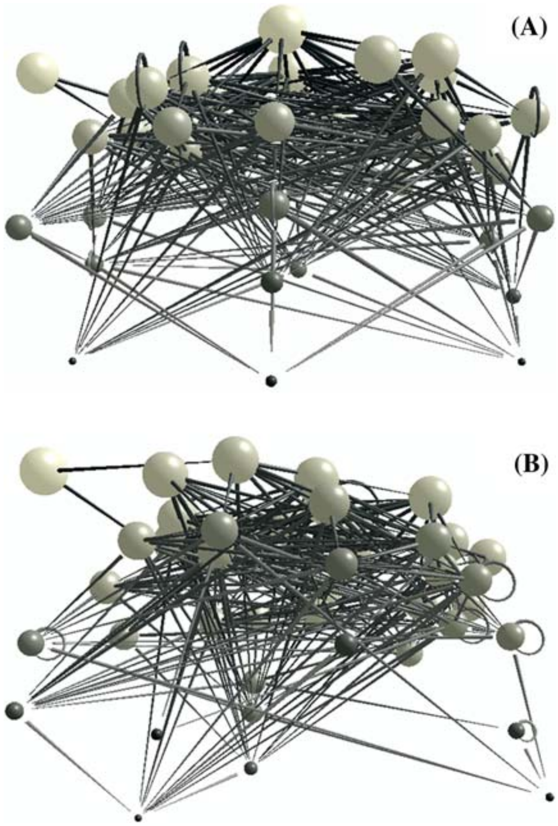

**Figure 2.** Visualization of (**A**) the South Catalan Sea and (**B**) the North-Central Adriatic Sea food webs from the mid-late 1990s. Images were produced with FoodWeb3D, written by R.J. Williams, Pacific Ecoinformatics and Computational Ecology Lab. Different coloured dots represent functional groups from different trophic levels with black = primary producers, dark grey = secondary producers, and the lightest grey being top predators, whereas the light and dark grey links represent feeding links.

Sea (1990s) and the fraction of species involved in looping (%Loop) for the Catalan Sea (1970s). Visualization of the food web in terms of links and nodes of the South Catalan Sea and the North-Central Adriatic Sea from the mid-late 1990s is shown in Figure 2 (a similar representation was obtained for the models in the 1970s; data not shown).

Overall, the 22 food-web properties calculated with the Niche and the Ecopath model were very similar for the North-Central Adriatic and South Catalan food webs in the mid-late 1970s and the mid-late 1990s (Tables 3 and 4). There were no significant differences between the two time periods, but a few statistically significant differences between areas (see supplementary material, Table 1): The Adriatic Sea showed significantly higher Gen and lower mean trophic level of the community (mTLco, excluding TL = 1), lower fraction of omnivore species (SOI) and lower %Loop, all suggesting a higher degradation of food-web structure regarding overexploitation of higher trophic levels and food-web simplification. In addition, there was a lower percentage of biomass of top predators (%BTP) in the Adriatic, showing an impoverishment of biomass at the highest trophic levels. The South Catalan Sea showed significantly lower overall system biomass (Bt, considering both all trophic levels and trophic levels $>1$) and lower biomass/production ratio ($B/P$) that indirectly reflects the mean size of organisms in the ecosystem, suggesting a higher degradation regarding productivity and biomass. Its food-web structure was also characterized by a significantly lower maximum trophic level (maxTLi), lower $C$ and lower mean trophic path lengths (both Path and FPath), also indicators of overexploitation of high trophic levels and food-web simplification.

Multivariate analyses (Table 5, tests 1 and 2, Figure 3A) of the 22 food-web properties indicated that, as a whole, the South Catalan and North-Central Adriatic models were more than 96% similar, whereas models representing the 1970s and the 1990s from both sites were more than 97% similar. At a finer level, comparison of connectivity (Co), vulnerability (Vul), generality (Gen), short-weighted trophic level (SWTL) and mean path length (Path) characterizing the trophic groups of each ecosystem (Table 1) also showed similarities between regions and time periods (Table 5, tests 3 and 4). In general terms, functional groups of the South Catalan models and the North-Central Adriatic models representing both the mid-late 1970s and the mid-late 1990s were more than 75% similar. Although not significant, functional groups of the South Catalan models showed higher generality, lower trophic level and lower path length; functional groups from the North-Central Adriatic models showed lower vulnerability and lower connectivity (Figure 3B).

## Comparison of Mediterranean with Other Marine Food Webs

To determine the state of food-web degradation in the Mediterranean in regard to other marine regions, we compared the South Catalan and North-Central Adriatic Sea models with those from the Southern Benguela, Caribbean Sea and US continental shelf. We found significant differences between Mediterranean and non-Mediterranean models with 91% similarity among the two groups (Table 5, test 5). The Mediterranean was most

**Table 4.** Ecopath Model Results for Food-Web Properties of the South Catalan Sea and North-Central Adriatic Sea (Mid-Late 1970s and Mid-Late 1990s) and Three Non-Mediterranean Systems

| Properties | Catalan Sea | | Adriatic Sea | | Southern Benguela | Caribbean Sea | US cont. shelf |
|---|---|---|---|---|---|---|---|
| | 1970 | 1990 | 1970 | 1990 | | | |
| (a) Overexploitation of high TL | | | | | | | |
| %$T$ | 0.14 | 0.14 | 0.16 | 0.16 | 0.06 | 0.00 | 0.07 |
| %$I$ | 0.80 | 0.80 | 0.78 | 0.78 | 0.88 | 0.94 | 0.86 |
| %$B$ | 0.07 | 0.07 | 0.07 | 0.07 | 0.06 | 0.06 | 0.07 |
| mTLco (all TLs) | 1.44 | 1.51 | 1.41 | 1.39 | 2.10 | 1.40 | 1.57 |
| mTLco (TL $>$ I) | 2.39 | 2.37 | 2.17 | 2.13 | 2.72 | 2.20 | 2.58 |
| maxTLi | 4.39 | 4.39 | 4.49 | 4.55 | 5.20 | 4.24 | 4.53 |
| (b) Simplification of food web | | | | | | | |
| $L/S$ | 7.50 | 7.81 | 7.34 | 7.50 | 7.06 | 11.40 | 10.85 |
| $C'$ | 0.20 | 0.20 | 0.20 | 0.20 | 0.22 | 0.23 | 0.20 |
| SOI | 0.22 | 0.22 | 0.17 | 0.19 | 0.26 | 0.23 | 0.25 |
| %Can | 0.28 | 0.28 | 0.27 | 0.27 | 0.38 | 0.42 | 0.25 |
| Finn's path length | 2.40 | 2.56 | 3.30 | 3.34 | 3.28 | 4.72 | 2.30 |
| (c) Changes in biomass and productivity | | | | | | | |
| Bt (all TLs)$^{1}$ | 116.75 | 129.34 | 335.07 | 331.04 | 231.19 | 5,047.98 | 527.13 |
| Bt (TL $>$ 1)$^{1}$ | 36.71 | 48.77 | 117.68 | 113.65 | 147.71 | 1,707.98 | 188.73 |
| %BT | 0.01 | 0.01 | 0.003 | 0.002 | 0.03 | 0.004 | 2.02 |
| %BI | 0.31 | 0.37 | 0.35 | 0.34 | 0.61 | 0.33 | 0.64 |
| %BB | 0.69 | 0.62 | 0.65 | 0.66 | 0.36 | 0.66 | 0.34 |
| $B/P$ | 0.03 | 0.03 | 0.09 | 0.08 | 0.01 | 0.11 | 0.03 |
| TST$^{2}$ | 3797.00 | 3845.00 | 3786.00 | 4038.00 | 8496.00 | 23673.49 | 11210.32 |
| FD/TST | 0.01 | 0.01 | 0.00 | 0.00 | 36.75 | 4.69 | 21.27 |
| TE | 12.10 | 10.00 | 11.50 | 12.20 | 12.10 | 12.90 | 16.50 |

*$^{1}$t km$^{-2}$; $^{2}$ t km$^{-2}$ y$^{-1}$.*

*Legends as expressed in Table 1 for food web properties.*

similar to the Southern Benguela (differing up to 7%), followed by the US continental shelf (9%), and the Caribbean Sea (11%) (Figure 4A). There were no significant differences among the three non-Mediterranean models (Table 5, tests 6–8).

Biomass (total and fractional) and total system throughput (TST) were the two most important parameters differentiating Mediterranean and non-Mediterranean webs. As these two variables are not necessarily linked with degradation and could differ due to difference in productivity due to regional features, we repeated the analysis excluding these two properties. As a result, dissimilarity between Mediterranean and non-Mediterranean models decreased to 5%, although differences were still significant between both groups (Table 5, test 9). In this case, Mediterranean models showed more similarities to Southern Benguela (differing up to 3%), followed by Caribbean Sea (5%) and US continental shelf (5%) (Figure 4B).

In general, 16 of the 22 (73%) network properties analyzed (Table 2) indicated a more degraded state in Mediterranean compared to non-Mediterranean models with respect to overexploitation of high trophic levels, simplification of food webs and decreases in productivity and biomass (Table 6). Exceptions were found for Southern Benguela with values of linkage density ($L/S$), fraction of omnivore species (%Omn) and $B/P$ similar to the Mediterranean areas. The Caribbean Sea showed similar values of %BTP, the percentage of biomass of intermediate predators and basal species (%BI and %BB), and mTLco with the Mediterranean Sea. On the other hand, %$T$, Vul and the fraction of cannibalism (%Can) indicated a less degraded state for Mediterranean compared to non-Mediterranean systems, whereas unclear signs were found in the maxTLi and Fpath.

## Comparison of Modelling Approaches: Ecopath and Niche Model

Similar quantitative results were obtained using both Niche and Ecopath models for several of the 22 calculated food-web properties (Tables 3, 4, 6). Moreover, both models showed qualitative comparable trends of higher degradation of food-web structure in Mediterranean compared to non-

**Table 5.** Results of ANOSIM (Global *R*, *P*-value) and SIMPER for Comparison of Ecosystem Models

| | ANOSIM | | SIMPER % dissimilarity | Test description | Properties contributing to % dissimilarity |
|---|---|---|---|---|---|
| | *R* | *P*-value | | | |
| Test 1 | 1.00 | 0.333 | 3.35 | Catalan versus Adriatic models pooled over time (ST) | Bt (TL > 1), Bt (all TLs) (>50%) |
| Test 2 | −0.75 | 1.000 | 2.03 | Mediterranean models 1970 versus 1990 pooled over sites (ST) | Bt (TL > 1), Bt (all TLs) (>50%) |
| Test 3 | −0.06 | 0.797 | 23.13 | Catalan versus Adriatic models pooled over time (FG) | Demersal fish (1), Crabs, Shrimps, Demersal fish (2), Other benthic invert., Benthop. fish., Discards, Dolphins, Benthic cephalop., Benthop. cephalop., European pilchard, Seabirds, Polychaetes, Macrozooplankton (>50%) |
| Test 4 | −0.10 | 0.990 | 22.77 | Mediterranean models 1970 versus 1990 pooled over sites (FG) | Demersal fish (1), Crabs, Shrimps, Demersal fish (2), Other benthic invert., Benthop. fish., Discards, Dolphins, Benthic cephalop., European pilchard, Benthop. cephalop., Polychaetes, European anchovy, Demersal sharks (>50%) |
| Test 5 | 0.74 | **0.029** | **9.17** | Mediterranean versus non-Mediterranean models pooled over sites (ST) | TST, Bt (TL > 1), Bt (all TLs) (>50%) |
| Test 6 | 0.00 | 0.667 | 7.07 | Southern Benguela versus Caribbean and US continental shelf models (ST) | TST, Bt (all TLs), Bt (TL > 1), %BB, %BI (>50%) |
| Test 7 | 1.00 | 0.333 | 9.30 | Caribbean Sea versus Southern Benguela and US continental shelf models (ST) | Bt (all TLs), Bt (TL > 1), TST (>50%) |
| Test 8 | −1.00 | 1.000 | 6.52 | US continental shelf versus Caribbean Sea and Southern Benguela models (ST) | Bt (all TLs), Bt (TL > 1), TST, L/S (>50%) |
| Test 9 | 0.61 | **0.029** | **4.81** | Mediterranean versus non-Mediterranean models, excluding biomasses and total fluxes | L/S, FPL, TE, %Loop (>50%) |

*Bt: total system biomass (t km$^{-2}$), TST: total system throughput (t km$^{-2}$ y$^{-1}$), %BI: percentage of biomass of intermediate predators, Fpath: Finn's trophic path length, %BB: percentage of biomass of basal species, FD/TST: the fraction of overall flows to detritus over total flows, C: connectance, B/P: overall biomass/production ratio, %Can: fraction of cannibalism, %Omn: fraction of omnivore species, mTLco: mean trophic level of the community. ST = structural properties, FG = functional groups.*

Mediterranean models. Of the 22 food-web indicators, 4 were only partly comparable between models due to differences in how the property was calculated (Table 2). However, despite different absolute values (Tables 3 and 4), similar results were obtained regarding the degradation of the Mediterranean Sea. The only exception was for Path and FPath where unclear results were shown (Table 6). They slightly increased when comparing the South Catalan Sea Niche models with time, and slightly decreased comparing the Adriatic Niche models; it was higher for Mediterranean Niche models compared with non-Mediterranean models and showed intermediate values for Ecopath Mediterranean models when comparing with non-Mediterranean.

In the case of the mean trophic levels of the community, SWTL of the Niche model showed higher values compared to mTLco calculated from the more information-rich flow-weighted data of the mass-balance model. Omnivory from the Niche model was calculated as the fraction of species that feed directly on more than one trophic level and have food chains of different lengths (%Omn), whereas in Ecopath the system omnivory index (SOI) is calculated as the average omnivory index (average of trophic levels of consumer's prey groups) of all consumers weighted by the logarithm of each consumer's food intake. This explains the differences found between the modelling approaches with larger values for %Omn compared to SOI. Connectance ($C$) was slightly lower from the Niche model as it is calculated as the proportion of actual links ($L$) to all possible links ($S^2$), while the Ecopath model defines possible links as $(S-1)^2$ where $S$ is the number of living groups, and it

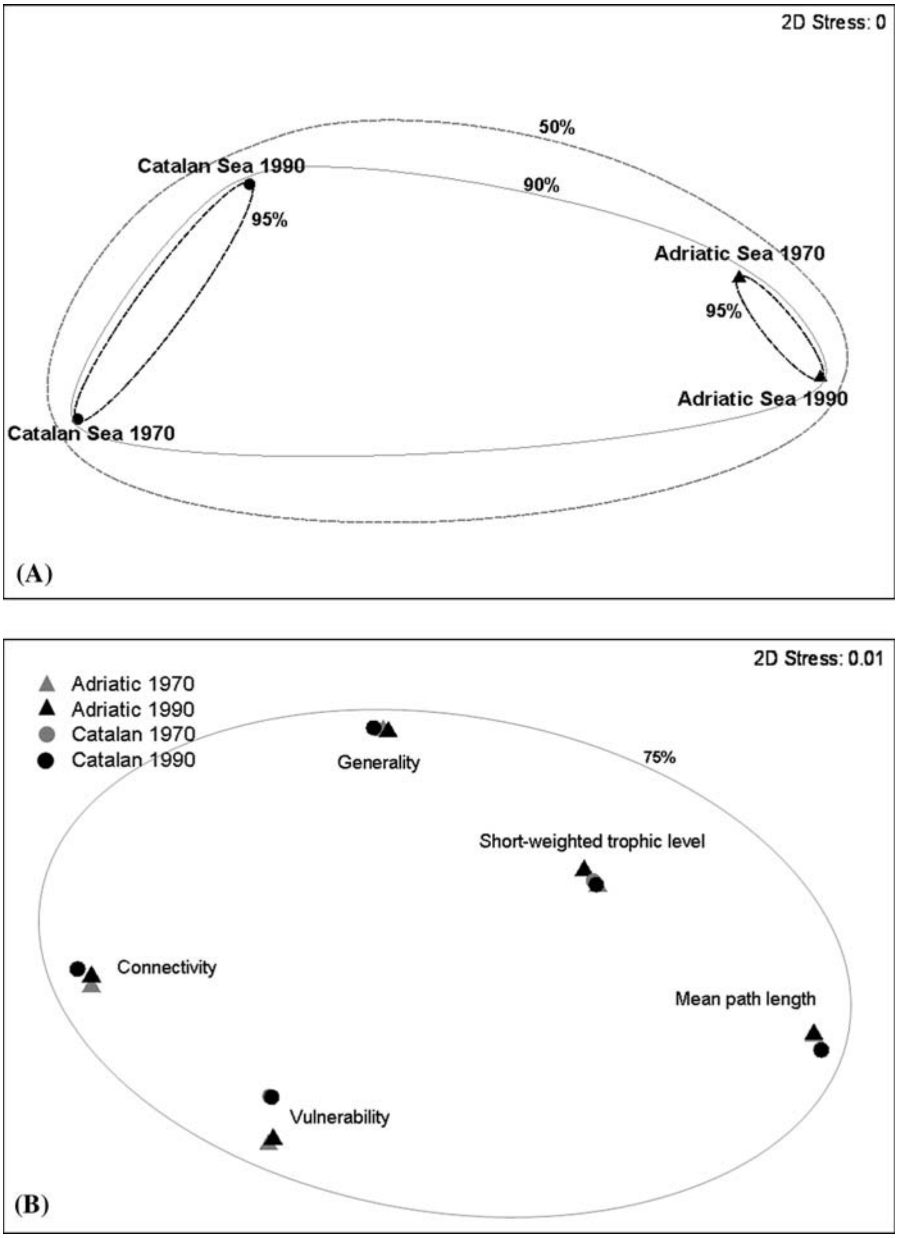

**Figure 3.** Two-dimension MDS ordination of the four Mediterranean food-web models based on Bray-Curtis similarities comparing (**A**) 22 network properties (see Table 1) and (**B**) five selected properties by functional group. Encircling lines represent percentages of similarity.

excludes cannibalism. Finally, the trophic path length was calculated as the average number of groups that an inflow or outflow passes through in Ecopath (Finn's path length index, Fpath), which showed higher values compared to the mean shortest path length between species pairs in the Niche model (Path).

## Robustness of Mediterranean Food Webs to Species Loss

Simulated species removals resulted in similar consequences for the South Catalan and North-Central Adriatic Sea (Figure 5). Removing the most connected species resulted in additional species loss or secondary extinctions after removal of 25–30% of species in the original food webs. Randomly removing taxa and removing the less connected taxa resulted in intermediate to low levels of secondary extinctions. These results are in line with previous studies on other marine food webs (Dunne and others 2004). Removing most commercial species resulted in additional species loss after removal of 5–25% of species in the original food webs, and notably increased after removal of 40–50% of taxa (Figure 5). Interestingly, in the case of the North-Central Adriatic Sea during the mid-late 1970s and the South Catalan Sea during the mid-late 1990s, removing the most commercial species resulted in higher secondary extinctions

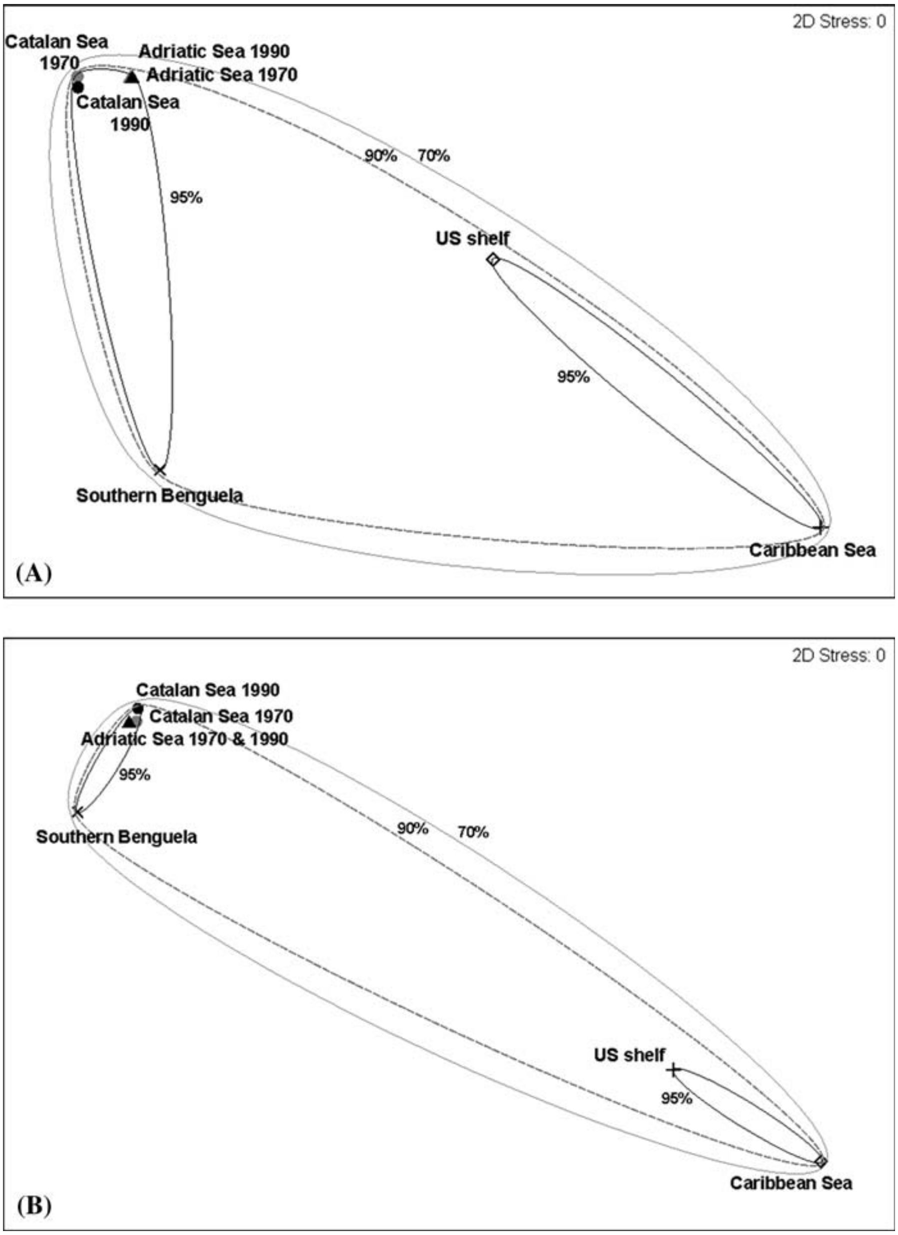

**Figure 4.** Two-dimension MDS ordination of the four Mediterranean and three non-Mediterranean food-web models based on Bray-Curtis similarities comparing (**A**) 22 network properties (see Table 1) and (**B**) all network properties excluding indices of biomasses and trophic flows. Encircling lines represent percentages of similarity.

compared with random removals (Figure 5). Secondary extinctions were also slightly higher in the Catalan Sea food web during the mid-late 1970s after removal of 50% of species in the original web.

Comparing trends of secondary extinctions after removal of the most connected species in Mediterranean and non-Mediterranean food webs revealed much higher robustness against secondary extinctions in the Caribbean Sea and US shelf compared to Southern Benguela and the Mediterranean systems (Figure 6). The structural robustness ($R_{50}$) of food webs to species removal was lower in all Mediterranean systems and Southern Benguela for both randomly removing species or removing the most connected ones. The robustness of food webs to removal of most connected species including results from Mediterranean and non-Mediterranean models varied significantly with total system biomass (t km$^{-2}$) ($r = 0.877$, $P = 0.010$).

## DISCUSSION

Human activities have led to significant changes in species abundance and composition of marine food webs due to overexploitation, habitat transformation, species invasions, pollution and climate change. Using two different trophic modelling approaches we could show that Mediterranean food webs are structurally more degraded and less robust to species extinctions than food webs from

**Table 6.** Qualitative Comparison of 22 Network Properties (see Table 1) from Mediterranean and Non-Mediterranean Models and Description of Directions Suggesting a more Degraded State for Overexploitation of High Trophic Levels, Simplification of Food Webs and Decrease of Productivity and Biomass

| Network properties | Mediterranean versus non-Mediterranean areas | | |
|---|---|---|---|
| | Niche | Ecopath | Direction |
| (a) Overexploitation of high TL | | | |
| 1 %*T* | ↑ | ↑ | Improvement |
| 2 %*I* | ↓ | ↓ | Degradation |
| 3 %*B* | ↑ | ↑ | Degradation |
| 4 GenSD | ↑ | | Degradation |
| 5 VulSD | ↑ | | Improvement |
| 6 SWTL&mTLco | ↓ | ↓* | Degradation |
| 7 maxTLi | X | X | Unclear |
| (b) Simplification of food web | | | |
| 8 *L*/*S* | ↓ | ↓ | Degradation |
| 9 *C*&*C*′ | ↓ | ↓ | Degradation |
| 10 %Omn&SOI | ↓ | ↓ | Degradation |
| 11 %Can | ↓ | ↓ | Improvement |
| 12 %Loop | ↓ | | Degradation |
| 13 ChLen | ↓ | | Degradation |
| 14 Path&Fpath | ↑ | X | Unclear |
| (c) Changes in productivity and biomass | | | |
| 15 Bt | | ↓* | Degradation |
| 16 %BTP | | ↓ | Degradation |
| 17 %BI | | ↓ | Degradation |
| 18 %BB | | ↑ | Degradation |
| 19 *B*/*P* | | ↓ | Degradation |
| 20 TST | | ↓ | Degradation |
| 21 FD/TST | | ↑ | Degradation |
| 22 TE | | X | Unclear |

*When the direction is not clear the X symbol is applied; (*) = properties that were measured with two different indicators from Ecopath models (data of the analyses are shown in Tables 2 and 3, and data of non-Mediterranean models are modified from Dunne and others 2004).*

the Caribbean, eastern US continental shelf and Southern Benguela. Within the Mediterranean, however, food-web models from the North-Central Adriatic and South Catalan Sea from the mid-late1970s and mid-late 1990s, respectively, showed similar structural food-web properties suggesting similar levels of ecological degradation in terms of overexploitation of high trophic levels, food-web simplification, and changes in biomass and productivity prior to the 1970s. Both modelling approaches used delivered comparable results suggesting that they both capture fundamental information about how food webs are structured.

## Comparison of Ecopath and Niche Models

The stochastic Niche model satisfactorily predicted the structure of four Mediterranean food webs from two regions and two time periods. The application of the Niche model to Mediterranean food webs complements previous modelling efforts with mass-balance Ecopath modelling in the region (Coll 2006; Coll and others 2006a, b, 2007, 2008) and thus enhances our understanding of current food-web structure and functioning in Mediterranean systems.

Both the Niche model and the Ecopath model delivered comparable results among Mediterranean areas and between Mediterranean and non-Mediterranean sites regarding structural food-web properties and degradation gradients in terms of overexploitation of high trophic levels and simplification of food-web structure. These results indicate that both modelling approaches capture fundamental components of food-web structure in similar ways. A combination of both methodologies can be a useful tool to examine and validate changes in food-web structure and enables us to derive more reliable and general patterns in food-web degradation. By adding trophic flows and biomass-related indicators from mass-balance

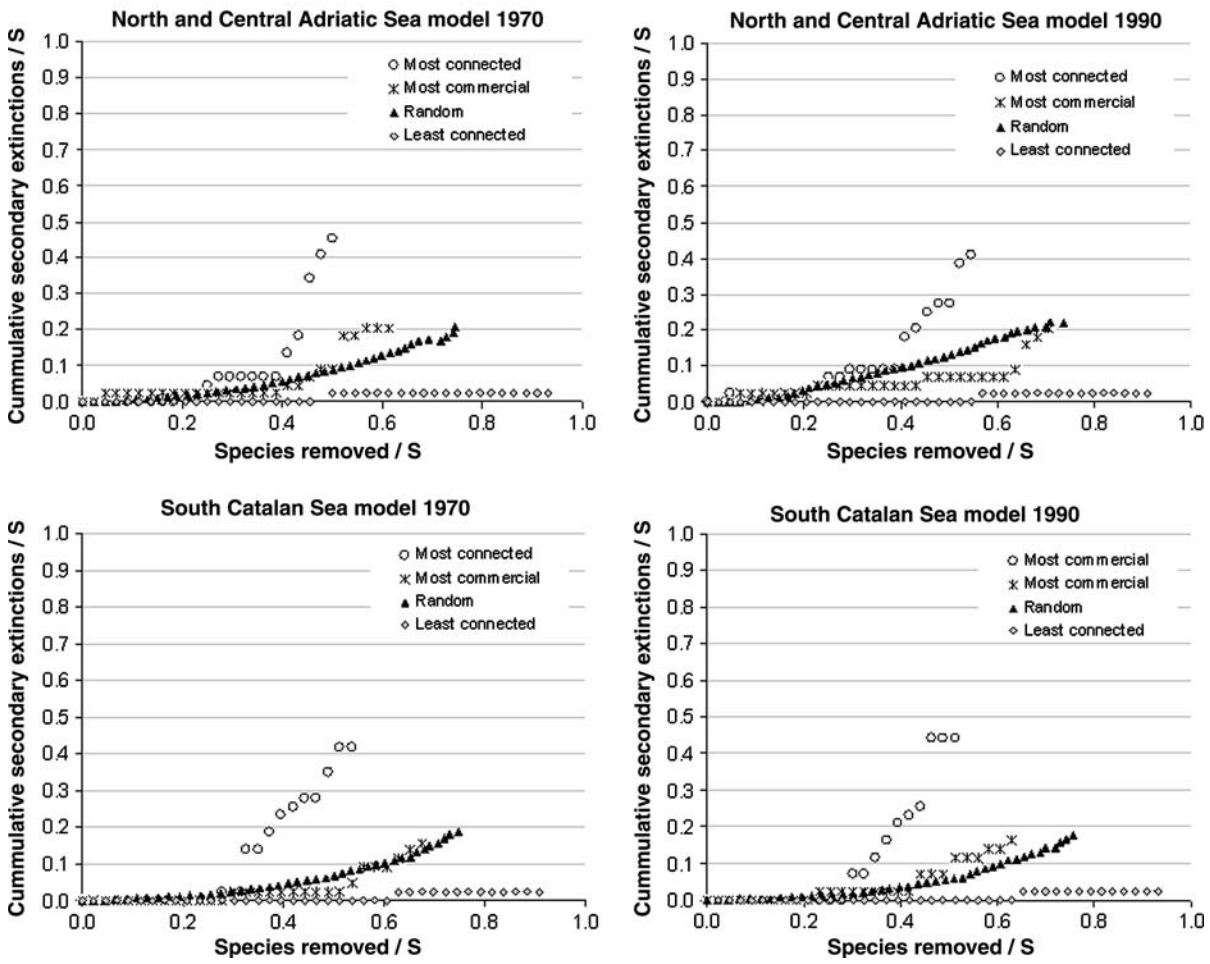

**Figure 5.** Secondary extinctions resulting from primary species loss in four Mediterranean food webs from the South Catalan Sea and the North-Central Adriatic Sea during mid-late 1970s and mid-late 1990s.

Ecopath models, the structural results can also be compared with changes in biomass and productivity across a degradation gradient.

## Similarities in Mediterranean Systems

Both the South Catalan Sea and the North-Central Adriatic Sea during the mid-late 1970s and mid-late 1990s, respectively, showed similar structural food-web properties. This suggests that both areas share similar biological and ecological features, and that both areas have been exposed to similar levels of anthropogenic impacts in the past (for example, Bianchi and Morri 2000; Coll 2006; Ferretti and others 2008). These results also suggest that both food webs were already degraded prior to the 1970s, because changes in overall food-web structure between the 1970s and 1990s were not severe despite distinct changes in individual species groups such as small pelagic fish or jellyfish (Piccinett and Piccinetti Mandrin 1984; Santojanni and others 2003; Palomera and others 2007). However, the ecological degradation in both systems was emphasized in different structural properties. For the South Catalan Sea, lower total system throughput, lower total system biomass and a lower biomass/production ratio suggest higher degradation of the ecosystem regarding productivity and biomass. This is in agreement with general patterns of primary production and eutrophication in the Mediterranean basin, with more oligotrophic conditions in the western basin (Bosc and others 2004). The South Catalan food web also showed a decrease in maximum trophic level from the 1970s to the mid-late 1990s, a decrease which is likely due to the new development of long line fisheries that target demersal top predators, such as adult hake and conger ell (Coll and others 2006b). In contrast to the South Catalan food web, the North-Central Adriatic Sea food web showed higher food-web degradation regarding overexploitation of higher trophic levels and simplification of food-web

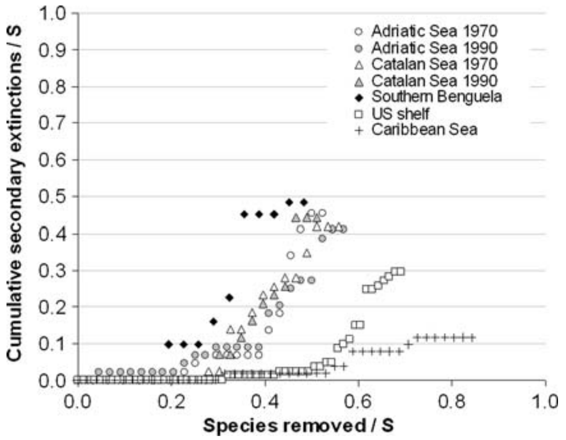

**Figure 6.** Comparison of secondary extinctions resulting from primary species loss of most connected species in Mediterranean and non-Mediterranean food webs.

structure with lower omnivory, species involved in looping and mean trophic level of the community, and higher generality. This can be related to fisheries catch trends showing a significant decrease of fish catch with time and a maintenance of invertebrate catches (Coll and others 2007).

## Higher Degradation in Mediterranean Compared to Non-Mediterranean Systems

In our analysis, Mediterranean food webs showed stronger overexploitation of higher trophic levels as indicated by the lower fraction of intermediate taxa and higher fraction of basal taxa, as well as lower trophic height and higher generality. The two Mediterranean systems also showed higher simplification of food-web structure compared to non-Mediterranean systems as indicated by lower fraction of omnivores, decreased connectance, decreases in the number of species involved in loops and shorter chain length. We also found important differences in productivity and biomass, with lower biomass at higher trophic levels and higher biomass at lower trophic levels in the Mediterranean compared to non-Mediterranean systems. The production of trophic flows to detritus, previously suggested as an indicator of disruption of energy transfer from lower to higher trophic levels (Walsh 1981; Odum 1985; Shannon and others in press), was higher within the Mediterranean Sea. This indicates that the vertical transfer of trophic flows may have decreased due to simplification and overexploitation, and as a consequence there has been an increase of trophic flows towards detritus or horizontal transport (Odum 1985; Christensen and Pauly 1993).

Our results suggest that human pressure in the Mediterranean has homogenized the food webs towards shorter, fatter and less productive systems (McCann 2007) in line with Dell and others (2005). The higher ecological degradation and simplification of food-web structure of Mediterranean compared to other marine ecosystems has also been highlighted in a comparative study of the South Catalan Sea model with upwelling models (Coll and others 2006a).

These results complement those of Pauly and others (1998), who found a lower mean trophic level of the fisheries catch in the Mediterranean Sea in the 1950s compared to other oceanic areas of the world. They are also consistent with regional data as well. Margalef (1985) suggested that Western Mediterranean coastal areas had already been overfished by the early 1900s. Moreover, within the Mediterranean Sea, many species groups have experienced long-term declines. Ferretti and others (2008) found that declines of large sharks in the Mediterranean Sea, which ranged between 96% and 99.9% over the last 50–200 years, and the mean size of sharks landed in Mediterranean pelagic fisheries is among the lowest in the world (Megalofonou and others 2005). Tuna fishing data and historical records on fishing development in the Mediterranean showed important declines of these organisms before the advent of industrial fishing (Florido 2004; Garrido 2006). Sub-fossil remains of hake otoliths indicating very large individuals have been documented in shallow Hellenic waters where such mature segments of the population do not occur nowadays (CIESM 2000). Large pelagic fish and dolphins were regularly fished at least from the fourteenth century in the Catalan Sea (Garrido 2006), and other marine mammals have also shown important historical declines (Bearzi and others 2004). The endemic monk seal (*Monachus monachus*) was already intensively hunted by the Romans and was ecologically extinct from the ecosystem in 1800–1900. After large organisms were exploited and became scarce, fishermen moved on to exploit smaller organisms, such as smaller demersal and pelagic fishes, and extended their fishing range from the coastal areas to the shelf systems and the deep sea, showing a continuous process of technology innovation and development (Garrido 2006).

Thus, the higher degradation of Mediterranean food webs may reflect the longer history of exploitation in the Mediterranean basin, where humans have exerted strong top-down control and the first signs of depletion of coastal resources occurred during Roman times, approximately

2,500 years ago (Hughes 1996; Lotze and others 2006). In contrast, exploitation of marine resources in the Benguela region increased with the arrival of European seafarers in the fourteenth century (Griffiths and others 2004). European colonization of American coastal areas initiated intense commercial exploitation of marine resources in the sixteenth and seventeenth centuries (Steneck and Carlton 2001; Jackson and others 2001; Pandolfi and others 2003; Lotze and others 2006). Interestingly, our results matched this chronology of the history of marine exploitation in the study areas with Mediterranean and Southern Benguela being more degraded than the Caribbean Sea and US continental shelf. However, whether the degree of degradation is related to the length of exploitation history requires further testing.

Differences between Mediterranean and non-Mediterranean models could also be partially due to methodological limitations such as the different resolution of ecosystem models and ecosystem information (Fulton and others 2003; Dunne 2005). For example, differences in the fraction of top predators, which are slightly higher in the Mediterranean than in the other marine webs, may be due to the lack of detailed links for predation on the juveniles of top predators in the Mediterranean webs. The trophic position of top predators without any juvenile predators was higher in the Mediterranean webs than in other webs, where information for ontogenetic fractions of species is available. However, two other indicators capturing similar information, the percentage of biomasses of top predators and the mean trophic level of the community, gave similar results towards higher degradation in Mediterranean systems. Similar problems could be important for the comparison of other indicators (especially connectivity and system omnivory index) from Ecopath models of non-Mediterranean systems which are represented by different numbers (higher or lower) of trophic groups compared to Mediterranean systems (Christensen 1995; Pinnegar and others 2005). Despite these limitations, most indicators showed consistent results between the Niche and Ecopath models. This may be explained by the bias of all food-web models used towards fish components so they do not show strong differences between aggregation or removal of trophic weak links or links of species with low consumption in the system (Pinnegar and others 2005). This can only be further tested when data availability on low trophic level organisms increases. However, trophic species and standardized food webs have been shown to overcome many of the effects of different resolution in past food-web studies (Martinez 1999; Fulton and others 2003; Dunne 2005).

One of the indicators providing unclear results was the transfer efficiency calculated with the Ecopath models. The same problem has been encountered previously (Pauly and Christensen 1998). The transfer efficiency has shown an increase across ecosystems submitted to higher levels of fishing impact in studies analyzing calibrated Ecosim models through time (Libralato and others 2005) as well as using size-based production and stable isotope analysis (Jennings and others 2002). On the other hand, the transfer efficiency was suggested to decrease in stressed ecosystems (Odum 1985). Further analyses are needed to clarify this point. Unexpected results were also found for cannibalism. Mediterranean models showed lower values of cannibalism than non-Mediterranean systems, which was contrary to our initial hypothesis that cannibalism increases with food-web degradation. Cannibalism could alternatively be correlated to biomasses at higher trophic level, which means biomass of adult individuals of species involved in cannibalism. A significant correlation between cannibalism and trophic level of the community (SWTL) was found in this analysis (Spearman's correlation coefficient $r_s = 0.964$, $P = 0.000$). On the other side, lower rates of cannibalism by European hake (*Merluccius merluccius*) from the Mediterranean were found when comparing data with similar species in Southern and Northern Benguela (*M. gayi*) and Southern and Northern Humboldt (*M. capensis* and *M. paradoxus*) upwelling systems and were related to evolutionarily different behavioral strategies (Bozzano and others 2005; Coll and others 2006a). Trophic path length measured as Finn's Path Length gave unclear results for Ecopath models, whereas the characteristic path length (Path) from Niche models increased in the Mediterranean compared to non-Mediterranean areas. This is contrary to what we hypothesized but in line with the inverse relationship found between connectance and Path by Williams and others (2002).

## Lower Robustness of Mediterranean Food Webs to Species Loss

The rate of secondary extinctions resulting from primary loss of species showed similar results in Mediterranean areas compared to other marine food webs, and was higher compared to non-marine food webs which is in line with previous studies (Dunne and others 2004). However, differences in magnitude can be seen when comparing results from Mediterranean and non-Mediterranean systems. The highest impact of removing highly connected species was found in Southern Benguela and the Mediterranean. In these models we found lower values of species linkage, lower percentage of omnivory and lower connectance that could result in a higher impact of the loss of highly connected taxa. Lower values of omnivory have been highlighted to have important implications for food-web dynamics because omnivory is suggested to stabilize food webs and reduce the likelihood of trophic cascades within food webs (Fagan 1997; McCann and Hastings 1997; Bascompte and others 2005). Lower connectance of food-web networks has been related with higher probability of secondary extinctions (Dunne and others 2002). These results are similar to those obtained from comparing the 22 food-web properties from Mediterranean and non-Mediterranean models suggesting an underlying relationship between higher degradation of food-web structure and lower robustness to species loss and thus more proneness to species extinctions. However, we have not found a significant relationship between robustness and ecosystem structural properties, with the exception of total system biomass ($t \cdot km^{-2}$), probably due to our low sampling size and limited data.

In our analysis, removing commercial species from Mediterranean food webs had higher impacts than removing species randomly and lower impacts than removing the most connected species. In fact, the impact of removing commercial species depends on how connected these species are. In the case of the North-Central Adriatic Sea during the mid-late 1970s, 80% of the commercial taxa showed high connectance (we considered highly connected taxa those showing a connectance of ≥10). This percentage decreased to 60% during the mid-late 1990s due to a decline in fish and increase in invertebrates in the fisheries catch (Coll and others 2007). In the South Catalan Sea, 70% of the commercial taxa during both time periods showed high connectance. These differences in connectance of commercial species explained the observed results, and are in line with findings from simulations of realistic extinctions in freshwater lakes (Srinivasan and others 2007). According to the Food and Agriculture Organization of the United Nations (FAO), up to 24% of species are considered overexploited or severely exploited worldwide (SOFIA 2006), and 35% of commercial stocks in the Mediterranean were considered overexploited, depleted or recovering in 2004 (SOFIA 2004). Even if overexploited species are not extinct from the food web, they can lose their contribution to the structure of the ecosystem and could be considered ‘‘structurally extinct’’. Thus, the current situation of exploitation of marine resources could lead to additional species loss.

## CONCLUSIONS

Our results show that a cross-comparison of ecosystem models is a powerful tool to evaluate the robustness of food-web models and validate their results. This approach contributes to a better understanding of ecosystem structural and functional properties, as highlighted in other previous model comparisons (for example, Heymans and Baird 2000; Fulton and Smith 2004; Shin and others 2004, Dunne and others 2004). We have successfully applied the stochastic food-web Niche and mass-balance Ecopath modelling approaches to test the hypothesis of ecological degradation and overexploitation in the Mediterranean Sea. Both Mediterranean models showed similar food-web structure during the mid-late 1970s and 1990s, and higher levels of degradation compared to non-Mediterranean systems. Results from both mass-balance and stochastic food-web models were generally consistent despite fundamentally different assumptions and theories underlying both modelling approaches. Although food webs from different types of ecosystems with variable diversity and complexity share fundamental structural and ordering characteristics (Dunne and others 2004), our results indicate that some differences between Mediterranean and non-Mediterranean food webs could be related to an advanced state of degradation in the Mediterranean Sea, in line with insights from other global comparisons including the Mediterranean ecosystem (Libralato and others 2008). Secondary extinctions resulting from simulation of primary loss of species may underline a relationship between higher degradation of food-web structure and lower robustness to species loss. Future work including dynamic simulations and extending the comparison to other past and present food webs may provide further insights into ecosystem changes in the Mediterranean Sea.

## ACKNOWLEDGEMENTS

We acknowledge the co-authors of food-web models of the Mediterranean Sea: Isabel Palomera, Sergi Tudela, Francesc Sarda, Alberto Santojanni and Enrico Arneri. We also thank the authors of the non-Mediterranean food-web models used in this work: Jenniffer Dunne, Lynne Shannon, Silvia Opitz and Tom Okey. Thanks to Colette Wabnitz for advice on Caribbean Sea catch data, Jennifer Dunne, Neo Martinez and Paul Yoon for supporting this work and giving advice on the Niche model and Villy Christensen for giving advice on the Ecopath model. MC was partially supported financially by a postdoctoral fellowship from the Spanish Ministry of Education and Science. This work was financially supported by the Sloan Foundation (Census of Marine Life, FMAP program) and the Natural Sciences and Engineering Research Council of Canada with grants to HKL. We thank two anonymous reviewers for comments and corrections on the manuscript.

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