



Dynamical effects of weak trophic interactions in a stochastic food web simulation

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Abstract: Network models are traditional in community ecology. For example, they provide a rich analytical toolkit to put higher predators into a multispecies context. Better understanding their top-down effects and the potential bottom-up control on them would be of key importance for predictive ecosystem management. Food web architecture may be used to predict community dynamics, but it is an old question how reliable are the studies considering only static information. A general and intuitive assumption is that stronger links (with larger weights) mediate stronger effects. We study this statement and use an illustrative case study. We investigate the trophic structure of the Prince William Sound food web in terms of biomass flows, and study its simulated dynamics in a stochastic modelling framework. We aim to understand bottom-up effects of preys on consumers: we focus on the fluctuations of top predator populations, following disturbance on their prey. Several disturbance regimes are studied and compared. Food web structure and link weight generally predict well the average impacts of preys on top-predators, with larger flows mediating stronger effects. Most exceptions appear for weak links: these are less predictable, some of them can be surprisingly important.

1. Introduction

There is increasing interest in better understanding the role and dynamics of higher predators. Some of them are close to extinction, others are seriously over-exploited. Although a lot of research had already been made on their pairwise predator-prey interactions, it has been suggested that only multispecies models can really help understanding their role in the community (May et al. 1979). One of the key questions here is the dominant mechanism of community control: whether top-predators primarily exert top-down control (Stevens et al. 2000), they are mostly driven by bottom-up forces (Perry et al. 2010) or play their role under a wasp-waist control regime (Cury et al. 2000). Understanding these mechanisms can be easier in a spatial context (Yen et al. 2004) but most models are non-spatial, focusing on trophic structure and dynamics.

It is a classical assumption in food web ecology that larger biomass flows imply stronger trophic effects (e.g., Patten 1959, Hannon 1973). This assumption is the basis for several static studies on trophic networks, including mixed trophic impact analysis (Ulanowicz and Puccia 1990). Understanding the validity of this intuition is especially important, since several studies on strong and weak links have been published in community ecology (e.g., Paine 1980, 1992, McCann et al. 1998, Berlow 1999, Scotti et al. 2009) but the

role of weak links is still unclear (de Ruiter et al. 1995). Synthesis concerning the effects of interaction strength on dynamics is still poor (Berlow et al. 2004). Difficulties arise from the lack of a coherent definition of “interaction strength”: link weight may refer to energy transfer, biomass flux, elements of the interaction matrix, relative prey preference and consumption frequency, being the probably most typical cases (Berlow et al. 2004). Thus, key concepts of community ecology and systems ecology do overlap here without having been well integrated. Other reasons for our limited understanding here is the lack of comparable, high quality food web simulation results (preferably parameterized by real data) and the poor availability of good quantitative data. From a theoretical point of view, it is not easy to find general results for non-linear, richly parameterized dynamical systems. So, the best thing to do can be providing particular findings about individual case studies.

Our objective is to understand the relationship between biomass flows and simulated dynamical effects from a bottom-up perspective (donor-controlled). This might be an increasingly important issue in marine ecology and fisheries (Hollowed et al. 2000). Dynamical effects are measured as changes in the mean population size and its variance for top predators, after disturbing their prey. Only top predators are considered, as they are under exclusive bottom-up control, while other consumers face mixed (also top-down) control.

In a mixed regime it would be very hard to perform our analysis. We explore the importance of weak links using a real case study, the weighted food web of Prince William Sound, Alaska (Okey and Pauly 1999), where interactions are weighted by biomass transfer per unit area and unit time. For the dynamical food web simulations, we apply a stochastic approach.

We investigate (1) whether there is a positive relationship between biomass flux and dynamical effect from particular prey species, (2) whether this relationship, if exists, differs for the mean and for the variance of population size, (3) whether the above results are sensitive to the particular disturbance regime modelled (weak or strong, positive or negative disturbance) and (4) whether top-predator feeding habits differ from those of other consumers.

2. Data

We study the Prince William Sound food web (Okey and Pauly 1999, Okey 2004, Okey and Wright 2004, Fig. 1). It is composed of 51 compartments but we only analyze the subgraph of the 48 living ones ($S = 48$), with 355 trophic interactions ($m = 355$). The reason is that flows between living groups correspond to ingestion-assimilation events (trophic flows), showing a dynamics characteristically different from that of transfers between living and non-living compartments (Whipple 1998). Thus, we exclude from our analysis egestive transfers (i.e., from living to non-living and from non-living to non-living groups). We also excluded abiotic import, as we were interested in internal community dynamics.

The list of the 48 living trophic components is given in Table 1. The network is weighted by the intensity of trophic transfer (measured in terms of biomass flows; tonnes wet weight $\text{km}^{-2} \cdot \text{year}^{-1}$). For each trophic group, the number of

individuals was approximated from the biomass data (following Livi et al. 2011). The original model is an Ecopath with Ecosim (EwE) model (Christensen and Walters 2004, Okey 2004).

3. Methods

3.1. Structure

We characterize flow structure of the trophic network by the \mathbf{G} partial feeding matrix (Ulanowicz 2004). This matrix of $g_{i,j}$ values is estimated by normalizing all the prey-predator interactions by the total intake of each predator (Appendix A). Reading down j columns, \mathbf{G} provides information on the relative percentage of food that each prey i (in the rows) contributes to the full intake by consumer j . The partial feeding matrix summarizes dietary proportions and its columns sum to 1, summarizing bottom-up trophic effects on consumers. We focus only on top-predators, since other consumers are influenced both from the bottom up and from the top down. In this food web, there are six top-predators (with the number of prey species in parenthesis): #1 ($D_1 = 7$), #2 ($D_2 = 15$), #3 ($D_3 = 7$), #4 ($D_4 = 15$), #15 ($D_{15} = 7$), #26 ($D_{26} = 4$). Altogether, there are 45 prey-predator links. The list of prey for each predator is given in Appendix A.

3.2. Dynamics

3.2.1. Simulation model. Having identified the interactions between species i and j , it is of interest how strong is their effect on each other (a_{ij} and a_{ji}). We use a stochastic simulation model written in the process algebra-based BlenX language (Dematté et al. 2007, 2008). A brief introduction to this language is given in Appendix D. This makes it possible to simulate parameter-rich models of parallel ecological processes in a truly stochastic way (Livi et al. 2011), using

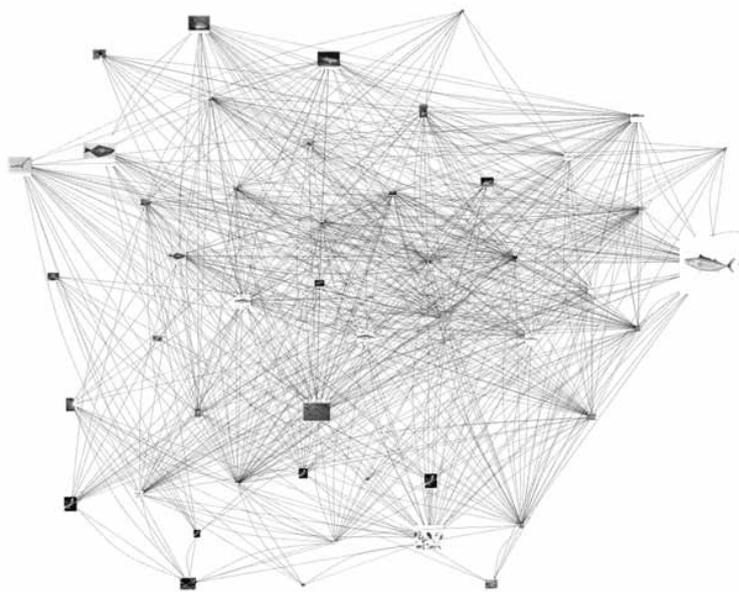


Figure 1. The food web of the Prince William Sound ecosystem (data from Okey 2004). Conventionally, producers are at the bottom and top predators are at the top. The size of the nodes is proportional to the importance of trophic groups based on stochastic dynamical simulations (measured by NRR on mean in the DIV2 disturbance regime; drawn by COSBILAB Graph, Valentini and Jordán 2010).

the Gillespie algorithm (Gillespie 1977). Stochastic, individual-based simulations in ecology (Powell and Boland 2009, Okuyama 2009) are being increasingly used to complement our knowledge based on the already available deterministic models (even if these may also contain stochastic terms: Jordán et al. 2002).

3.2.2. Sensitivity analysis. The model is run $K = 20$ times and the population size for each compartment is recorded after time t (a pilot study showed no difference for larger K). We calculate the mean and variance of population size values (in a stochastic modeling framework, the latter provides essential information, compared to deterministic models). Then, the number of individuals is changed for each compartment (disturbance), one by one, and for each case 20 simulations are run. We study four disturbance regimes: dividing (DIV) or multiplying (PER) the population size of the disturbed group by 2 or 4 (DIV2, DIV4, PER2, PER4). After a constant time t , population sizes of each species are recorded.

The dynamical effect of species i on species j is calculated for both the mean and the variation, similarly. For estimating the effect of species i on the mean population size of species j , we first define the reference value of population density for species j (A_j) in absence of any disturbance

$$A_j = \frac{\sum_{k=1}^K a_{k,*j}(t)}{K} \tag{1}$$

where K simulations are performed and, for each run k , the

population size of species j in the undisturbed system ($a_{k,*j}$) is recorded at time t . The value of population density for species j , after disturbing species i is

$$A_{ij} = \frac{\sum_{k=1}^K a_{k,ij}(t)}{K}, \tag{2}$$

and the relative response of species j to disturbing species i is

$$RR_{ij} = \frac{|A_j - A_{ij}|}{A_j}. \tag{3}$$

The relative response is normalized over all the living species ($S = 48$):

$$NRR_{ij} = \frac{RR_{ij}}{\sum_{i=1}^S RR_{ij}}, \tag{4}$$

The effects on variability are calculated similarly, but using the variance (V) instead of the mean (M) in (1) and (2). We obtain the $NRR_{ij}(M)$ and the $NRR_{ij}(V)$ measurements for each of the four disturbance regimes, accordingly. Measuring the responses of species to disturbing others is possible in several ways and our NRR is an adapted version of the Hurlbert index (Hurlbert 1997). In Figure 2, we provide an example for how to analyze biomass flows and dynamical effects of preys to their consumer, the sea otter (#26). Appendices B and C present the NRR results for each disturbance regime, for M and V , respectively.

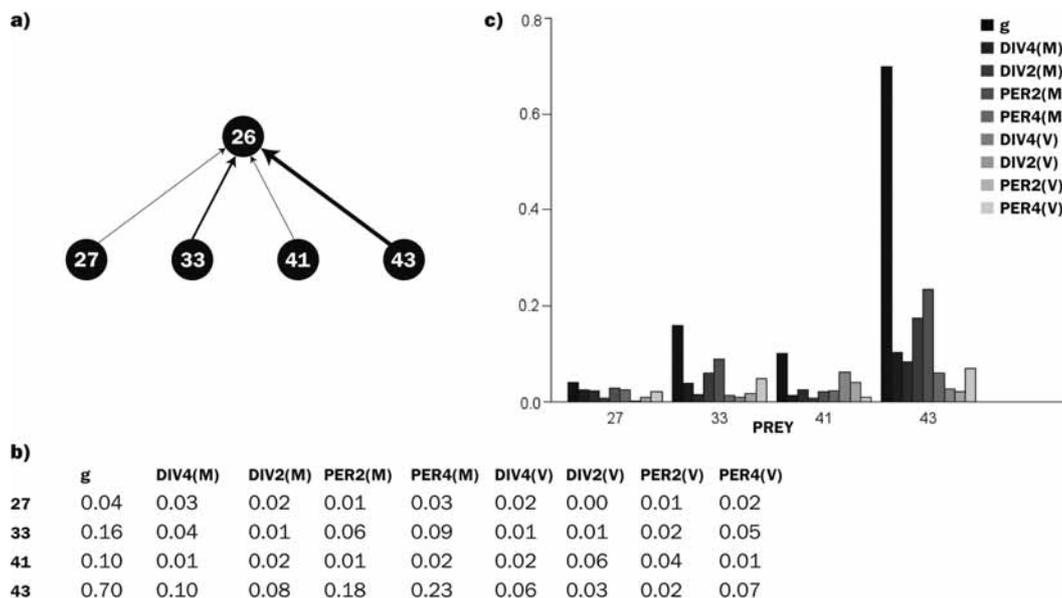


Figure 2. Trophic in-flows to Sea Otter (#26) and the dynamical effects of disturbing its prey species. In (a) we show the prey groups of Sea Otter in the Prince William Sound ecosystem. Link width shows the magnitude of trophic in-flows (b shows also the numerical values of the g partial feeding coefficients). Appendix A provides information on prey codes. Figure (b) also shows the dynamical effects of its four prey species. Histograms in (c) illustrate the same values visually (M and V stand for mean and variance, respectively). For a counter-intuitive result, see the difference between #41 and #43: the latter provides more food (larger g value) but its effect on Sea Otter variability can be smaller (e.g., in the DIV2 regime). Thus, the 41-26 link seems to be weak but can have a surprisingly large effect.

Table 1. The 48 living components of the Prince William Sound food web and their trophic positions (TP), based on Okey and Wright (2004).

ID	Compartment	TP
1	Transient Orca	5.41
2	Salmon sharks	5.10
3	Resident Orca	4.92
4	Sleeper sharks	4.88
5	Halibut	4.52
6	Pinnipeds	4.45
7	Porpoise	4.40
8	Lingcod	4.27
9	Adult Arrowtooth	4.25
10	Adult Salmon	4.18
11	Pacific Cod	4.06
12	Sablefish	4.03
13	Juvenile Arrowtooth	4.01
14	Spiny dogfish	3.96
15	Avian Predators	3.92
16	Octopods	3.80
17	Seabirds	3.80
18	Deep demersals	3.77
19	Pollock 1+	3.76
20	Rockfish	3.74
21	Baleen Whales	3.65
22	Salmon Fry 0-12	3.51
23	Nearshore Demersals	3.35
24	Squid	3.26
25	Eulachon	3.25
26	Sea otters	3.23
27	Deep Epibenthos	3.16
28	Capelin	3.11
29	Adult Herring	3.10
30	Pollock 0	3.07
31	Invertebrate-eating Birds	3.07
32	Sandlance	3.06
33	Shallow Large Epibenthos	3.06
34	Juvenile Herring	3.03
35	Jellies	2.96
36	Deep Small Infauna	2.25
37	Nearshore Omnivorous Zooplankton	2.25
38	Omnivorous Zooplankton	2.25
39	Shallow Small Infauna	2.18
40	Meiofauna	2.11
41	Deep Large Infauna	2.10
42	Shallow Small Epibenthos	2.05
43	Shallow Large Infauna	2.00
44	Nearshore Herbivorous Zooplankton	2.00
45	Herbivorous Zooplankton	2.00
46	Nearshore Phytoplankton	1.00
47	Offshore Phytoplankton	1.00
48	Macroalgae	1.00

First, we compare the relative food contribution of the dominant prey of each predator to the alternative prey groups. We perform this analysis for each predator and highlight the patterns for top-predators. The difference between the feeding patterns of top-predators and that of other consumers is measured by the Kruskal-Wallis test. Second, we are interested in the relationship between the biomass flow from i to j and the simulated effect of i on j (i.e., when species i is disturbed according to a particular regime, how does species j respond to it). Third, we use the Kruskal-Wallis test for comparing the structure to dynamics relationships for the mean and the variance of population sizes. Fourth, we inves-

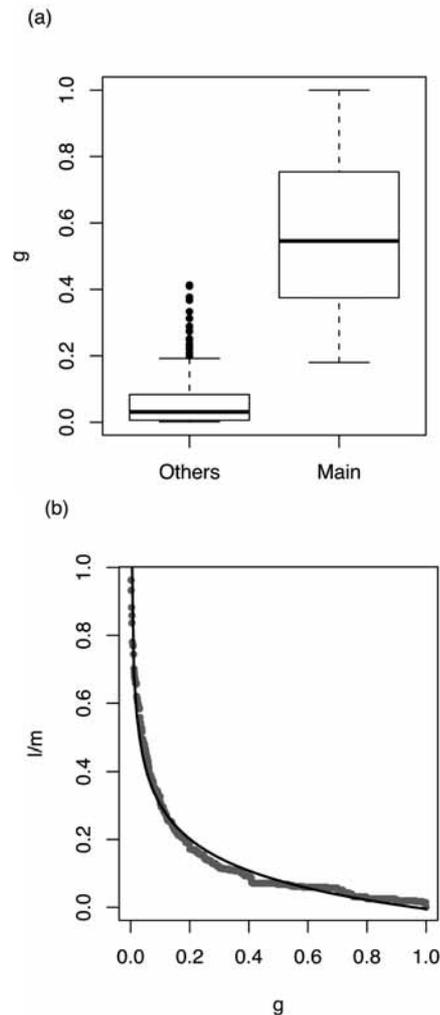


Figure 3. a: For each of the 45 predator-prey interactions where the predator is a top predator, we plot the average and variation of g partial feeding coefficients coming from their dominant prey ("Main", $mean = 0.580$, $sd = 0.270$). This significantly differs from the same done for all of the 310 other g values for inflows ("Others", $mean = 0.061$, $sd = 0.078$). Dominant food items are thus significantly different from the rest, the distribution of trophic inflows is highly skewed. **b:** In the whole weighted food web, more than 80% of the g partial feeding coefficients are less than 0.2 but some of them may have strong dynamical effects.

tigate whether the previous relationship depends on disturbance regime: we compare the effects of weak (DIV2 and PER2) and strong (DIV4 and PER4) disturbances and we compare the effects of positive (PER2 and PER4) and negative (DIV2 and DIV4) disturbances. All these issues are tested by estimating Pearson's product-moment correlations (r) and related p -values.

4. Results

First we study the 45 dominant trophic in-flows of the consumers (the 3 primary producers, nodes #46, #47 and #48, do not feed on living groups). The relative contribution of these dominant flows is different from that of average in-

teractions ($p < 0.001$, Kruskal-Wallis test; see Fig. 3a). For more than 80% of trophic links (293 out of 355), the partial feeding coefficient is less than 0.2 (Fig. 3b). For these patterns, no significant difference is detected between top-predators and other species ($p = 0.789$, Kruskal-Wallis test, for dominant flows and $p = 0.314$, Kruskal-Wallis test, for partial feeding coefficients). This means that considering top-predators only provides a representative characterization of flow distributions within the community.

The feeding patterns of top-predators are studied both structurally (partial feeding coefficients) and dynamically (sensitivity to prey disturbance). We find significant linear correlation between trophic transfer and simulation effect on the mean population size (M), for all of the four disturbance regimes (DIV2(M): $r = 0.418$, $p = 0.001$; PER2(M): $r = 0.730$, $p < 0.001$; DIV4(M): $r = 0.476$, $p < 0.001$; PER4(M): $r = 0.751$, $p < 0.001$; see Figs 4a, 4b, 4e, 4f). When preys providing larger in-flows are disturbed, predators give linearly larger responses. However, notable deviations from this general pattern are observed. In case of halving (DIV2) or dividing by four (DIV4) the population density of Adult Salmon (#10), a dominant prey ($g_{10,3} = 0.74$) of Resident Orca (#3), the $NRR_{10,3}$ values are very low: DIV2(M) = 0.008 and

DIV4(M) = 0.026 (see these outlier values on Fig 4a and 4e). A different relationship is found between Adult Arrowtooth (#9) and Salmon Sharks (#2): the prey, providing only a little food to the consumer ($g_{9,2} = 0.01$), has an unexpectedly strong effect on it (for DIV4(M), $NRR_{9,2} = 0.166$), see Figure 4e. Similar, surprisingly strong dynamical effects are found between Nearshore Demersals (#23) and their two consumers, Resident Orca (#3) and Avian Predators (#15): $g_{23,3} = 0.01$ and $g_{23,15} = 0.06$, while for DIV2(M), $NRR_{23,3} = 0.087$ and $NRR_{23,15} = 0.076$ (see two more outliers on Fig. 4a).

For the relationship between g and NRR , measured in terms of variance (V), only the strong disturbance scenarios (DIV4 and PER4) show significant linear correlation (DIV2(V): $r = 0.036$, $p = 0.797$; PER2(V): $r = -0.049$, $p = 0.722$; DIV4(V): $r = 0.378$, $p = 0.004$; PER4(V): $r = 0.460$, $p < 0.001$; see Figs 4c, 4d, 4g and 4h). The relationship for PER2(V) is not significant (Fig. 4d), and DIV2(V) is clearly nothing like linear (Fig. 4c). Except for the case of DIV2(V), we do not find extreme outliers. In this disturbance regime (DIV2), halving the population size of Nearshore Demersals (#23) results in outstanding responses in the variability of three top-predator populations, Resident Orca (#3), Sleeper Sharks (#4) and Avian Predators (#15): $g_{23,3} = 0.01$, $g_{23,4} =$

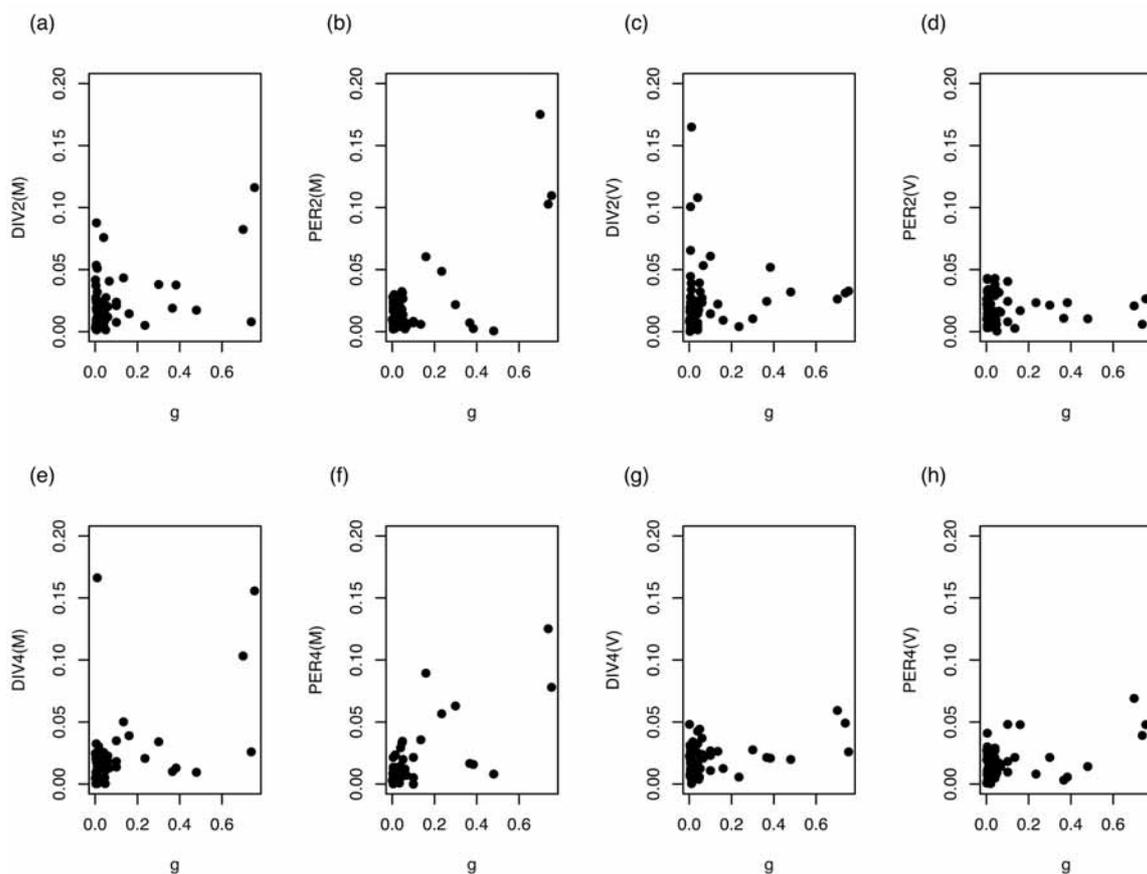


Figure 4. Correlations between structural (g on X axis) and dynamical (NRR on Y axis) effects. All of the 45 prey-predator links are presented, where the predator is a top-predator of the food web. The eight plots show the results of four prey disturbance scenarios (DIV2 in **a** and **c**, DIV4 in **e** and **g**, PER2 in **b** and **d**, and PER4 in **f** and **h**), measuring the effect on both the mean (M in **a**, **b**, **e** and **f**) and the variance (V in **c**, **d**, **g** and **h**) of the top-predator population. Particular prey disturbance regimes differ a lot in how predator is affected even in the same interaction.

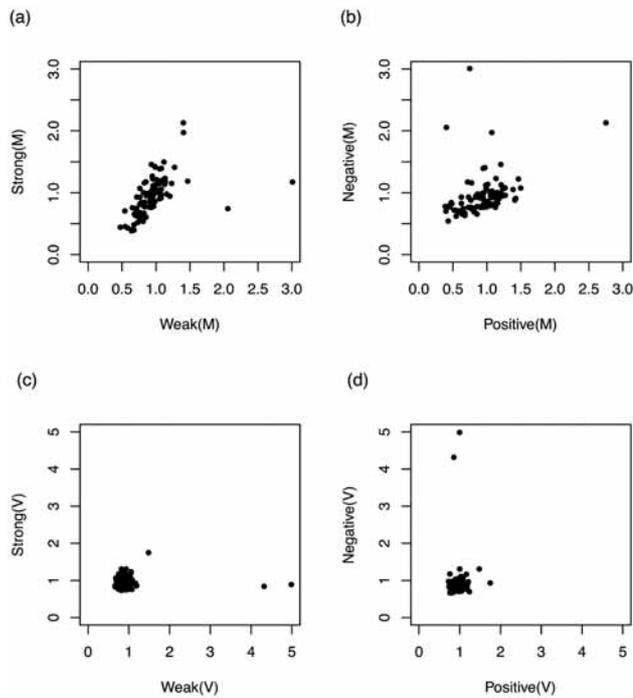


Figure 5. We compared the effects of different kinds of disturbances on top-predators. (a) shows the relationship between strong (PER4 and DIV 4 pooled) and weak (PER2 and DIV2 pooled) disturbances. (b) shows the same between positive (PER4 and PER2 pooled) and negative (DIV4 and DIV2 pooled) disturbances. Both in (a) and (b) effects are measured in terms of mean behavior (M), while (c) and (d) report the changes in variance (V).

0.01 and $g_{23,15} = 0.06$, while $NRR_{23,3} = 0.101$, $NRR_{23,4} = 0.165$ and $NRR_{23,15} = 0.108$ (see Fig. 4c).

Five of the six top-predators (but Sea Otter, #26) are influenced by at least one prey in a surprisingly strong or weak way. Five of the 27 prey species (Pinnipeds #6, Porpoise #7, Adult Arrowtooth #9, Adult Salmon #10 and Nearshore Demersals #23) do not follow the patterns described by linear correlations (provide surprising outlier values).

We observe that the structure to dynamics (g to NRR) relationship does not depend on either strong (DIV4 and PER4) versus weak (DIV2 and PER2) or positive (PER2 and PER4) versus negative (DIV2 and DIV4) disturbance regimes in terms of mean population sizes (strong vs. weak: $r = 0.656$, $p < 0.001$; positive vs. negative: $r = 0.360$, $p < 0.001$), see Figures 5a and 5b. Although, notably, the clear positive correlations vanish when outcomes are measured in terms of variance (strong vs. weak: $r = -0.017$, $p = 0.870$; positive vs. negative: $r = 0.033$, $p = 0.750$), see Figures 5c and 5d.

Based on Figure 5, we have statistically defined the outlier nodes and determined the set of preys whose dynamical effect is sensitive to the disturbance regime. We used Pearson's product-moment correlation (with 95% confidence interval), as we aimed to test linearity (even if some of these relationships clearly appear to be non-linear). In each of the four cases, whether it is mean or variance, and whether it is strong/weak or positive/negative, three species provide 15 of the 16 outlying values: Adult Arrowtooth (#9), Nearshore Demersals (#23) and Herbivorous Zooplankton (#45). Also, for Juvenile Herring (#34) it matters whether positive or negative disturbance is applied, in terms of its effect on mean top-predator population size (this is the sixteenth outlier). These three (or four) species are of significantly higher trophic positions (TP) than the average ($p = 0.010$, Kruskal-

Wallis test), see Table 1. Values of trophic position are obtained from Okey and Wright (2004).

Prey ranking changes when their dynamical effects on top-predators are quantified in terms of mean or variance ($p = 0.005$, Kruskal-Wallis test). Strong dynamical effects on the mean population density of the top-predator is often characterized by a small effect on its variance. For intermediate levels of mean effect, larger variance is observed.

5. Discussion

We compare the magnitude of biomass transfer (expressed as weights on links in a trophic flow network) to dynamical effects (expressed as response to disturbing the partner) between pairs of species i and j . Both measures can indicate important interactions (and be considered as interaction strength, in different senses). Structural information was derived from an EwE modeling framework, while the stochastic dynamical sensitivity analysis was performed in a BlenX language-based platform. We focused on top-predators in order to analyze exclusively bottom-up effects. We study the Prince William Sound ecosystem model, a well-studied and richly described community (Okey 2004).

First, we find that the in-coming flow distribution for top-predators provides a representative sample of the whole community. Second, we find a generally positive, linear correlation between the relative magnitude of biomass flow (g) and the dynamical effect from the prey to the predator (NRR). This correlation in itself is an intuitive result. What is more interesting here is to see the outliers: in these cases, a strong prey-predator flow can result in a weaker dynamical effect and vice versa. Our results support that generally only a fraction of species has a strong effect on food web stability (de Ruiter et al. 1995). The majority of outlier effects are weaker

than expected based on the **G** matrix (Fig. 4a,e). When these prey species are perturbed, the population size of the consuming top-predators remains relatively stable. The reason can be the stabilizing effect of many weak interactions that buffer variations involving strong prey-predator connections (MacArthur 1955, Emmerson and Yearsley 2004). In other cases, minor flows can have quite strong dynamical effects (c.f. Berlow 1999, McCann 2000). Here, the flow is so small that disturbing the prey can result in qualitative, structural change (disappearing link). The inconsistent behavior of outliers does not allow to conclude for a stabilizing effect of weak links. For example, Nearshore Demersals under the scenario DIV2 (M) have large effect on the population size of Resident Orca and Avian Predators, even if they provide only little food for them (see Fig. 4a).

The dynamical effects of several prey species are different on the mean and the variance of population size of their consumer top-predators. This might have interesting conservation consequences: as variability is a key to adaptability, the conservation value of some species may be related also to the variability of their populations. Variation is inherent in biological systems, and conservation biology begins to recognize that it should be understood and considered instead of neglected (Feest et al. 2010). Our stochastic simulation framework provides essential information to this, complementing deterministic dynamical models (as well as essentially deterministic models with added stochastic components). For an example, Shallow Large Infauna (#43) have a very large effect on the mean population size of Sea Otter (#26) but only a little effect on their variability (see Figures 4b and 4d), under the same disturbance regime (PER2).

Prey species may have inconsistent effects under different disturbance regimes, and there is only a restricted number of species that deviates from the positive correlation linking structure to dynamics, each being at higher positions of the food web. The consistent dynamical effects of prey providing food for Sea Otter (#26) is also associated with the lower trophic position of its prey. Our findings also demonstrate that Sea Otter differs from the patterns of all the other top-predators ($p = 0.006$, Kruskal-Wallis test). Thus, inconsistent dynamical effects (outlier points) may be the result of both the particular behavior of some populations and their trophic position in the community (Scotti and Jordán 2010). Moreover, there is evidence in the literature about the role of Sea Otter in controlling herbivorous invertebrate populations: the removal of Sea Otter by Russian fur traders prevented its top-down control and triggered the population explosion of sea urchins (Estes and Palmisano 1974). This may be in concert with our findings that highlight the predictable community effects of Sea Otter. Our results confirm that the majority of food web interactions are weak (de Ruiter et al. 1995, McCann et al. 1998). The variation in simulated dynamical effects was largest for these weak links, in concert with earlier findings on interaction strength (Berlow 1999).

Let us note here that all of our results concern a single ecological system model, the Prince William Sound case

study. Similar studies on several comparable systems are under progress, this study serves primarily as introducing the approach. A major possible future extension would be to perform the same analysis based on deterministic simulations. Beyond characterizing the binary topology (Montoya and Solé 2002, Jordán et al. 2003, Luczkovich et al. 2003, Ortiz et al. 2009, Navia et al. 2010) and the weighted structure (Scotti et al. 2009) of food webs, also binary/weighted comparisons (Scotti et al. 2007) and structure to dynamics comparisons (Jordán et al. 2008, Jordán 2009) are needed to have a more complete systems view on community organization. Since stochasticity can be of higher importance for rare species and weak interactions, our approach may be especially relevant in a conservation context (if wisely complemented by alternative modeling tools, Hollowed et al. 2011).

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Appendices

Appendix A. The g_{ij} partial feeding coefficients from prey in row i to its top-predator consumer in column j .

Appendix B. NRR -values expressing dynamical effects of prey in row i on the mean size of top-predator populations in column j , according to four disturbance regimes (DIV2, PER2, DIV4, PER4).

Appendix C. NRR -values expressing dynamical effects of prey in row i on the variation of top-predator population size in column j , according to four disturbance regimes (DIV2, PER2, DIV4, PER4).

Appendix D. A brief description of the modelling language we used for the stochastic simulation model.

The file may be downloaded from the web site of the publisher at www.akademai.com.