1   Architecture of Marine Food Webs: to be or not be a 'small-world'

2

3

4   Tomás Ignacio Marina[1,2,3#], Leonardo A. Saravia[2,3#], Georgina Cordone[1,2,4¶], Vanesa Salinas[1,2¶], Santiago

5   R. Doyle[2¶] and Fernando R. Momo[2,3¶]

6

7   [1] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

8   [2] Instituto de Ciencias, Universidad Nacional de General Sarmiento, Los Polvorines, Argentina

9   [3] INEDES, Universidad Nacional de Luján, Luján, Argentina

10   [4] Centro Para el Estudio de Sistemas Marinos (CESIMAR), Centro Nacional Patagónico (CENPAT),

11   Puerto Madryn, Chubut, Argentina

12

13   * Corresponding author

14   E-mail: tomasimarina@gmail.com ORCID: 0000-0002-9203-7411

15

16   [#] These authors contributed equally to this work.

17   [¶] These authors also contributed equally to this work.

Abstract

The search for general properties in network structure has been a central issue for food web studies in recent years. One such property is the small-world topology that combines a high clustering and a small distance between nodes of the network. This property may increase food web resilience but make them more sensitive to the extinction of connected species. Food web theory has been developed principally from freshwater and terrestrial ecosystems, largely omitting marine habitats. If theory needs to be modified to accommodate observations from marine ecosystems, based on major differences in several topological characteristics is still on debate. Here we investigated if the small-world topology is a common structural pattern in marine food webs. We developed a novel, simple and statistically rigorous method to examine the largest set of complex marine food webs to date. More than half of the analyzed marine networks exhibited a similar or lower characteristic path length than the random expectation, whereas 39% of the webs presented a significantly higher clustering than its random counterpart. Our method proved that 5 out of 28 networks fulfilled both features of the small-world topology: short path length and high clustering. This work represents the first rigorous analysis of the small-world topology and its associated features in high-quality marine networks. We conclude that such topology is a structural pattern that is not maximized in marine food webs; thus it is probably not an effective model to study robustness, stability and feasibility of marine ecosystems.

Introduction

Food webs are complex networks of feeding (trophic) interactions among diverse species in communities or ecosystems (Dunne 2009). Studies characterizing and modelling food web structure have suggested the existence of general properties (Link 2002, Williams et al. 2002, Montoya and Solé 2003, Vermaat et al. 2009), as well as simple models that predict the complex structure of these networks (Cohen et al. 1985, Williams and Martinez 2000, Allesina et al. 2008, Digel et al. 2014, Johnson et al. 2014).

Although some of the earliest food web studies were done considering marine examples (Petersen 1918, Hardy 1924), food web theory has been developed principally from freshwater and terrestrial habitats, largely omitting marine ecosystems (Link et al. 2005). Led by Link (2002) and Dunne et al. (2004), the number of marine food web studies has increased considerably in the last decade (Bodini et al. 2009, Rezende et al. 2009, Riede et al. 2010, de Santana et al. 2013, Kortsch et al. 2015, Bortanowski et al. 2016, Navia et al. 2016, Marina et al. 2018, among others). Despite the amount

31   of new marine food web data, whether food web theory needs to be modified to accommodate

32   observations from marine ecosystems, based on major differences in several topological characteristics

33   (i.e. higher link density, connectance, mean chain length and omnivory), is still on debate (Link 2002). It

34   has been suggested that more evenly and highly resolved networks are required in order to decide

35   whether current patterns are artifacts or whether they reflect more significant similarities or differences

36   between marine and non-marine food webs (Dunne et al. 2004, Vermaat et al. 2009).

37   In this regard, the presence of the small-world (SW) topology (Watts and Strogatz 1998) in

38   marine food webs is also an open question. This topology, inspired by the "six degrees of separation"

39   sociology experiment by Milgram (1967), has emerged as a suitable framework to study the global

40   structure of food webs (Amaral et al. 2000). Two network properties are typically analyzed in order to

41   gain insight into this pattern: the characteristic path length, a global property of the network that refers to

42   the average shortest distance between pairs of nodes; and the clustering coefficient, a local property of

43   the network defined by the average fraction of pairs of nodes connected to the same node that are also

44   connected to each other (Watts and Strogatz 1998). These features are usually compared to its random

45   counterpart web (equal size and link density or connectance), with the aim of investigating how much

46   does the empirical food web deviate from the random one (Watts 1999). A SW network needs to display

47   a high clustering coefficient and a short characteristic path length, compared to a random graph. The

48   latter property gives the name "small-world" to these networks, because it is possible to connect any two

49   vertices in the network through just a few links (Amaral et al. 2000).

50   Furthermore, SW networks may display three of the following scale patterns: scale-free, broad-

51   scale or single-scale (Amaral et al. 2000). The first one describes a network with very few nodes highly

52   connected and most nodes poorly connected, following a power-law degree distribution (Barabási et al.

53   2000, Montoya and Solé 2002). On the other hand, a broad-scale pattern is characterized by a degree

54   distribution that has a truncated power-law regime or a power-law regime followed by a sharp cutoff

55   (Montoya et al. 2006). Finally, single-scale networks present a degree distribution with a fast decaying

56   tail, such as exponential or Gaussian (Amaral et al. 2000). Most studies of empirical food webs show

57   that degree distributions rarely differ from any of these scale patterns (Camacho et al. 2002, Dunne et al.

58   2002a, 2002c, Montoya and Solé 2003, Stouffer et al. 2005), meaning that this structural feature (i.e.

59   degree distribution) would not be essential to determine whether food webs display a SW topology or

60   not.

Disregarding its habitat (e.g. marine, freshwater or terrestrial), several studies have considered whether empirical food webs display the SW topology similar to many other real-world networks (Camacho et al. 2002, Dunne et al. 2002c, Montoya and Solé 2002, Bornatowski et al. 2016, Navia et al. 2016). Most of these explored individual marine food webs or considered few networks belonging to this habitat; while some suggested the presence of the SW topology (Montoya and Solé 2002, Gaichas and Francis 2008, Navia et al. 2016, Bornatowski et al. 2016), others stated that food webs do not display such topology (Camacho et al. 2002, Dunne et al. 2002c).

Why is it important to explore the SW topology in marine food webs? There is no doubt that network topology can have important implications for network function (Strogatz 2001). More detailed knowledge on food web topology in marine ecosystems will help to understand the dynamics of complex systems, historically subject to intense fisheries pressure and subsequent regime shifts and collapse (Pauly et al. 1998, Jackson et al. 2001, Rocha et al. 2015, Gårdmark et al. 2015, Gilarranz et al. 2016). In general, consequences of SW topological pattern in food webs are of great importance in recognizing evolutionary paths and the vulnerability to perturbations (Montoya and Solé 2002). A short characteristic path length showed by SW food webs imply a rapid spread of an impact (e.g. invasion, population fluctuation, local extinction) throughout the network (Williams et al. 2002). However, based on its high clustering coefficient SW networks are associated with rapid responses to disturbances resulting in a high resilience (Solé and Montoya 2001, Montoya and Solé 2002). Recently, extinction simulations in three marine food webs displaying this topology presented opposite results regarding susceptibility to the loss of highly connected species (Gaichas and Francis 2008, Bornatowski et al. 2016, Navia et al. 2016). In this sense, the analysis of large mobile predators might shed light on this issue, as they are highly connected species, energy-channel couplers and ubiquitously affected by anthropogenic disturbances (Rooney et al. 2008). Therefore, it is not certainly known neither if the SW topology is a common pattern in marine food webs, nor if the most connected species in such networks (e.g. species of commercial interest, top predators) should be protected to avoid structural and functional impacts in ecosystems that cover more than 70% of the planet´s surface.

As stated above, research on marine food web properties on individual networks is abundant, yet topological studies analyzing the global structure in large sets of well-resolved marine food webs are scarce (e.g. Dunne et al. 2004, Riede et al. 2010). The SW topology, a pattern that gives a clear overview of organization and resistance in trophic networks (Bornatowski et al. 2016), has been difficult

91   to detect in empirical food webs because of incompatibility in used approaches and insufficient

92   methodological rigour (e.g. Montoya and Solé 2002, Gaichas and Francis 2008, Navia et al. 2016).

93   In this work, our aim was to analyze the SW structural pattern in empirical marine food webs.

94   For this, we gathered a broad range of high-quality marine food webs, some of which have never been

95   examined using a topological network approach. We developed and implemented a simple and rigorous

96   method to determine whether food webs presented the SW topology. This method is rigorous because it

97   considers the structural properties of interest (i.e. characteristic path length, clustering coefficient and

98   degree distribution) and statistically tests the probability of presenting such topology, taking into

99   account the position of the empirical values for the structural properties in the confidence interval (99%)

100   of the equivalent random networks. Our results were compared with that of Humphries and Gurney

101   (2008), who proposed a quantitative and continuous small-world-ness metric for complex networks.

102   Finally, we hypothesized about possible implications of the SW topology for ecosystem functioning in

103   marine habitats.

Methodology

105   We compiled and selected a large set of well-resolved marine food webs, many of which are

106   included for the first time in network topology analyses. We limited our inclusion to food webs with a

107   minimum size (= number of trophic species), following Link et al. (2005) recommendation of

108   considering only networks with 20-25 nodes at least. The studied food webs represent a wide range of

109   number of trophic species (27 – 513) and connectance (0.01 – 0.27). The assembled marine food webs

110   cover from pelagic to coastal habitats, and tropical to polar regions (Table 1). The list is by no means

111   exhaustive, but the high taxonomic resolution of the webs and the variety of regions that comprises

112   likely make this list the most representative and comprehensive picture of the topology in real-world

113   marine food webs.

114   We studied the cumulative degree distribution, or the fraction of trophic species $P(k)$ that have k

115   or more trophic links, for each network (Albert and Barabási 2002). The use of cumulative distributions

116   gives a more accurate picture of the shape of the distribution in small, noisy data sets (Dunne et al.

117   2002c). Model fit was done using maximum likelihood (McCallum 2008), and model selection was

118   performed by computing the Akaike Information Criterion corrected for small sample size (AICc)

119   (Burnham and Anderson 2002).

120   In order to explore the SW phenomenon among these empirical marine food webs, we analyzed

the properties of interest: characteristic path length (CPL) and clustering coefficient (CC). The CPL is defined as the average shortest path length between all pairs of nodes and represents a global property of the network (Watts and Strogatz 1998). Here, CPL was calculated as the average number of nodes in the shortest path $CPL_{Min}(i,j)$ between all pairs of nodes $V(i,j)$ in a network averaged over $n(n-1)/2$ nodes (Montoya and Solé 2002):

$$CPL = \frac{2}{n(n-1)} \sum_{i=1}^{n} \sum_{i=1}^{n} CPL_{Min}(i,j)$$

On the other hand, CC quantifies the local interconnectedness of the network and it is defined as the fraction of the number of existing links between neighbours of node i among all possible links between these neighbours. In this study, the CC of each food web was determined as the average of the individual clustering coefficients CCi of all the nodes in the network. Individual CCi were determined as follows:

$$CCi = \frac{2\,Ei}{Ki(Ki-1)}$$

where Ei is the effective number of interactions between ki nearest-neighbor nodes of node i and the maximal possible number of such interactions (Albert and Barabási 2002, Newman 2003).

With the aim of testing whether marine food webs presented the SW topology, we compared the empirical values of CPL and CC with those resulted from 1000 randomly generated networks with the same size (S) and number of links (L). Random webs were created using the Erdös-Rényi model, where links are added to the complete set of nodes (S) and chosen uniformly randomly from the set of all possible links (Erdös and Rényi 1959). Small-world networks are considered to present similar or lower CPL values between empirical and random webs (CPL empirical $\leq$ CPL random), and a much higher CC in empirical than in random webs (CC empirical $\gg$ CC random) (Watts and Strogatz 1998, Bollobás 2001).

The rigurosity of our method lies in the use of confidence intervals (CI 99%) for the empirical-random comparison of the CPL and CC properties. If the empirical value for a particular food web was positioned within or to the left (=lower than) the CI 99% of the random CPL, and to the right (=higher

150 than) the CI 99% of the CC, then the food web was considered to present the SW topology. We also

151 calculated the ´small-world-ness´ S^{ws} metric proposed by Humphries and Gurney (2008) for each studied

152 food web, and compared these results with our method. If $S^{ws} > 1$ and $S^{ws} > S^{ws}$ CI 99% (confidence

153 interval), then the food web was said to be a SW network.

154 The complete source code for generating the random networks and statistical analyses was done in R (R

155 Core Team 2017), and is available at GitHub

156 (https://github.com/lsaravia/MarineFoodWebsSmallWorld).

Results

158 The analysis of the topological properties associated with the SW pattern showed that the

159 characteristic path length (CPL) and the clustering coefficient (CC) among the studied marine food webs

160 varied from 1.20 to 3.41 and from 0.0026 to 0.66, respectively. Connectance range for these food webs

161 was 0.01 – 0.27, considering networks comprising from 27 to 513 trophic species (Table 1).

162 The cumulative degree distributions of the marine food webs fitted to a broad variety of models:

163 exponential, power-law, truncated power-law (power-law regime with a sharp cutoff), lognormal,

164 uniform. To our surprise some networks displayed a poisson distribution. The majority of the networks

165 exhibited 'power-law-like' (i.e. power-law and truncated power-law = 40%) or uniform (25%)

166 cumulative degree distributions (Table 1).

167 More than half of the analyzed food webs (19/28) exhibited similar or lower CPL than expected

168 for random networks. Following the CPL empiric results, minimum and maximum

169 $CPL_{Empirical}/CPL_{Random}$ ratios were exhibited by those food webs with the lowest and highest empiric

170 values (i.e. SW Pacific Ocean and Sanak nearshore, respectively). Only 39% of the webs presented

171 higher CC than its random counterpart. A small number of food webs showed both features: low CPL

172 and high CC, compared to random networks (Figure 1).

173 The comparison between the small-world-ness metric (S^{ws}) defined by Humphries and Gurney

174 (2008), and our method to determine SW topology in complex networks reflected differences. While the

175 first one registered that 11 out of 28 webs presented the SW topology, our method proved that only five

176 food webs exhibited such pattern. These five empiric networks displayed a similar or lower CPL and a

177 higher CC, compared to the confidence interval 99% of the random networks for each of the topological

178 properties (Figure 1). Supplementary information S1 presents detailed results on the comparison

179 between these methods.

180   Following Watts (1999), we positioned each food web in the coordinate system x = CPL

181   empirical/random ratio, and y = CC empirical/random ratio (Figure 2). Our method demonstrated that

182   the only well-resolved marine food webs that clearly present the SW topology are: Gulf of Lions,

183   Florida, Caribbean reef (l), Barents Sea Arctic and Weddell Sea (Figure 2b). Values of CPL and CC

184   ratios for the SW marine food webs are: 0.98 and 1.35 (Gulf of Lions), 0.91 and 1.60 (Florida), 0.98 and

185   1.49 (Caribbean reef (l)), 0.86 and 2.37 (Barents Sea Arctic), 0.67 and 2.04 (Weddell Sea). It is worth

186   noting that network size in these food webs varies from 39 to 442 trophic species; connectance ranges

187   from 0.01 to 0.12 (an order of magnitude of difference); and that the degree distribution was: truncated

188   power-law, uniform, uniform, exponential and lognormal, respectively (Table 1).

189

190   Table 1. Network properties of high quality marine food webs, ordered by decreasing connectance. S = Size, L = Links, C =

191   Connectance (L/S^2), CPL = Characteristic Path Length, CC = Clustering Coefficient. DD = fit for cumulative degree

192   distribution. * model fit using maximum likelihood and AICc. References are given for the source of the original network

193   data.

Network	Region	Size	Links	C	CPL	CC	DD	Reference
La Guajira	Tropical	27	198	0.27	1.53	0.66	Uniform*	Criales-Hernández et al. (2006)
Benguela	Temperate	29	203	0.24	1.6	0.3	Uniform	Yodzis (1998)
NE US Shelf	Temperate	81	1482	0.23	1.6	0.31	Uniform	Link (2002)
Gulf of Cadiz	Temperate	42	410	0.23	1.99	0.56	LogNormal*	Torres et al. (2013)
Baltic Sea	Temperate	33	191	0.18	1.41	0.31	Poisson*	Yletyinen et al. (2016)
Beagle Channel	Temperate	33	183	0.17	1.46	0.32	Uniform*	Riccialdelli et al. (2017)
Angola	Subtropical	28	127	0.16	1.61	0.36	Uniform*	Angelini & Vaz-Velho (2011)
Chilean rocky	Temperate	106	1362	0.12	1.34	0.11	Truncated power-law*	Kéfi et al. (2015)
Gulf of Lions	Temperate	39	189	0.12	1.77	0.34	Truncated power-law*	Banaru et al. (2013)
Florida	Tropical	48	221	0.1	1.76	0.31	Uniform*	Christian & Luczcovich (1999)
Simon Bay	Temperate	30	70	0.08	1.7	0.12	Poisson*	Filgueira & Castro (2011)
Celtic Sea	Temperate	48	169	0.07	2.3	0.3	Exponential*	Woodward et al. (2010)
Cuba	Tropical	240	3874	0.07	1.86	0.11	Truncated power-law*	Roopnarine & Hertog (2012)
Jamaica	Tropical	249	4105	0.07	1.84	0.12	Truncated power-law*	Roopnarine & Hertog (2012)
Cayman Is.	Tropical	242	3766	0.06	1.85	0.11	Truncated power-law*	Roopnarine & Hertog (2012)
Monterey Bay	Temperate	37	79	0.06	1.4	0.09	Truncated power-law*	Glynn (1965)
Barents Sea Boreal	Tropical	180	1546	0.05	2.28	0.25	Exponential	Kortsch et al. (2015)
Caribbean reef (l)	Temperate	249	3312	0.05	1.9	0.16	Uniform	Opitz (1996)

|								
Potter Cove	Subtropical	91	307	0.04	1.82	0.09	Exponential*	Marina et al. (2018)
Southern Brazil	Polar	139	837	0.04	3.25	0.07	Truncated power-law	Bornatowski et al. (2016)
Barents Sea Arctic	Subtropical	159	848	0.03	2.06	0.16	Exponential	Kortsch et al. (2015)
Beach Peru	Polar	46	74	0.03	1.71	0.09	Exponential*	Koepcke & Koepcke (1952)
Sanak intertidal	Polar	235	1804	0.03	3.06	0.15	Truncated power-law*	Dunne et al. (2016)
Sanak nearshore	Polar	513	6774	0.03	3.41	0.18	LogNormal*	Dunne et al. (2016)
SW Pacific Ocean	Temperate	109	202	0.02	1.2	0.02	Truncated power-law*	Dambacher et al. (2010)
Gulf of Alaska	Tropical	406	1057	0.01	2.59	0.00[1]	Power-law	Gaichas & Francis (2008)
Gulf of Tortugas	Polar	256	647	0.01	1.65	0.02	LogNormal	Navia et al. (2016)
Weddell Sea	Polar	442	1915	0.01	2.05	0.04	LogNormal*	Jacob (2005)

194   Note: [1] clustering coefficient for Gulf of Alaska food web is 0.0026.

195
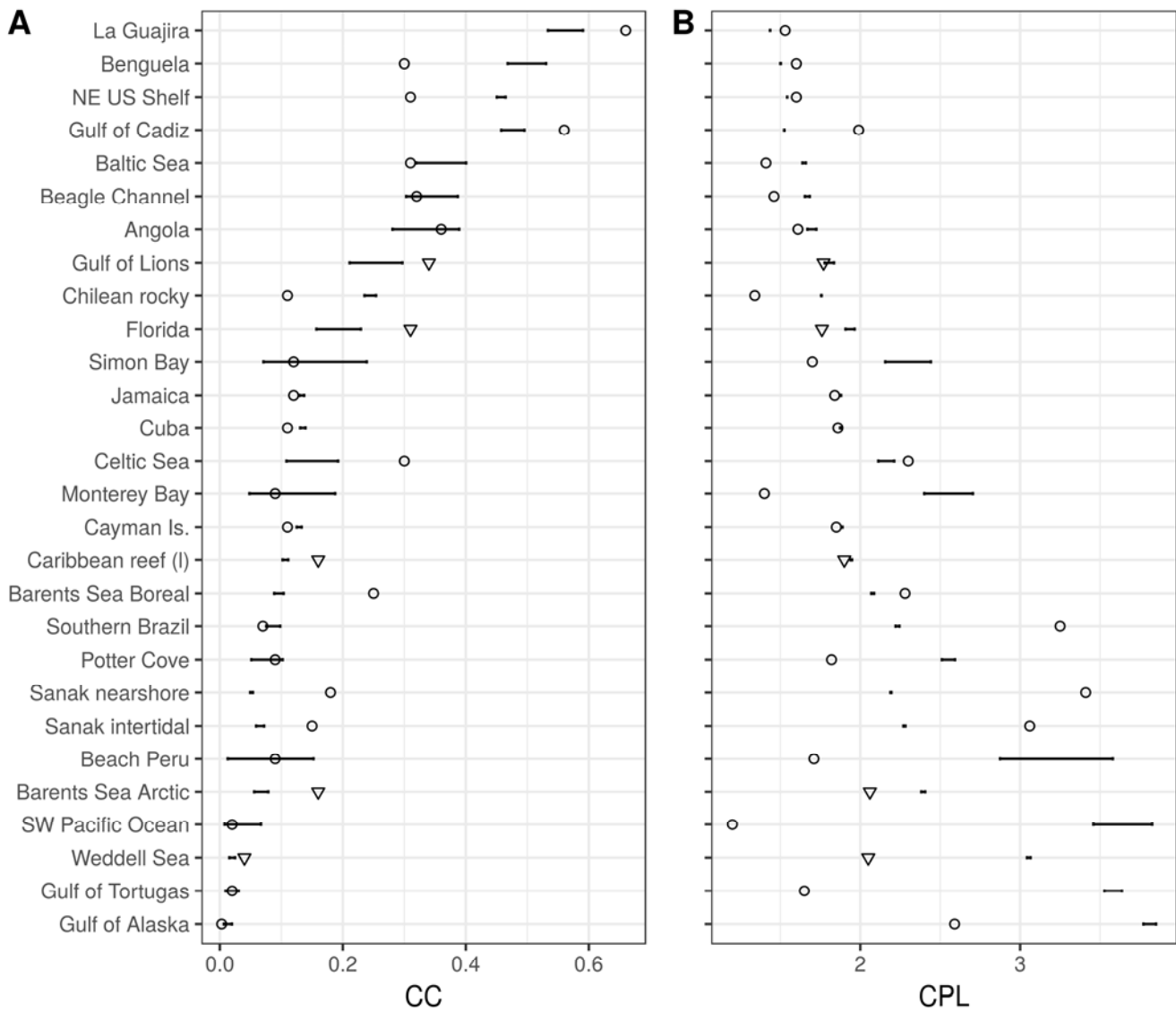
Figure 1. A) Clustering Coefficient (CC) and B) Characteristic Path Length (CPL) for empirical and random networks (ordered by decreasing connectance), generated with the same size (S) and number of links (L). Horizontal line for each food web corresponds to the confidence interval (99%) of the 1000 random networks. The inverted triangule symbol indicates food webs that follow the SW topology according to our method.
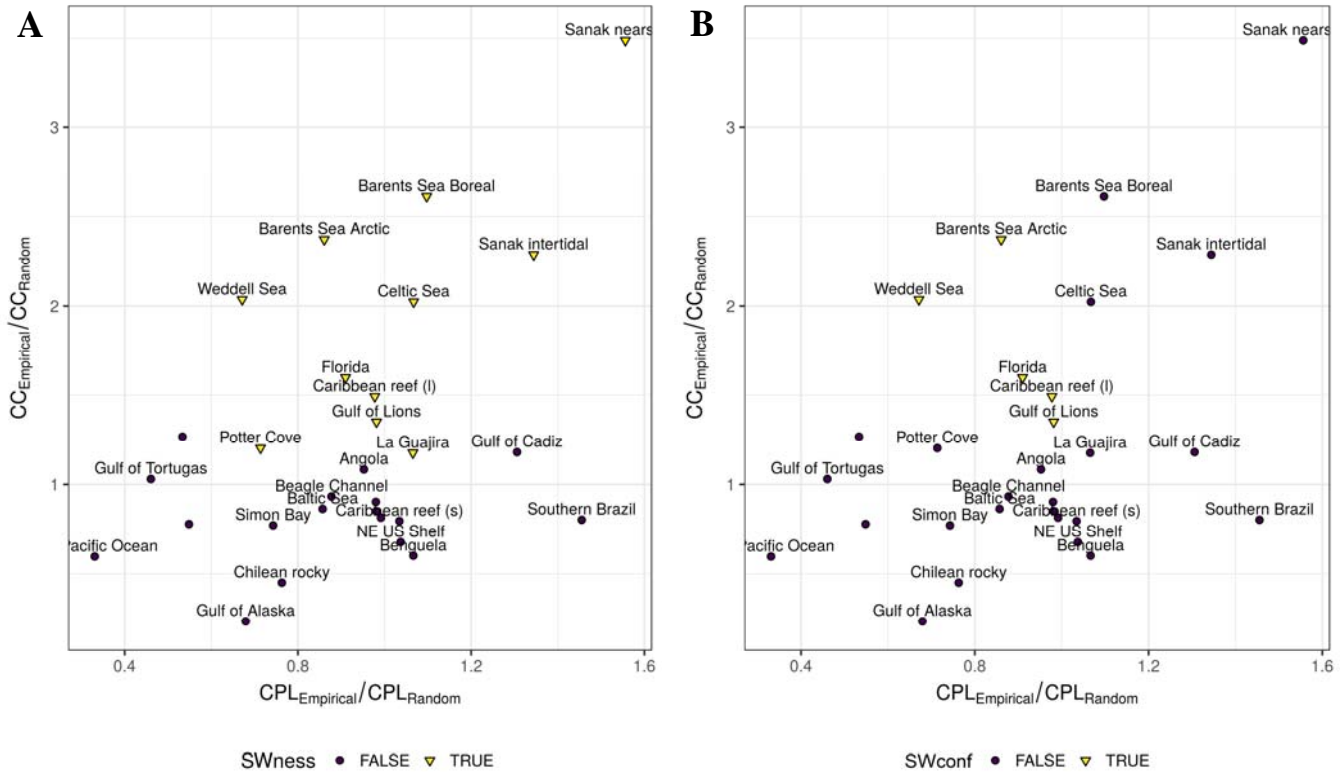
Figure 2. Characteristic Path Length (CPL) and Clustering Coefficient (CC) empirical/random ratios. Marine food webs that follow a SW topology according to A) small-world-ness metric (SWness), and B) our method (SWconf). SW networks are indicated with an inverted yellow triangle.

Discussion

The method developed and applied in this study to determine whether high quality food webs present the SW topology showed that most of the marine networks analyzed do not display such topology. Likewise, Dunne et al. (2002c) argued that food webs are not SW networks, though other studies identify several individual or small sets of food webs as having the SW topology (Solé and Montoya 2001, Camacho et al. 2002, Montoya and Solé 2002, Gaichas and Francis 2008, Navia et al. 2016, Bornatowski et al. 2016).

The first condition for a network to exhibit a SW topology is a short distance between all nodes of the web. All studies looking at this topology in food webs have reported short path lengths similar to random expectations, coincident with one aspect of such structural pattern (Dunne 2006). Consistently,

214 the majority of the CPL empiric values for the analyzed marine food webs in the present study were
215 similar or lower than the random webs.

216 Previously suggested dependence of CPL on connectance (i.e. path length decreases with increasing
217 connectance) (Williams et al. 2002, Vermaat et al. 2009, Riede et al. 2010) was not found among the
218 largest and most complex marine food webs available to date. In this regard, the lowest and highest
219 values for CPL in the analyzed networks were displayed by marine food webs with relatively very low
220 connectance (C = 0.02 and 0.03, respectively). On the other hand, CPL might be sensitive to network
221 size in marine food webs, but with an opposite scaling relationship as described by Riede et al. (2010),
222 since the shortest CPL occured in SW Pacific Ocean food web, S = 109, and the longest CPL was found
223 in Sanak nearshore web (S = 513), a food web five times larger than the first one. There is no doubt that
224 the mechanisms responsible for short path lengths and potentially scaling correlations with other
225 structural properties in marine food webs deserve further investigation.

226 In spite of short path lengths, similar to random expectations, currently available food web data
227 clearly deviate from the SW topology due to a low clustering coefficient compared to random networks
228 (Dunne et al. 2002c). Although analyses of compartmentalization in aquatic and terrestrial ecosystems
229 and food web models are profused (May 1972, Krause et al. 2003, Allesina and Pascual 2009, Stouffer
230 and Bascompte 2011), few studies have evaluated the presence of clusters (i.e. subsets of species that
231 interact more frequently among themselves than with other species in the community, compared to
232 random networks) in well-resolved marine food webs. In this sense, Pérez-Matus et al. (2017) reported 5
233 compartments for the Chilean subtidal food web (not included here due to lack of information), and
234 Rezende et al. (2009) found for the Caribbean reef food web (included here) a significant
235 compartmentalized structure, higher than that expected for its random counterpart. However, the present
236 study demonstrates that in general marine food webs tend to have low clustering coefficients (<< 1); less
237 than half of the networks (11 out of 28) showed a significantly higher empiric clustering coefficient
238 compared to the random expectation (i.e. $CC_{Empiric} > CC_{Random}$ CI 99%). As a result,
239 compartmentalization in marine ecosystems is very small, meaning that food webs are characterized by
240 trophic species highly interconnected between each other. It has been suggested that being
241 compartmentalized is advantageous to a community because compartments buffer the propagation of
242 extinctions, and that the observed architecture of empirical food webs (e.g. SW topology) increases both
243 the persistence and resilience against perturbation (Stouffer and Bascompte 2011, Gilarranz et al. 2017).
244 Therefore, the fact that the analysis of the largest set of complex marine food webs statistically showed

245   that the minority of the networks displays high clustering coefficients brings to light that: 1) current
246   marine food webs are predicted to be fragile and susceptible to structural changes with consequent
247   alterations in the functioning of the ecosystem, or 2) the influence of the clustering coefficient in the
248   stability and feasibility of large marine communities is not as significant as it is thought.

249   The drivers of a lower empiric clustering coefficient than its random counterpart in food webs are
250   suggested to be small network size (i.e. low diversity) and high connectance, features displayed in
251   ecological networks compared to other network types (e.g. neuronal, social and technological) (Dunne
252   2006). On the contrary, we have showed that large food webs (> 100 trophic species) can also present
253   notably low clustering coefficient ratios (e.g. Chilean rocky, SW Pacific Ocean, Gulf of Alaska), similar
254   to what Camacho et al. (2002) have suggested. Regarding connectance, SW marine networks exhibited
255   one order of magnitude of difference (0.12 – 0.01). Neither network size nor complexity (= connectance)
256   seem to be playing an important role in explaining the lack of compartmentalized structures in marine
257   food webs; highly interconnected nodes might be the case for these networks. These findings imply that
258   species-rich food webs (i.e. high diversity) in the marine ecosystem might not be organized by
259   combining sub-web compartments, as previously suggested for food webs in general (Riede et al. 2010).

260   Small-world networks seem to exhibit a variety of degree distributions (Amaral et al. 2000). To
261   date, it has been reported and identified in SW food webs the presence of scale-free or 'power-law like'
262   structures (Montoya and Solé 2002, Gaichas and Francis 2008, Bornatowski et al. 2016, Navia et al.
263   2016) and exponential distributions (Camacho et al. 2002). Here, the majority of the marine food webs
264   identified as having the SW structural pattern showed neither 'power-law like' nor exponential degree
265   distributions; instead they fit to uniform and lognormal models. This is the first study that, using a robust
266   statistical methodology (i.e. maximum likelihood and Akaike Criterion), presents evidence for the
267   occurrence of uniform degree distribution in SW food webs. Added to the three classes of small-world
268   networks proposed by Amaral et al. (2000), we suggest a new class: uniform-scale networks,
269   characterized by a connectivity distribution with an approximately constant node degree. It has been
270   hypothesized that the presence of uniform degree distributions in food webs may occur in relatively
271   small (= few nodes) and high-connected networks (Dunne et al. 2002b). Food webs with this type of
272   distribution are expected to be more robust against intentional removal of the most connected nodes than
273   networks with more skewed distributions (Albert et al. 2000, Estrada 2007). Nearly all of the marine
274   food webs assessed in the current study follow the pattern suggested by Dunne et al. (2002b), with the
275   exception of the Caribben reef food web that is comparatively large (S=249) and low connected

276 (C=0.05). As it seems to occur in general with food web degree distributions (Dunne et al. 2002b), SW

277 networks in the marine ecosystem may display a broad variety of distribution models which proves the

278 minor influence of such property in the structural pattern of marine food webs. Furthermore, in contrast

279 with what is expected in real-world networks (Dunne et al. 2002b, Montoya and Solé 2002, Newman

280 2003), we have demonstrated that empiric marine food webs display poisson degree distributions (e.g.

281 Baltic Sea and Simon Bay).

282   It has been suggested that network size, connectance and the degree distribution pattern are

283 drivers of the SW topology in complex networks in general (Humphries and Gurney 2008) and in food

284 webs in particular (Thompson and Towsend 2000, Dunne et al. 2002c). After applying a novel small-

285 world-ness metric to examine several classes of real-world networks (e.g. social, information,

286 technological and biological), Humphries and Gurney (2008) concluded that high connectance results in

287 low SW-ness, confirming what was stated for food webs (Dunne 2006). Although we have not

288 performed correlation analyses, neither of the suggested drivers seems to be playing an important role in

289 the presence of the SW structural pattern in marine food webs: SW food web network size and

290 connectance ranged from 39 to 442 and from 0.12 to 0.01 (one order of magnitude of difference),

291 respectively. In addition, three different models fit their degree distributions: 'power-law like' (power-

292 law and truncated power-law), lognormal and uniform.

293   After examining the features of the SW topology (i.e. path length, clustering coefficient and

294 degree distribution) and exposing the discrepancies among studies, it seems more than appropriate the

295 application of a rigorous method like the one proposed here if the aim is to search for a universal,

296 generalized model explaining the structural pattern in food webs. Early suggested correlations between

297 path length, clustering coefficient and degree distribution with network size and connectance in food

298 webs (e.g. Dunne et al. 2002b, Williams et al. 2002, Vermaat et al. 2009, Riede et al. 2010) might not be

299 followed in the structure of marine networks. It is crucial to better understand the topology and possible

300 scaling relationships among food web properties in marine ecosystems, since network structure has deep

301 consequences in the functioning of exploited systems (Gaichas and Francis 2008, Bornatowski et al.

302 2014, Navia et al. 2016, Pérez-Matus et al. 2017).

303   In conclusion, this study represents the first rigorous analysis of the SW topology and its

304 associated features in the largest set of complex marine food webs examined to date. It attempts to

305 resolve the 'small-world controversy' in food webs. The SW topology is a structural pattern that is not

13

maximized in marine food webs; thus it is probably not an effective model to study the robustness, stability and feasibility of marine ecosystems.

Acknowledgments

References

1. Amaral LA, Scala A, Barthelemy M, Stanley HE. Classes of small-world networks. Proceedings of the national academy of sciences. 2000;97: 11149-52.

2. Angelini R, Vaz-Velho F. Ecosystem structure and trophic analysis of Angolan fishery landings. Scientia Marina. 2011;75: 309-19.

3. Albert R, Barabási AL. Statistical mechanics of complex networks. Reviews of modern physics. 2002; 74:47.

4. Albert R, Jeong H, Barabási AL. Error and attack tolerance of complex networks. Nature. 2000;406: 378.

5. Allesina S, Pascual M. Food web models: a plea for groups. Ecology letters. 2009;12: 652-62.

6. Allesina S, Alonso D, Pascual M. A general model for food web structure. science. 2008;320: 658-61.

7. Bănaru D, Mellon-Duval C, Roos D, Bigot JL, Souplet A, Jadaud A, Beaubrun P, Fromentin JM. Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. Journal of Marine Systems. 2013;111: 45-68.

8. Barabási AL. Linked: The new science of networks. Vol 1. Cambridge: Perseus; 2002.

9. Barabási AL, Albert R, Jeong H. Scale-free characteristics of random networks: the topology of the world-wide web. Physica A: statistical mechanics and its applications. 2000;281: 69-77.

10. Bodini A, Bellingeri M, Allesina S, Bondavalli C. Using food web dominator trees to catch secondary extinctions in action. Philosophical Transactions of the Royal Society B: Biological Sciences. 2009;364: 1725-31.

11. Bollobás B. Random Graphs. Cambridge: Cambridge University Press; 2001.

12. Bornatowski H, Barreto R, Navia AF, Amorim AF. Topological redundancy and 'small□world'patterns in a food web in a subtropical ecosystem of Brazil. Marine Ecology. 2016;38.

13. Burnham KP, Anderson DR. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media; 2002.

14. Camacho J, Guimerà R, Amaral LA. Robust patterns in food web structure. Physical Review Letters. 2002;88: 228102.

15. Cohen JE, Newman CM, Briand F. A stochastic theory of community food webs II. Individual webs. Proc. R. Soc. Lond. B. 1985;224: 449-461.

16. Criales-Hernández MI, B García C, Wolff M. Flujos de biomasa y estructura de un ecosistema de surgencia tropical en La Guajira, Caribe colombiano. Revista de biología tropical. 2006;54: 1257-82.

17. Christian RR, Luczkovich JJ. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. Ecological modelling. 1999;117: 99-124.

18. Dambacher JM, Young JW, Olson RJ, Allain V, Galván-Magaña F, Lansdell MJ, Bocanegra-Castillo N, Alatorre-Ramírez V, Cooper SP, Duffy LM. Analyzing pelagic food webs leading to top predators in the Pacific Ocean: a graph-theoretic approach. Progress in Oceanography. 2010;86: 152-65.

19. de Santana CN, Rozenfeld AF, Marquet PA, Duarte CM. Topological properties of polar food webs. Marine ecology progress series. 2013;474: 15-26.

20. Digel C, Curtsdotter A, Riede J, Klarner B, Brose U. Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. Oikos. 2014;123: 1157-72.

21. Dunne JA. The network structure of food webs. In: Pascual M, Dunne JA, editors. Ecological networks: linking structure to dynamics in food webs. Oxford University Press; 2006. pp. 27-86.

22. Dunne JA. Food webs. In: Meyers RA, editor. Encyclopedia of complexity and systems science; 2009. pp. 3661-3682.

23. Dunne JA, Williams RJ, Martinez ND. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology letters. 2002a;5: 558-67.

24. Dunne JA, Williams RJ, Martinez ND. Food-web structure and network theory: the role of connectance and size. Proceedings of the National Academy of Sciences. 2002b;99: 12917-22.

25. Dunne JA, Williams RJ, Martinez ND. Small networks but not small worlds: unique aspects of food web structure. SFI Working Paper; 2002c.

26. Dunne JA, Williams RJ, Martinez ND. Network structure and robustness of marine food webs. Marine Ecology Progress Series. 2004;273: 291-302.

27. Dunne JA, Maschner H, Betts MW, Huntly N, Russell R, Williams RJ, Wood SA. The roles and impacts of human hunter-gatherers in North Pacific marine food webs. Scientific reports. 2016;6: 21179.

28. Erdös P, Rényi A. On random graphs, I. Publicationes Mathematicae (Debrecen). 1959;6: 290-7.

29. Estrada E. Food webs robustness to biodiversity loss: the roles of connectance, expansibility and degree distribution. Journal of theoretical biology. 2007;244: 296-307.

30. Filgueira R, Castro BG. Study of the trophic web of San Simón Bay (Ría de Vigo) by using stable isotopes. Continental Shelf Research. 2011;3: 476-87.

31. Gaichas SK, Francis RC. Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web. Canadian Journal of Fisheries and Aquatic Sciences. 2008;65: 1965-82.

32. Gårdmark A, Casini M, Huss M, van Leeuwen A, Hjelm J, Persson L, de Roos AM. Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory. Phil. Trans. R. Soc. B. 2015;370: 20130262.

33. Gilarranz LJ, Mora C, Bascompte J. Anthropogenic effects are associated with a lower persistence of marine food webs. Nature communications. 2016;7: 10737.

34. Gilarranz LJ, Rayfield B, Liñán-Cembrano G, Bascompte J, Gonzalez A. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. Science. 2017;357: 199-201.

35. Glynn PW. Community composition, structure, and interrelationships in the marine intertidal Endocladia muricata–Balanus glandula association in Monterey Bay, California. Beaufortia. 1965;12: 1-98.

36. Hardy AC. The herring in relation to its animate environment I. The food and feeding habits of the herring with special reference to the east coast of England. Fish. Invest., Lond.. 1924;2: 53.

37. Humphries MD, Gurney K. Network 'small-world-ness': a quantitative method for determining canonical network equivalence. PloS one. 2008;3: e0002051.

38. Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP. Historical overfishing and the recent collapse of coastal ecosystems. Science. 2001;293: 629-37.

39. Jacob U. Trophic Dynamics of Antarctic Shelf Ecosystems, Food Webs and Energy Flow Budgets. Ph.D. Thesis, University of Bremen. 2005.

40. Johnson S, Domínguez-García V, Donetti L, Muñoz MA. Trophic coherence determines food-web stability. Proceedings of the National Academy of Sciences. 2014;111: 17923-8.

41. Kéfi S, Berlow EL, Wieters EA, Joppa LN, Wood SA, Brose U, Navarrete SA. Network structure beyond food webs: mapping non□trophic and trophic interactions on Chilean rocky shores. Ecology. 2015;96: 291-303.

42. Koepcke HW, Koepcke M. Sobre el proceso de transformación de la materia orgánica en las playas arenosas marinas del Perú. Mus Hist Nat Javier Prado. 1952;8: 1-25.

43. Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc. R. Soc. B. 2015;282: 20151546.

44. Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW. Compartments revealed in food-web structure. Nature. 2003;426: 282.

45. Link J. Does food web theory work for marine ecosystems?. Marine ecology progress series. 2002;230: 1-9.

46. Link JS, Stockhausen WT, Methratta ET. Food-web theory in marine ecosystems. In: Belgrano A et al, editors. Aquatic food webs: an ecosystem approach. Oxford University Press; 2005. pp. 98-114.

47. Marina TI, Salinas V, Cordone G, Campana G, Moreira E, Deregibus D, et al. The food web of Potter Cove (Antarctica): complexity, structure and function. Estuarine, Coastal and Shelf Science. 2018;200: 141-51.

48. May RM. Will a large complex system be stable? Nature. 1972;238: 413.

49. McCallum H. Population parameters: estimation for ecological models. John Wiley & Sons; 2008.

50. Milgram S. The small world problem. Phsychology Today. 1967;1: 61-7.

51. Montoya JM, Solé RV. Small world patterns in food webs. Journal of theoretical biology. 2002;214: 405-12.

52. Montoya JM, Solé RV. Topological properties of food webs: from real data to community assembly models. Oikos. 2003;102: 614-22.

53. Montoya JM, Pimm SL, Solé RV. Ecological networks and their fragility. Nature. 2006;442: 259.

54. Navia AF, Cruz-Escalona VH, Giraldo A, Barausse A. The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management. Ecological modelling. 2016;328: 23-33.

55. Newman ME. The structure and function of complex networks. SIAM review. 2003;45: 167-256.

56. Opitz S. Trophic interactions in Caribbean coral reefs. International Center for Aquatic Resources; 1996.

57. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. Fishing down marine food webs. Science. 1998;279: 860-3.

58. Perez-Matus A, Ospina-Alvarez A, Camus PA, Carrasco SA, Fernandez M, Gelcich S, Godoy N, Ojeda FP, Pardo LM, Rozbaczylo N, Subida MD. Temperate rocky subtidal reef community reveals human impacts across the entire food web. Marine Ecology Progress Series. 2017;567: 1-6.

59. Petersen CGJ. The Sea Bottom and Its Production of Fish-food. Report of the Danish Biological Station. 1918;21: 1-44.

60. Rezende EL, Albert EM, Fortuna MA, Bascompte J. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecology Letters. 2009;12: 779-88.

61. Riccialdelli L, Newsome SD, Fogel ML, Fernández DA. Trophic interactions and food web structure of a subantarctic marine food web in the Beagle Channel: Bahía Lapataia, Argentina. Polar Biology. 2017;40: 807-21.

62. Riede JO, Rall BC, Banasek-Richter C, Navarrete SA, Wieters EA, Emmerson MC, Jacob U, Brose U. Scaling of food-web properties with diversity and complexity across ecosystems. Advances in Ecological Research. 2010;42: 139-170.

63. Rocha J, Yletyinen J, Biggs R, Blenckner T, Peterson G. Marine regime shifts: drivers and impacts on ecosystems services. Phil. Trans. R. Soc. B. 2015;370: 20130273.

64. Rooney N, McCann KS, Moore JC. A landscape theory for food web architecture. Ecology Letters. 2008;11: 867-81.

65. Roopnarine PD, Hertog R. Detailed food web networks of three Greater Antillean coral reef systems: the Cayman Islands, Cuba, and Jamaica. Dataset Papers in Science. 2013.

66. Solé RV, Montoya M. Complexity and fragility in ecological networks. Proceedings of the Royal Society of London B: Biological Sciences. 2001;268: 2039-45.

67. Stouffer DB, Bascompte J. Compartmentalization increases food-web persistence. Proceedings of the National Academy of Sciences. 2011;108: 3648-52.

68. Stouffer DB, Camacho J, Guimera R, Ng CA, Nunes Amaral LA. Quantitative patterns in the structure of model and empirical food webs. Ecology. 2005;86: 1301-11.

69. Strogatz SH. Exploring complex networks. nature. 2001;410: 268.

70. Team RC. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; 2016.

71. Thompson RM, Townsend CR. Is resolution the solution?: the effect of taxonomic resolution on the calculated properties of three stream food webs. Freshwater Biology. 2000;44: 413-22.

72. Torres MÁ, Coll M, Heymans JJ, Christensen V, Sobrino I. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). Ecological modelling. 2013;265: 26-44.

73. Vermaat JE, Dunne JA, Gilbert AJ. Major dimensions in food⎕web structure properties. Ecology. 2009;90: 278-82.

74. Watts DJ. Networks, dynamics, and the small-world phenomenon. American Journal of Sociology. 1999;105: 493-527.

75. Watts DJ, Strogatz SH. Collective dynamics of 'small-world' networks. nature. 1998;393: 440.

76. Williams RJ, Martinez ND. Simple rules yield complex food webs. Nature. 2000;404: 180.

77. Williams RJ, Berlow EL, Dunne JA, Barabási AL, Martinez ND. Two degrees of separation in complex food webs. Proceedings of the National Academy of Sciences. 2002;99: 12913-6.

78. Woodward G, Blanchard J, Lauridsen RB, Edwards FK, Jones JI, Figueroa D, Warren PH, Petchey OL. Individual-based food webs: species identity, body size and sampling effects. Advances in ecological research. 2010;43: 211-266.

79. Yletyinen J, Bodin Ö, Weigel B, Nordström MC, Bonsdorff E, Blenckner T. Regime shifts in marine communities: a complex systems perspective on food web dynamics. InProc. R. Soc. B. 2016;283: 20152569.

80. Yodzis P. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology. 1998;67: 635-58.