

# Network structure and robustness of marine food webs

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## ABSTRACT

Previous studies suggest that food-web theory has yet to account for major differences between marine food webs and the trophic structure of other ecosystems. We examined this issue by analyzing the structure of food webs for Benguela (South Africa), a Caribbean reef, and the Northeast US shelf with 29, 50, and 81 taxa, respectively. Marine webs tend to have somewhat higher connectance (links/species<sup>2</sup>), link density (links/species), mean chain length, and fractions of intermediate, omnivorous, and cannibalistic taxa than food webs from other ecosystems. Given that most food-web properties are scale-dependent on network diversity and complexity, we used the empirically well corroborated “niche model” that accounts for such dependence to compare the structure of marine and other food webs. Our results show that the niche model accurately predicts 15 properties of the marine food webs 81% of the time, similar to the 79% success rate previously reported for other food webs. This suggests that common mechanisms underlie emergent network structure across ecosystems and that the uniqueness of marine food-web structure has been exaggerated. The structural robustness of marine food webs to species loss, in terms of potential secondary extinctions, was also consistent with trends from other food webs. Marine webs appear relatively robust to loss of most-connected taxa as well as random taxa, as expected given their relatively high connectance. However, the short average path length between marine taxa (1.6 links) also suggests that effects from perturbations such as overfishing can be transmitted more widely throughout marine ecosystems than previously appreciated.

KEY WORDS: Food Webs, Network Structure, Marine Ecosystems, Robustness, Connectance, Niche Model, Biodiversity Loss

## I. INTRODUCTION

Recent studies have described general properties of complex food-web structure as well as simple rules that accurately predict such structure in a wide variety of terrestrial and aquatic ecosystems (e.g., Williams & Martinez 2000, Camacho et al. 2002ab, Dunne et al. 2002ab, Williams et al. 2002). The data used in these studies have substantially higher diversity, complexity, and resolution than the earlier “ECOWeB” food-web data used to initiate topological food-web research (Cohen et al 1990). Analyses of improved data have modified earlier food-web theory and contributed new insights into the trophic network structure and robustness of ecosystems. However, food webs from marine ecosystems have been conspicuously absent from recent work (e.g., Williams & Martinez 2000). An earlier analysis of ECOWeB data, including 11 marine food webs with low average diversity (18 taxa), found strong contrasts between marine and other food-web networks (Cohen 1994). Similarly, a recent analysis of a more diverse, complex marine food web (81 taxa) for the Northeast US Shelf concluded, “it is clear that the emergent properties of this marine food web are very different than their terrestrial and freshwater counterparts” (Link 2002).

Here, we revisit comparisons of marine food webs to food webs from other types of ecosystems using three recently published marine webs with 29 to 81 taxa, including the NE US Shelf food web (Link 2002). In particular, we consider: (1) Do marine food webs show similarities to each other? (2) Do marine food webs look like other types of food webs? (3) Does food-web theory apply to marine ecosystems? and (4) What are the empirical limitations of recent marine food-web data? We also use the three marine food webs to simulate the potential effects of different types and magnitudes of

species loss in triggering cascading secondary extinctions. This allows a comparison of the potential robustness to biodiversity loss associated with the network structure of marine versus other types of food webs (Dunne et al. 2002a). This type of research into food-web structure and robustness is just one example of the statistical mechanics of “real-world” technology, information, social, and biotic networks (see Strogatz 2001, Albert & Barabási 2002 for reviews). Even in the absence of dynamical modeling, which is challenging even for relatively low diversity systems, analysis of network structure can have important implications for network function (Strogatz 2001). For marine ecosystems, historically subject to intense fisheries harvesting pressure and subsequent collapse (Jackson et al. 2001, Pauly et al. 1998, 2002), more detailed knowledge of the complex network of trophic relationships that encompass species of economic interest will be important for guiding more sustainable policy.

## II. METHODS

We analyzed the network structure of three recently published marine food webs with relatively detailed trophic interaction data. The first is a 29-taxa food web for the Benguela ecosystem off the southwest coast of South Africa (Field et al. 1991, Yodzis 1998, 2000). A second 50-taxa food web of a Caribbean coral reef ecosystem is reported for the Puerto Rico-Virgin Islands shelf complex (Opitz 1996). The third is an 81-taxa food web of the Northeast US shelf ecosystem (Link 2002). We refer to these ecosystems and their food webs as Benguela, Caribbean Reef, and NE US Shelf. All three ecosystems are subject to fisheries harvesting, and the food-web data reflect a strong fish bias, which represent  $\geq 50\%$  of the taxa in each web (Table 1). Invertebrates (22-41% of taxa) are

underrepresented and aggregated (Link 2002) and basal taxa are very highly aggregated into simplified groups such as “phytoplankton” and “detritus” (3-7% of taxa). All three food webs simplify more detailed trophic data in other ways. For example, the Caribbean Reef web aggregates 243 fish species into 25 fish groups based on size, activity level, and food type, while 41 nonfish taxa, many of which were already highly aggregated, were more subjectively aggregated into 25 nonfish groups (Opitz 1996). Still, all three food webs represent significant improvements over earlier low-diversity marine food-web data (e.g., Cohen et al. 1990). Two of the studies (Opitz 1996, Yodzis 1998) include extensive data beyond food-web structure (e.g., body size, diet preferences, population biomasses) and while Link (1998) focuses on food-web structure, his data are based on detailed stomach content data (Link & Almeida 2000).

We studied trophic species versions of the food webs, where the taxa reported by the original authors are aggregated into groups called ‘trophic species’ whose members share the same set of predators and prey (Briand & Cohen 1984). The use of trophic species, hereafter referred to as species or taxa ( $S$ ), is a widely accepted convention in structural food-web studies that reduces methodological biases of uneven resolution of taxa within and among food webs (Williams & Martinez 2000). Because all three studies focused on analyzing food webs with trophically distinct components, only the NE US Shelf web decreases slightly in diversity due to trophic species aggregation, from 81 to 79 taxa (Table 2).

For each food web, we calculated 17 network structure properties (Tables 2, 3). Two standard measures of food-web connectedness are reported: links per species ( $L/S$ ), the mean number of species’ predators and prey (also called link density); and connectance ( $C$ ), where  $C = L/S^2$ , the proportion of possible trophic links that are

actually realized. Seven properties give percentages of types of species in a food web: top ( $T$ ), intermediate ( $I$ ), and basal species ( $B$ ); cannibals (*Cannib*); omnivores (*Omniv*) (species with food chains of different lengths); herbivores (*Herb*); and species involved in looping (*Loop*) by appearing in a food chain twice. Most of these are commonly reported properties that have been reviewed elsewhere (e.g., Williams & Martinez 2000) although *Herb* has not been previously reported. The remaining eight properties quantify overall properties of network structure. Following Williams & Martinez (2000), we report the standard deviations of mean generality (*GenSD*) and vulnerability (*VulSD*), which quantify the variabilities of species’ normalized predator and prey counts (Schoener 1989); mean maximum trophic similarity of species pairs (*MxSim*); and three food chain length related measures, the mean (*ChnLg*) and standard deviation (*ChnSD*) of chain lengths and the log of the number of chains (*ChnNo*). Finally, we report two measures of “small-world” network structure (Watts & Strogatz 1998): characteristic path length (*Path*), the mean shortest path length between species pairs; and clustering coefficient (*Clust*), the mean fraction of species pairs connected to the same species that are connected to each other (Williams et al. 2002, Dunne et al. 2002b).

For each marine food web, we compared the ability of two simple stochastic food-web structure models, the cascade model (Cohen et al. 1990) and the niche model (Williams & Martinez 2000), to predict 15 of the 17 food-web properties. The models have only two input parameters: the number of trophic species ( $S$ ) and connectance ( $C$ ) of the food web being modeled. We ignore random network models (e.g., Erdős & Rényi 1960) because food-web structure, as well as the structure of most, if not all real-world networks, is clearly not random (Watts & Strogatz 1998, Williams & Martinez 2000).

The cascade model (Cohen et al. 1990) assigns each species a random value drawn uniformly from the interval [0,1] and each species has probability  $P = 2CS / (S-1)$  of consuming species with values less than its own. The niche model (Williams and Martinez 2000) builds on the cascade model, with each species similarly assigned a randomly drawn “niche value” ( $n_i$ ) from the interval [1,0] (Fig. 1). Each species is then constrained to consume all prey species within a range of values ( $r_i$ ) whose randomly chosen center ( $c_i$ ) is less than the consumer’s niche value. In the niche model, the placement of the feeding range relaxes the cascade model’s strict feeding hierarchy by allowing up to half a consumer’s range to include species with higher niche values than the consumer, thus allowing looping and cannibalism. Also, the consumer must feed on all species that fall within its feeding range, a contiguity that is absent from the cascade model. For each marine food web, we used Monte Carlo simulations to generate 1000 cascade and niche model webs with the same  $S$  and  $C$  as the empirical web, allowing calculation of a model mean and standard deviation for each property. If the normalized error (raw error divided by model SD) between the empirical property and the mean model value for that property falls within  $\pm 2$  model SD, the model is considered to be a good fit to the empirical data (Williams & Martinez 2000).

In another analysis, we simulated species loss in each marine food web by sequentially removing species selected by one of three criteria: (1) the most connected species, (2) randomly chosen species (1000 random removal sequences initiated for each web), and (3) the least connected species (Dunne et al. 2002a). The connectedness of a species is calculated as the sum of both predator and prey links. When the most and least connected species are targeted for “primary extinctions,” we protect basal species because removing such highly

aggregated species (e.g., phytoplankton) in marine food webs has obviously large and not particularly informative consequences. “Secondary extinctions” result when a consumer species loses all of its prey items or when a cannibalistic species loses all of its prey items except itself. The most or least connected species in a web was determined at each step of the simulation, i.e., after the web had reconfigured after the previous removal and any resulting secondary extinctions. The structural “robustness” of each food web to the three types of species loss was calculated as the fraction of species that had to be removed in order to result in total species loss (i.e., primary species removals plus secondary extinctions) of  $\geq 50\%$  of the species in the original web. Maximum robustness (0.50) occurs when no secondary extinctions follow primary extinction of 50% of the species and minimum ( $1/S$ ) occurs when the first primary extinction leads to 50% total loss of species (Dunne et al. 2002a).

To examine the relationship between robustness and the trophic level of species being removed, we calculated mean “prey-averaged” trophic level for each food web and subsets of taxa. The prey-averaged trophic level for a particular taxon is one plus the mean trophic level of all the taxon’s trophic resources. It is computed using the matrix algebra method of Levine (1980) based on summing an infinite geometric series that includes the contributions from all loops. This and other trophic level measures are defined in more detail and reviewed by Williams and Martinez (2003).

### III. RESULTS AND DISCUSSION

#### Direct comparisons of food webs

Direct comparison of some representative food-web properties suggests that the three marine food webs have strong structural similarities (Tables 1,2). For

example, they have similar numbers of top (0-4%), intermediate (92-94%), and basal taxa (4-7%), as well as omnivores (76-86%). Mean shortest path length among all pairs of taxa is nearly identical (~1.6 links) and  $C$  ranges from 0.22 to 0.27. Consistent with current food-web theory (e.g., Martinez 1992),  $L/S$  and chain length vary strongly among the marine webs, increasing with  $S$ . Thus, Benguela, with 29 taxa, has the smallest values ( $L/S = 7.9$ , mean chain length = 6.5) and NE US Shelf, with 79 taxa, has the largest values ( $L/S = 18.1$ , mean chain length = 15.5).

How do the marine food webs compare with food webs from other types of ecosystems? First, direct comparisons of food-web properties across and often within ecosystem types reveal a wide range of values (Table 2). Since most food web properties are known to be scale-dependent (e.g., Martinez 1994, Dunne et al. 2002b), this variation is both unsurprising and not necessarily indicative of fundamental differences among food webs. However, given that caveat, it is interesting to note that marine food webs have high levels of intermediate taxa, omnivores, and cannibals (IOC) compared to many, but not all, other food webs. Their levels are comparable to two small webs, Coachella Valley and Skipwith Pond, as also noted by Link (2002). The high levels of IOC in the Coachella Valley desert food web are largely artifacts of high aggregation of taxa, but in the highly resolved Skipwith Pond food web the high levels are due to the predominance of generalist (wide-diet) insect species. Whether high IOC in marine webs is the result of methodological problems (e.g., bias towards fishes), or is a fundamental attribute of marine ecosystems (e.g., widespread generalist feeding habits related to gape size and filtering), is an open question (Link 2002) that requires more detailed and evenly resolved data to settle (Cohen et al. 1993). The low percentage of basal taxa in these marine food webs compared to other systems is clearly an

artifact of poor resolution of primary producers and consumer links to them. Better resolution at the basal level would tend to mitigate, but probably would not erase, current high levels of IOC taxa in marine food webs.

As also discussed by Link (2002) for the NE US Shelf web and Cohen (1994) for a set of 11 highly aggregated, low-diversity marine food webs, marine webs have high  $L/S$  and mean chain lengths compared to food webs from other ecosystems (Table 2). This is the case even when the marine webs are compared to food webs with similar or larger  $S$ . In particular, the Caribbean Reef and NE US Shelf webs have higher values of  $L/S$  and chain length than any other food web shown. Cohen (1994) goes through a detailed discussion (which we do not repeat here) of a variety of biological and methodological reasons that marine webs might display higher  $L/S$  and chain lengths. Interestingly, the more highly resolved data summarized here have not eliminated the patterns Cohen found in the early data; indeed the patterns are exaggerated in the more recent data. However, the current marine food webs, while more diverse than earlier marine webs, still have obvious empirical problems, particularly the over-emphasis on fish taxa and high aggregation of basal taxa.

The three marine food webs also have relatively high connectance values from 0.22 to 0.27, although they fall within the range of connectances observed for a variety of high quality food webs (0.03 to 0.3) (Table 2, Dunne et al. 2002a). We do not use Link's (2002) "interactive connectance" measure,  $connectivity = L / [ S (S-1) / 2 ]$ . The denominator precludes cannibalism and mutual predation while the numerator includes such links and therefore results in double counting, exaggerated connectance, and other misrepresentations (Martinez 1991). Empirical data suggest that food webs, including the current marine webs, often

include cannibalism and mutual predation (e.g., Polis 1991). The connectance measure we use, also called “directed connectance” ( $C = L/S^2$ ), avoids these problems by allowing the numerator to reflect the fact any species has the potential to feed on any species in a web. Thus, Link’s (2002) assertion that order-of-magnitude higher connectivity in the NE US Shelf food web is an indicator of dramatic differences between marine and other types of ecosystems is incorrect. Instead, marine food webs display connectance above the mean but within the range seen in non-marine food webs when consistent methodology is employed.

#### Comparisons using the niche model

As mentioned above, direct comparisons of properties can be misleading due to the scale-dependence of food-web network properties. Comparing observed food webs against model food webs that incorporate ecological scale-dependence mitigates this problem. If a particular model accurately predicts the network structure of a range of food webs, those food webs can be considered to have a similar structure. Two such food-web models are the cascade model (Cohen et al. 1990) and the niche model (Williams & Martinez 2000). These simple models, described previously, use only two input parameters,  $S$  (species richness) and  $C$  (connectance), equal to the  $S$  and  $C$  of the empirical food web being modeled. The use of these two parameters embodies the notion that the network structure of food webs will vary in predictable ways in accordance with their diversity (i.e., number of taxa) and complexity (i.e., number of interactions).

The cascade model fails to accurately predict marine food-web structure. Of 15 properties assessed for the Benguela and Caribbean Reef food webs, only 5 are well-matched by the cascade model, and only 3 of 12 are properties are well-matched for the NE

US Shelf food web (results not shown). Overall, the cascade model accurately predicts only 31% of the properties examined in the marine food webs. This is very similar to what was found for an analysis of 2 lake, 1 pond, 2 estuary, and 2 terrestrial food webs (Williams & Martinez 2000, Table 2), where the overall success rate of the cascade model was 27%. In contrast, the niche model closely predicts the structure of the three marine food webs. Of 42 niche model means (15 properties of two webs and 12 properties of one web), 81% are within 2 model SD of the empirical data (Table 3). This is very similar to the 79% overall success rate for the niche model found by Williams and Martinez (2000) for 12 properties of seven non-marine food webs. The similar high level of niche model predictive success for marine, estuary, freshwater, and terrestrial food webs suggests that marine food webs have remarkably similar network structure to food webs from other ecosystems.

The niche model does particularly well for the Benguela and Caribbean Reef webs, with accurate predictions for 13 of 15 properties each. In the Benguela food web, the niche model underestimates the variability in species’ normalized prey counts, and overestimates the degree that species are clustered. In the Caribbean Reef web, it underestimates the amount of cannibals and also the mean maximum trophic similarity of species. Only 8 of 12 properties are well predicted for the NE US Shelf food web. The niche model overestimates the mean maximum trophic similarity of species and the amount of omnivorous taxa. It underestimates the variability of species’ normalized predator counts, and dramatically underestimates the amount of herbivorous taxa, which may result from the hyper-aggregation of basal taxa. Any of these mismatches could stem either from problems with the data or with the model; more highly resolved data would help to resolve that issue.

## Structural robustness of marine food webs

When species are systematically removed from the three marine food webs in biodiversity loss simulations, potential secondary extinctions resulting from the loss of all prey items varied among the webs and due to different types of species removed (Fig. 2). Very few secondary extinctions occurred as a result of removing taxa with very few connections, whereas removing random taxa and the most connected taxa did result in additional species loss, once >25% of the species in the original webs were removed. Benguela showed the most dramatic effects and differences among the three targeting strategies where removal of ~30% of most connected, random, and least connected taxa resulted in ~20%, 11%, and 3% of the taxa undergoing secondary extinctions, respectively. In general, the Caribbean Reef and NE US Shelf web displayed very high robustness to species removals, with >50% primary removals required to induce >5% secondary extinctions.

Marine food webs generally show high structural robustness to species loss compared to other food webs analyzed previously (Solé & Montoya 2001, Dunne et al. 2002a), which appears related to their relatively high connectance (Dunne et al. 2002a, Fig. 3). Structural robustness, when most connected or random species are targeted, increases significantly with increasing connectance, and saturates at 0.50, which is the point at which there are no secondary extinctions as a result of 50% primary removals (Fig. 3). Benguela is an outlier compared to the other 2 marine and 16 non-marine webs represented, with lower robustness than expected for both types of species removals. For all 19 food webs, structural robustness did not vary significantly with species richness ( $S$ ), and because of the very low secondary extinctions associated with targeting the least connected taxa while protecting basal species, there was no

relationship between that type of species loss and either  $S$  or  $C$  (linear regression data not shown, see Dunne et al. 2002a).

Why is Benguela an outlier? The first 10 most and least connected taxa removed in the simulations are shown for each food web in Table 4. A qualitative look at the most connected taxa suggests that in the Benguela food web, there are highly connected taxa such as macro- and mesozooplankton that are fairly low in the food web, unlike in the Caribbean Reef and NE US Shelf webs. Quantitatively, the three marine food webs have similar mean (3.5 to 3.6) and maximum (5.0 to 5.4) trophic levels, and the average trophic level of least connected taxa (the first 25% of  $S$  removed) is similar to the mean trophic level for each web (Table 5). However, the mean trophic level of the most connected species is much lower for Benguela (3.7) than the Caribbean Reef and NE US Shelf food webs (4.3, 4.1). This suggests that from a structural perspective, removing highly connected lower trophic level taxa is more destabilizing than removing highly connected upper trophic level taxa.

## IV. CONCLUSION

Previous examinations of marine food-web structure concluded that marine food webs are fundamentally different from other kinds of food webs (Cohen 1994, Link 2002). In the current study, measures of food-web structure such as  $L/S$ , connectance, omnivory, and cannibalism suggest that marine food webs (1) tend to look similar to each other, and (2) have higher values for those properties than the means of previously studied estuary, freshwater, and terrestrial ecosystems. Marine webs thus appear to have relatively large trophic interaction richness. However, in most cases marine food webs do fall within previously reported ranges of observed food-web properties from non-marine systems. More evenly and highly resolved data from

marine and non-marine systems will help to decide whether current patterns are artifacts or whether they reflect more significant similarities or differences among and within different types of ecosystems (Cohen et al. 1993).

Even given apparent differences in food-web properties between marine and other ecosystems, it does *not* appear that “food web theory needs to be modified to accommodate observations from marine ecosystems” (Link 2002). Instead, our study shows that when species richness and connectance are taken into account, observations from marine food webs strongly corroborate current food-web theory. In particular, the niche model of food-web structure very accurately predicts the structure of marine food webs, as it does for other types of food webs (Williams & Martinez 2000). This suggests that the emergent network structure of food webs is a general property of ecosystems. It also suggests that the simple rules of the niche model, which specify a relaxed feeding hierarchy that allows cannibalism and looping as well as a contiguity of feeding within a niche, may point to common ecological, evolutionary, and thermodynamic mechanisms shaping the complex network structure of food webs from all types of ecosystems examined thus far (Williams & Martinez 2000, Camacho et al. 2002ab, Dunne et al 2002ab, Montoya & Solé 2002, Williams et al. 2002).

Food webs are of particular interest in marine ecosystems because of the intense economic harvesting pressure, overexploitation, and the collapse of many coastal and shelf marine fisheries (e.g., Boreman et al. 1997, Jackson et al. 2001). What can network structure tell us about the potential robustness of food webs to biodiversity loss? Current and previous results (Dunne et al. 2002a) suggest that highly connected communities will tend to be more robust to species loss than low connectance communities, and that the loss of

highly-connected taxa will tend to induce higher levels of secondary extinctions than loss of random taxa (Albert et al 2000, Solé & Montoya 2001). This suggests that marine systems, with relatively high connectance, will have greater inherent structural robustness than other ecosystems. However, other structural effects can come into play. First, extinctions in marine systems do not appear random, particularly with regard to anthropogenic effects over the last several centuries. Humans tend to selectively and intensively harvest marine taxa at high trophic levels (Pauly et al. 1998, Jackson et al. 2001), which are often the taxa that are highly connected (Table 5). Also, the mean shortest path length between pairs of taxa within marine webs is low (1.6 links) compared to other types of food webs, which have values ranging from 1.3 to 3.7 (Table 2, Dunne et al. 2002b). This suggests that most species in marine food webs are potentially very close “neighbors,” and that negative effects can spread rapidly and widely throughout the food web (Williams et al. 2002). However, the rich network of interactions quantified by high connectance and low path length may also suggest that strong effects can rapidly disperse throughout marine food webs, thus decreasing the overall impact of any particular fluctuation (Link 2002). This perspective provides support from a structural perspective for MacArthur’s hypothesis about community stability and complexity (1955).

This analysis, like other structural food-web studies, does not consider the dynamics of interacting taxa (e.g., May 1973). Useful predictions of ecosystem response to perturbations such as population or biomass fluctuations and species losses or introductions requires modeling that integrates ecologically plausible network structure with non-linear interaction dynamics of species (Williams & Martinez 2001). Dynamical studies that that overly simplify structure, focusing on small modules of the most

“important” species, may provide poor and unreliable approximations of dynamics in complex systems with diffuse interactions (Yodzis 2000). Marine food webs, particularly those impacted by humans, may be the ideal test case for developing and applying integrated models, as explored in the Benguela food web (Yodzis 1998, 2000), for two reasons. First, the drastic need for more sophisticated ecological (and economic) modeling and prediction to guide fisheries and marine reserve policy is clear. Second, groups such as the Partnership for Interdisciplinary Study of Coastal Oceans (PISCO) and the Marine Ecosystem Dynamics (MED) consortium are developing an excellent empirical foundation necessary for applied ecosystem modeling. An improved understanding of marine food-web structure, which explicitly focuses on the complex network of interactions in which harvested taxa are embedded, will be a cornerstone of future marine ecosystem research and policy.

#### ACKNOWLEDGEMENTS

This work was supported by NSF grants DEB/DBI-0074521 (JAD), DEB-0083929 (NDM), DBI-0234980 (NDM, JAD, RJW), and DBI-9904777 (RJW). This work was conducted during JAD’s residence at SFI.

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Table 1. The number and percentage of different types of taxa within three marine food webs.

	Benguela	Caribbean Reef	NE US Shelf
All taxa	29	50	81
Fishes	18 (62.1%)	25 (50.0%)	41 (50.6%)
Other vertebrates	3 (10.3%)	2 (4.0%)	5 (6.2%)
Invertebrates	6 (21.7%)	18 (36.0%)	33 (40.7%)
Basal groups	2 (6.9%)	3 (6%)	2 (2.5%)

Table 2. Some commonly reported structural food-web properties for 14 food webs from a variety of ecosystem types. \* shows food webs analyzed in Williams & Martinez (2000). Taxa = number of taxa from original food web,  $S$  = number of trophic species,  $C$  = connectance ( $L/S^2$ ),  $L/S$  = links per species,  $ChLg$  = mean food chain length,  $Path$  = characteristic path length,  $T$  = % top species,  $I$  = % intermediate species,  $B$  = % basal species,  $Cannib$  = % cannibalistic species,  $Omniv$  = % omnivorous species. References: Coachella Valley (Polis 1991), St. Martin Island (Goldwasser & Roughgarden 1993), UK Grassland (Memmott et al. 2000), Skipwith Pond (Warren 1989), Bridge Brook Lake (Havens 1992), Little Rock Lake (Martinez 1991), Canton Creek and Stony Stream (Townsend et al. 1998), Chesapeake Bay (Baird & Ulanowicz 1989), St. Mark's Estuary (Christian & Luczkovich 1999), Ythan Estuary (Hall & Raffaelli 1991), Benguela (Yodzis 1998), Caribbean Reef (Opitz 1996), NE US Shelf (Link 2002).

	Taxa	$S$	$C$	$L/S$	$ChLg$	$Path$	$T$	$I$	$B$	$Cannib$	$Omniv$
TERRESTRIAL											
Coachella Valley*	30	29	0.31	9.0	6.7	1.4	0	90	10	66	76
St. Martin Island*	44	42	0.12	4.9	5.2	1.9	17	69	14	0	60
UK Grassland	75	61	0.03	1.6	3.2	3.7	31	56	13	0	21
LAKE/POND											
Skipwith Pond*	35	25	0.32	7.9	6.2	1.3	4	92	4	32	60
Bridge Brook Lake*	75	25	0.17	4.3	4.0	1.9	0	68	32	12	40
Little Rock Lake*	182	92	0.12	4.9	7.3	1.9	1	86	13	14	38
STREAM											
Canton Creek	108	102	0.07	6.8	3.2	2.3	25	22	53	1	8
Stony Stream	112	109	0.07	7.6	3.1	2.3	17	27	56	2	10
ESTUARY											
Chesapeake Bay*	33	31	0.07	2.2	4.0	2.7	32	52	16	3	52
St. Marks Estuary	48	48	0.10	4.6	6.6	2.0	17	69	12	6	71
Ythan Estuary*	92	83	0.06	4.8	5.9	2.2	37	54	9	4	54
MARINE											
Benguela	29	29	0.27	7.9	6.5	1.6	0	93	7	24	76
Caribbean Reef	50	50	0.22	11.1	9.8	1.6	0	94	6	42	86
NE US Shelf	81	79	0.23	18.1	15.5	1.6	4	92	4	31	77

Table 3. Comparison of 15 empirically observed structural food-web properties with niche model means (in parentheses) for three marine food webs. Empirical values whose normalized error falls within  $\pm 2$  model SD, demonstrating a good fit between the model and empirical data, are shown in bold. Niche model food chain properties were not calculated for the NE US Shelf food web due to the excessive computing time required. *T* = % top species, *I* = % intermediate species, *B* = % basal species, *Herb* = % herbivores, *Cannib* = % cannibals, *Omniv* = % omnivores, *Loop* = % species in loops, *GenSD* = generality standard deviation, *VulSD* = vulnerability standard deviation, *MxSim* = mean maximum similarity, *ChLg* = mean food chain length, *ChSD* = food chain length standard deviation, *ChNo* = log food chain number, *Path* = characteristic path length, *Clust* = clustering coefficient. \* shows properties not previously evaluated by Williams and Martinez (2000).

	Benguela	Caribbean Reef	NE US Shelf
<i>T</i>	<b>0</b> (4)	<b>0</b> (4)	<b>4</b> (2)
<i>I</i>	<b>93</b> (86)	<b>94</b> (87)	<b>92</b> (92)
<i>B</i>	<b>7</b> (10)	<b>6</b> (9)	<b>4</b> (6)
<i>Herb</i> *	<b>7</b> (4)	<b>6</b> (3)	19 (2)
<i>Cannib</i>	<b>24</b> (37)	42 (29)	<b>32</b> (31)
<i>Omniv</i>	<b>76</b> (81)	<b>86</b> (83)	77 (88)
<i>Loop</i>	<b>41</b> (65)	<b>68</b> (68)	<b>67</b> (80)
<i>GenSD</i>	1.22 (0.87)	<b>0.90</b> (0.93)	<b>0.91</b> (0.92)
<i>VulSD</i>	<b>0.66</b> (0.54)	<b>0.61</b> (0.55)	0.71 (0.54)
<i>MxSim</i>	<b>0.94</b> (0.92)	0.85 (0.73)	0.92 (0.96)
<i>ChLg</i>	<b>6.52</b> (7.73)	<b>9.82</b> (10.2)	----
<i>ChSD</i>	<b>1.46</b> (1.64)	<b>2.05</b> (1.91)	----
<i>ChNo</i>	<b>3.91</b> (4.47)	<b>6.29</b> (6.37)	----
<i>Path</i> *	<b>1.62</b> (1.52)	<b>1.60</b> (1.60)	<b>1.58</b> (1.58)
<i>Clust</i> *	0.30 (0.39)	<b>0.36</b> (0.34)	<b>0.31</b> (0.34)

Table 4. The first ten taxa eliminated from three marine food webs when targeting the most and least connected taxa, with basal taxa protected from removal. Qualifiers in parentheses refer to body size classes (int. = intermediate). Names are drawn from the original studies.

Most connected taxa

	Benguela	Caribbean Reef	NE US Shelf
1	Sharks	Sharks/rays (large)	Cod
2	Hakes	Carnivorous reef fish #3 (int.)	Red hake
3	Squid	Shrimps/hermit crabs/stomatopods	Spotted hake
4	Birds	Carnivorous reef fish #2 (int.)	White hake
5	Macrozooplankton	Carnivorous reef fish #1 (small)	Silver hake
6	Other groundfish	Omnivorous reef fish #1 (small)	Spiny dogfish
7	Mesozooplankton	Crabs	Goosefish
8	Anchovy	Gastropods	Little skate
9	Benthic carnivores	Carnivorous reef fish (large)	Man
10	Goby	Omnivorous reef fish #2 (small)	Winter skate

Least connected taxa

	Benguela	Caribbean Reef	NE US Shelf
1	Bacteria	Kyphosidae	Snails
2	Zooplankton, gelatinous	Gobiidae (small)	Tunicates
3	Microzooplankton	Groupers (large)	Billfish
4	Lightfish	Hemiramphidae	Birds
5	Other pelagics	Scaridae (large)	Pteropods
6	Yellowtail	Scaridae (int.)	Sponges
7	Geelbek	Scaridae (int.)	Sea cucumbers
8	Whales & dolphins	Sea turtles	Seals
9	Benthic carnivores	Lobsters	Baleen whales
10	Tunas	Jacks (large)	<i>Calanus</i> sp.

Table 5. Trophic level data for three marine food webs. MeanTL = the mean trophic level for the web across all taxa. MaxTL = the maximum trophic level observed for a taxon within each web. MostTL = the mean trophic level of most connected taxa removed, where n = 25% of original taxa (*S*). LeastTL = as for MostTL, but for least connected taxa.

	MeanTL	MaxTL	MostTL	LeastTL
Benguela	3.7	5.0	3.7	3.8
Caribbean Reef	3.6	5.4	4.3	3.6
NE US Shelf	3.5	5.2	4.1	3.4

Figure 1. Diagram of the niche model.  $S$  (trophic species richness) and  $C$  (connectance) are set at the observed values for the empirical web being modeled. Each of  $S$  species (here  $S = 7$ , shown by inverted triangles) is assigned a 'niche value' ( $n_i$ ) drawn uniformly from the interval  $[0,1]$ . Species  $i$  consumes all species falling in a range ( $r_i$ ) that is placed by uniformly by drawing the center of the range ( $c_i$ ) from the interval  $[r_i/2, n_i]$ . Thus, in this diagram, species  $i$  consumes 4 species (shaded triangles) including itself. The size of  $r_i$  is assigned by using a beta function to randomly draw values from the interval  $[0,1]$  whose expected value is  $2C$  and then multiplying that value by  $n_i$  to obtain a  $C$  that matches the  $C$  of the empirical web being modeled.

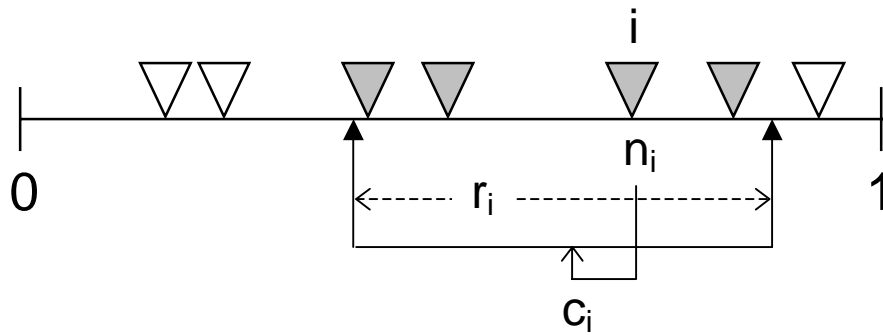


Figure 2. Secondary extinctions resulting from three types of primary species removal in three marine food webs. 95% error bars for random species removals fall within the size of the symbols and are not shown. The dashed line shows the points at which there is  $\geq 50\%$  total species loss (primary species removals plus secondary extinctions) in a food web for each type of species removal. The proportion of species that must be removed to reach that point is referred to as “structural robustness.”

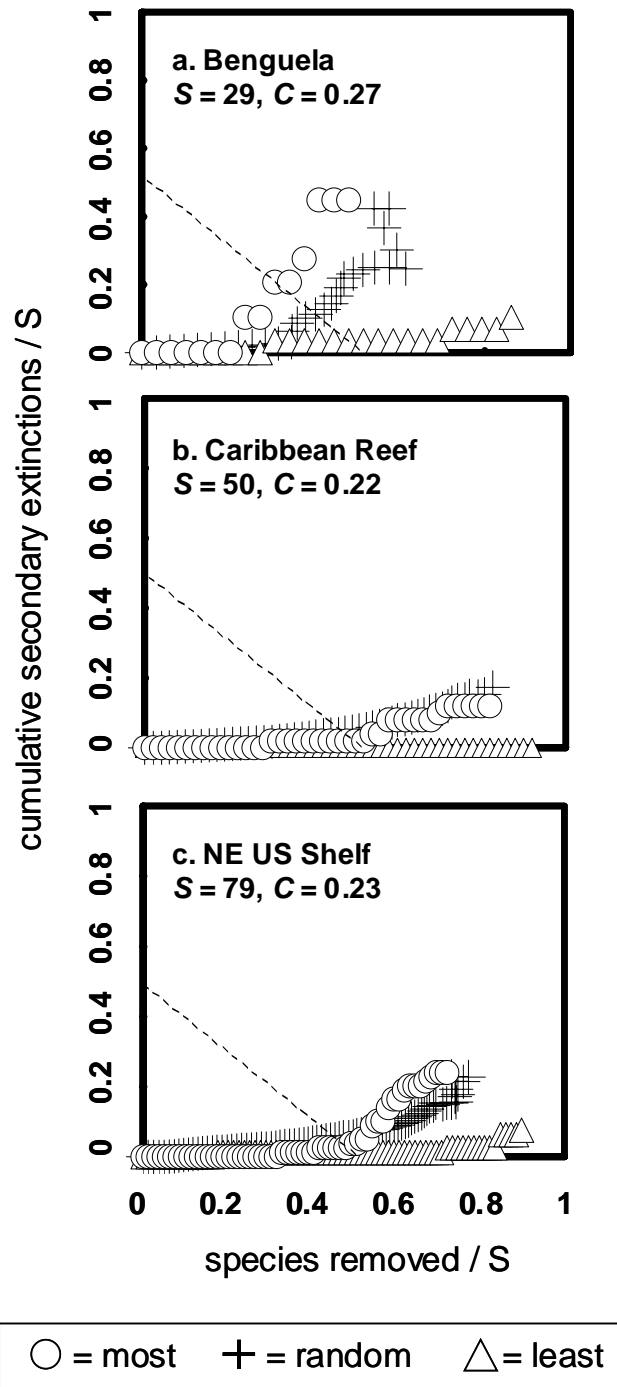


Figure 3. Structural robustness (the proportion of primary species removals required to induce a total loss of  $\geq 50\%$  of species) as a function of connectance ( $L/S^2$ ) in 16 food webs from Dunne et al. (2002a) plus three recent marine food webs (labeled and circled data points). Data shown for loss of most-connected taxa are for deletion sequences where basal taxa are protected from removal. Maximum robustness value = 0.50 (i.e., no secondary extinctions).

