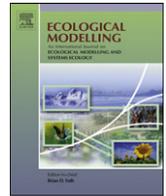




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Identifying key species in ecosystems with stochastic sensitivity analysis

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ABSTRACT

The development of approaches to estimate the vulnerability of biological communities and ecosystems to extirpations and reductions of species is a central challenge of conservation biology. One key aim of this challenge is to develop quantitative approaches to estimate and rank interaction strengths and keystone-ness of species and functional groups, i.e. to quantify the relative importance of species. Network analysis can be a powerful tool for this because certain structural aspects of ecological networks are good indicators of the mechanisms that maintain co-evolved, biotic interactions. A static view of ecological networks would lead us to focus research on highly-central species in food webs (topological key players in ecosystems). There are a variety of centrality indices, developed for several types of ecological networks (e.g. for weighted and un-weighted webs). However, truly understanding extinction and its community-wide effects requires the use of dynamic models. Deterministic dynamic models are feasible when population sizes are sufficiently large to minimize noise in the overall system. In models with small population sizes, stochasticity can be modelled explicitly. We present a stochastic simulation-based ecosystem model for identification of “dynamic key species” in situations where stochastic models are appropriate. To demonstrate this approach, we simulated ecosystem dynamics and performed sensitivity analysis using data from the Prince William Sound, Alaska ecosystem model. We then compare these results to those of purely topological analyses and deterministic dynamic (Ecosim) studies. We present the relationships between various topological and dynamic indices and discuss their biological relevance. The trophic group with the largest effect on others is nearshore demersals, the species mostly sensitive to others is halibut, and the group of both considerable effect on and sensitivity to others is juvenile herring. The most important trophic groups in our dynamical simulations appear to have intermediate trophic levels.

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1. Introduction

Food web modelling focuses either on the structural analysis of complex trophic networks (Martinez, 1991; Dunne et al., 2002; Jordán et al., 2007) or on dynamic simulations of smaller, mostly hypothetical, networks (Abrams, 1999; Jordán et al., 2002). It is only recently that dynamic simulation of large food webs has become feasible (Christensen and Walters, 2004; Okey, 2004; Okey et al., 2004), due to growth in computational capacity and available methodology (Walters et al., 1997). Dynamic simulations enable new kinds of quantitative measure of the relative importance of species, following the relatively large set of topological importance indices that mostly focus on node centrality (Harary, 1961; Jordán and Scheuring, 2004; Estrada, 2007). These measures are based on dynamic sensitivity analyses, i.e. the relative responses of the biological community to simulated perturbations on particular species (Hurlbert, 1997). Some of the species causing large com-

munity response may also be keystone species (with large effects relative to their proportional biomass; Power et al., 1996). The development of increasingly useful measures (indicators, indices) is key to improving (1) general understanding of ecosystem functioning, (2) prediction of secondary extinctions and (3) ranking of conservation priorities.

We find and argue in this paper that stochastic food web modelling can be more appropriate than deterministic modelling based on ODEs (ordinary differential equations), under certain circumstances. However, the latter aims to provide more general results (Montoya et al., 2009). We present a stochastic dynamic framework for food web analysis and use it to simulate the dynamics of the Prince William Sound ecosystem in Alaska. Furthermore, we present dynamic importance metrics adapted to this modelling framework.

2. Methods

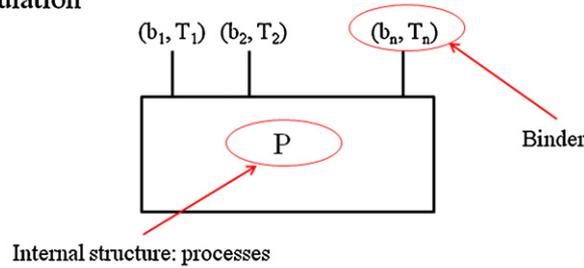
2.1. The approach

If the size of a population is relatively small, its temporal behaviour is noisy. For example, the actual number of sexually

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A. Single population



B. Population interactions

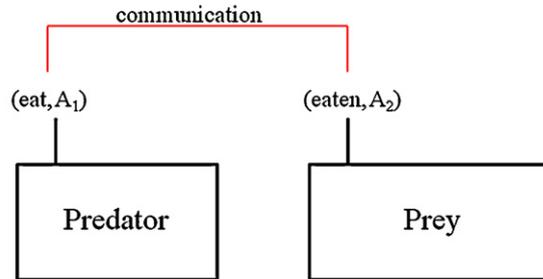


Fig. 1. A simple illustration of the BlenX-based representation of biological systems. Single populations are represented by internal dynamics and interaction capabilities (A), while interspecific interactions happen if interaction capabilities match, according to well-defined rates and actual densities of the two species (B).

mature individuals depends on time as a form of demographic noise. Birth and death also contribute to this form of stochasticity: differential equations describing the biomass of phytoplankton or herring can be quite accurate, however, the living biomass of killer whales in a small area changes in a characteristically step-wise manner (as the number of individuals is an integer). Spatial heterogeneity (e.g. lekking), individual-level differences among conspecifics (e.g. different strategies), local rules instead of global determination (Okuyama, 2009), priority effect in competition (Doak and Marvier, 2003), and the multiplicity of interactions all typically increase the stochastic component of population dynamics.

Moreover, while the average of several stochastic simulations is generally similar to the outcome of deterministic simulations, the former also describes the variability of different runs. In analysing the states of a dynamic system, the “width” of the possible trajectories can be at least as important as the shape of the average trajectory. In conservation biology, there is emerging interest in using variability as an indicator for evaluating biodiversity (Feest et al., 2010). In fact, variability can be the key to adaptability and evolvability. For example, during climate change, successful species are characterized by phenotypes that are not necessarily “good” but flexible enough.

Finally, stochastic simulation makes it possible to explicitly model extinction. In the typically used continuous, deterministic models, extinction is impossible: it can only be modelled as population size decreasing below a certain critical threshold value. In case of small populations, local extinction (and possible recolonization) is a realistic scenario.

2.2. The BlenX modelling framework

BlenX is a process algebra-based programming language (Dematté et al., 2007), supported by the Beta Workbench environment (Dematté et al., 2008). In BlenX, individuals are represented by boxes with internal dynamics (e.g. reproduction) and external interaction capabilities (Fig. 1a) abstracted by binders. The propensity of communication between boxes is quantified by the

affinity (rate) between the different types of binders, measuring interaction strength. An important feature of process algebras is compositionality: the meaning of the model depends on the features of its components and how they depend on each other (how it is composed). Wise composition has several advantages: model development can be modular, standardization is relatively easy and the evaluation can be rigorous. Over a certain level of model complexity, developing the model does not become more complicated. Model development requires adding simple elements instead of rewriting major parts of the code. An initial model can be easily fine-tuned according to pilot studies or sensitivity analyses, or can be simply extended and modified. These features are advantageous for recurrent application and standardization. The first ecological applications addressed social insect colonies (Tofts, 1993) and epidemiology (Norman and Shankland, 2004).

Fig. 1b presents a predator–prey interaction representation (Dematté et al., 2007, 2008; Livi, 2009). Both the predator (B_1) and the prey (B_2) are represented as biological processes depicted as boxes. Binders are identified by names and types (for instance, B_1 has one binder of type “A₁”, named “eat”). For simplicity, we only indicate the name of the set processes describing the internal behaviour of the box (for instance, the set of processes in B_1 is called “Predator”). A predator–prey interaction can be represented as a communication between B_1 and B_2 through the binders (eat, A_1) and (eaten, A_2), being realized when the affinity between A_1 and A_2 is non-zero.

Since it is an event-based description, combinatorial explosion in parameter-rich, complex models can be efficiently reduced by its use. BlenX is an efficient tool to implement the Gillespie algorithm (Gillespie, 1977) for stochastic simulations of biosystems. In biology, this has already been richly used for simulating the stochastic behaviour of molecules in the cell (Dematté et al., 2008). Ecological applications were also suggested recently: indirect effects and cycling (Finn, 1976) were measured by the particle tracking method of Kazanci et al. (2009), while hypothetical food webs were generated and studied by Powell and Boland (2009). Here we use an inherently stochastic model, instead of an inherently deterministic

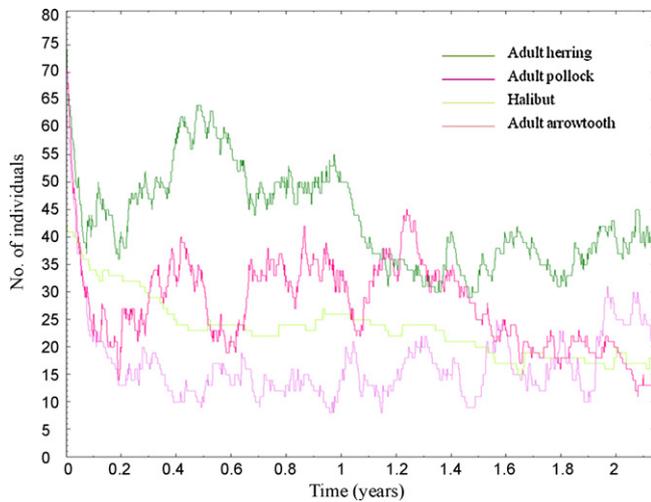


Fig. 2. An illustrative part of one simulation run. Curves of different colours represent the population size (Y axis) of four species in time (X axis).

system with some added stochastic component (e.g. Jordán et al., 2003).

2.3. The model

2.3.1. Data

The Ecopath with Ecosim (EwE) model of the Prince William Sound (Alaska) food web has been described and analysed in detail (Okey and Pauly, 1999; Okey, 2004; Okey and Wright, 2004). The network model contains 48 living components (Table 1). The non-living components (#49, #50, #51) as well as self-loops (“cannibalistic” trophic flows) have been omitted from the model. The original network model is a weighted graph, assigning trophic flow values to each link.

2.3.2. Implementation

We have translated the EwE-model (Okey, 2004) to BlenX (Livi, 2009). Biomass values of trophic groups have been translated to numbers of individuals, based on species-specific body size data (from www.fishbase.org and literature data). For simplicity, we have used the logarithm of number of individuals and then multiplied by 10. Trophic flows were directly translated to interaction rates. We excluded all external effects (e.g. material flows) and supposed that the system is close to equilibrium. Thus, death rates were chosen from a realistic range (from 0.001 to 0.1, typically 0.01) to fine-tune the model to quasi-equilibrium (note here that some authors use mortality as a sum of natural mortality and predation, like Okey (2004), and it is not easy to separate them).

We describe the dynamics in a way that is similar to (and adopted from) modelling molecular kinetics in the cell. Simple rates are assigned to single-individual (cf. mono-molecular) interactions (like reproduction, birth, death), while the kinetics of pairwise (bi-molecular) interactions follow mass-action:



and



meaning that there is a rate for “eat and reproduce” (k_1) and another for “eat” (k_2). In the first case, the predator eats the prey and produces another predator individual, while the prey disappears. In the second case, the predator eats the prey and the prey disappears. The k_1/k_2 ratio determines how many items of prey B are needed for

Table 1

The list of species (or trophic groups) in the Prince William Sound model, after omitting the three non-living components (Okey, 2004).

1	Transient Orca
2	Salmon sharks
3	Resident Orca
4	Sleeper sharks
5	Halibut
6	Pinnipeds
7	Porpoise
8	Lingcod
9	Adult Atooth
10	Adult Salmon
11	Pac. Cod
12	Sablefish
13	Juv. Atooth.
14	Spiny dogfish
15	Avian predators
16	Octopods
17	Seabirds
18	Deep demersals
19	Pollock 1+
20	Rockfish
21	Baleen Whales
22	Salmon Fry 0-12
23	Nshore demersal
24	Squid
25	Eulachon
26	Sea otters
27	Deep Epibent
28	Capelin
29	Adult Herring
30	Pollock 0
31	Invert-eat Bird
32	Sandlance
33	Shal Lg Epibent
34	Juv. Herring
35	Jellies
36	Deep sm infauna
37	Near Omni-zoo
38	Omni-zooplankto
39	Shal sm Infauna
40	Meiofauna
41	Deep Lg Infauna
42	Shal Sm Epibent
43	Shal Lg infauna
44	Near Herbi-zoo
45	Herbi-zooplankt
46	Near phytoplkn
47	Offshore Phyto.
48	Macroalgae/gras

the reproduction of A individuals. This is a very simplistic description of a prey–predator interaction but simple kinetic rules seem to apply quite well in several ecological situations: for example, the number of shark-bitten pinnipeds is proportional to shark and

Table 2

Community-based importance measures used in this study. Degree, weighted degree and betweenness measure the centrality of graph nodes in networks. Trophic level measures the distance from producers in the directed food web. Interaction strength measures species importance based on deterministic dynamic sensitivity analysis, while the Hurlbert response-based importance measure was used in the stochastic dynamic sensitivity analysis.

Formula	Measure of Importance
Topology	
D	Degree
wD	Weighted degree
BC	Betweenness
TL	Trophic level
Dynamics (deterministic)	
ISI	Interaction strength
Dynamics (stochastic)	
I_H	Effect
I_H'	Sensitivity

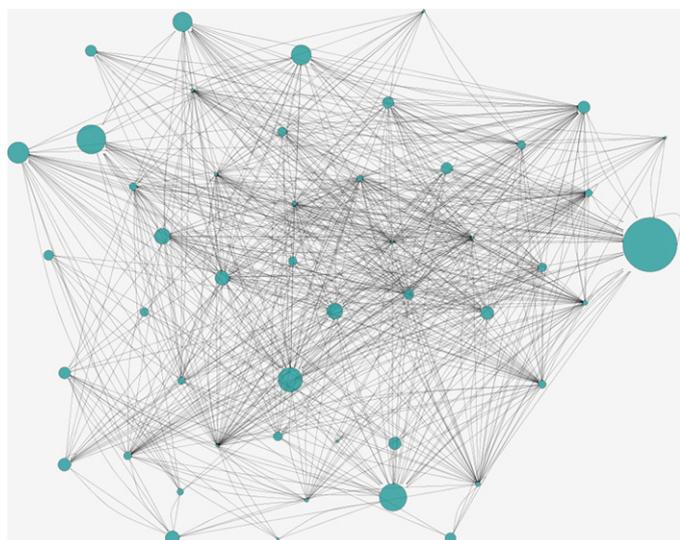


Fig. 3. The Prince William Sound food web: size of nodes is proportional to the mean-based I_H value of species or trophic groups (figure drawn by CoSBI Lab Graph, see Valentini and Jordán, 2010). Producers are at the bottom and top predators are at the top, following conventions.

pinniped abundance, while community shift in exploitative competition is proportional to prey availability, relative competitive abilities and the relative densities of consumers (Stevens et al., 2000). These parameters correspond to kinetic rates and concentrations in simple chemical reactions: if two molecules A and B have compatible functional groups, they may react and the probability of the reaction depends on the concentration of both molecules and the reaction rate (also on the concentration of products if the reaction is reversible). The simplest kinetics for an interspecific interaction may follow the same logic: prey density, predator density and the prey preference of the predator are three parameters describing the probability of feeding.

Our approach makes it possible to define a number of details in order to realistically describe eco-dynamics at the level of the individuals. The most essential biological detail here is what determines the k_1/k_2 ratio and how to describe the state of the individual. For example, Powell and Boland (2009) assume that only sated individuals (A^*) can reproduce and only hungry individuals (A) can be eaten. One challenge here is to integrate ecological stoichiometry (Sterner and Elser, 2002) with our model. It needs to specify how many feeding events, of exactly which prey, is enough for reproduction (this could also be expressed in rates). More complicated dynamical scenarios (e.g. various non-linear functional responses) are not considered in this paper but are possible future extensions. As reference, 20 simulations were run in 40,000 steps, corresponding to a 30 years period (Fig. 2 shows a small fragment of the simulation). Based on these runs with the same initial conditions and parameters, we can measure the variability of system behaviour.

2.4. Sensitivity analysis

2.4.1. Perturbation

We performed pulse perturbations, reducing the population size of each functional group by half, one by one, in different runs. We also made perturbations where population sizes were divided by 4, multiplied by 2 and multiplied by 4. The chosen mode of perturbation is comparable with the one in deterministic sensitivity analysis conducted by Okey (2004), but note that a variety of perturbation techniques have been used in the study of other systems (e.g. halving reproduction rates, Okey, 2004). Here we have not performed

Table 3

The rank of trophic groups based on stochastic dynamic sensitivity analysis. I_H and I_H^* quantify species importance based on effect on others mean population size and the effect of others on the studied group's mean population size, respectively.

	I_H		I_H^*
Nshore	230,3824	Halibut	985,93
Adarrowtooth	147,4819	Juvherring	271,61
Herbizoo	141,3665	Adsalmon	254,60
Seabird	119,7005	Shaligepi	237,64
Sleepershark	107,3609	Inverteat	126,30
Salmonshark	106,6122	Pinniped	112,05
Juvherring	105,6032	Pacificcod	103,69
Juvsalmon	103,555	Omnizoo	98,94
Juvatooth	103,0092	Sablefish	93,86
Adpollack	98,07455	Adpollack	93,29
Nearphyto	97,64756	Deepepi	86,59
Capelin	93,63991	Capelin	86,42
Shalsminf	92,28596	Spiny	85,88
Deepginf	91,28188	Jellies	81,16
Pacificcod	90,8476	Octopod	79,82
Jellies	88,49004	Seaotter	73,60
Lingcod	86,63624	Nearomnizoo	70,96
Pinniped	85,45055	Lingcod	68,47
Macroalge	84,65765	Offshorephyto	64,40
Adherring	84,5612	Deepginf	62,50
Resorca	82,71365	Deepsminf	60,99
Porpoise	81,85864	Macroalge	60,65
Deepsminf	79,39852	Adarrowtooth	57,55
Salmonfry	79,31558	Nearherbizoo	56,24
Baleen	78,1507	Salmonfry	54,75
Seaotter	78,06681	Seabird	54,30
Sandlance	77,67761	Sleepershark	49,15
Adsalmon	76,01381	Shalsmepi	48,94
Inverteat	75,63834	Eulachon	48,45
Nearomnizoo	75,61472	Avian	47,59
Deepdemfish	75,17384	Nearphyto	47,50
Octopod	75,02065	Salmonshark	42,38
Shaliginf	72,4026	Juvatooth	39,88
Spiny	69,01359	Baleen	36,01
Shaligepi	68,32205	Nshore	32,21
Rockfish	66,4884	Resorca	28,61
Shalsmepi	66,0483	Adherring	27,43
Nearherbizoo	63,47351	Shalsminf	23,47
Deepepi	61,13831	Meiofauna	21,90
Meiofauna	60,15124	Rockfish	20,46
Omnizoo	58,75869	Herbizoo	18,73
Sablefish	58,54705	Juvsalmon	13,92
Halibut	56,25068	Porpoise	9,78
Eulachon	56,17952	Squid	8,94
Avian	54,91904	Transorca	5,68
Transorca	52,8482	Shaliginf	4,05
Squid	52,25344	Deepdemfish	0,88
Offshorephyto	48,0378	Sandlance	0

sensitivity analysis where combinations of parameters have been changed simultaneously.

2.4.2. Response

We used several response functions but, for simplicity, present only results based on a metric very similar to the Hurlbert response index (Hurlbert, 1997; the only difference is that we compare the population sizes in the reference interval for the control and the perturbed simulation runs instead of two states in the same simulation, before and after perturbation). The Hurlbert response-based importance of species i ($I_{H(i)}$) is calculated by:

$$I_{H(i)} = \sum_{j=1}^{48} |P_j^i - P_j^*| \quad (3)$$

where P_j^* is the number of individuals of species j at time t in the reference simulation (without perturbation), and P_j^i is the mean number of individuals of j in time t based on 20 simulations when species i was perturbed. We have excluded self-effects realized

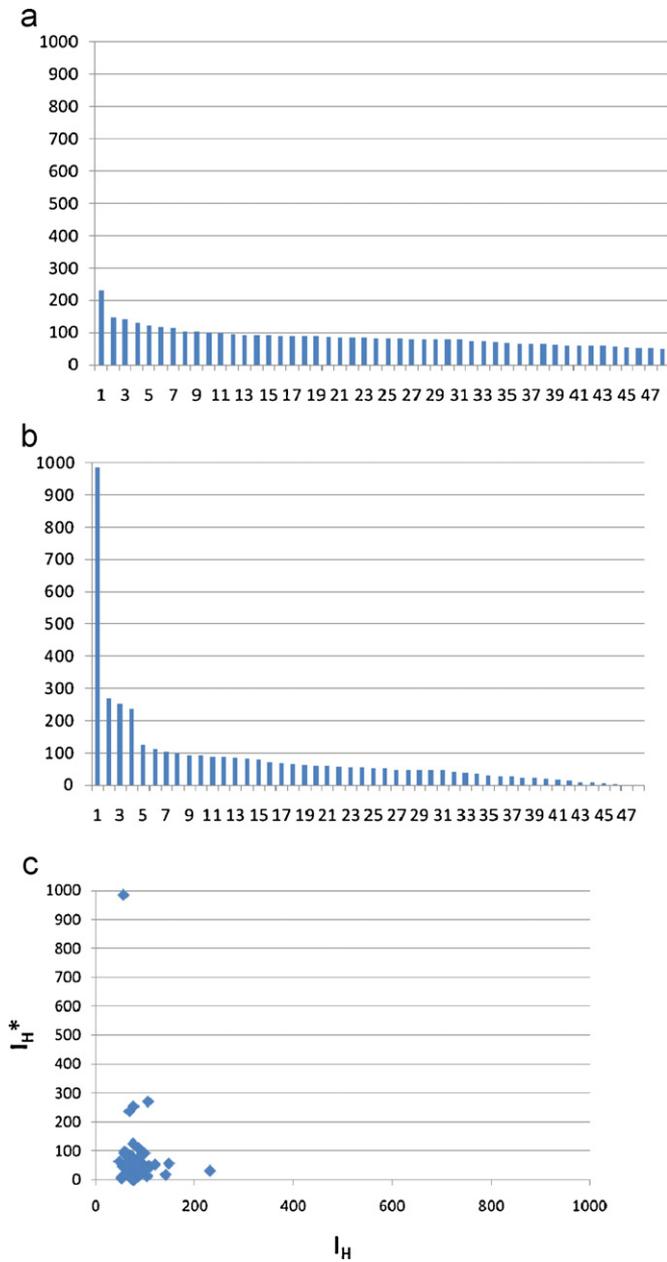


Fig. 4. The mean-based species importance quantified as the effect on other species (I_H , a), the effects of other species on the studied species (I_H^* , b), and their relationship (c). The distribution is uniform in (a) and shows a keystone pattern-like distribution in (b).

through indirect pathways (let $i \neq j$). This measure quantifies how large the community-wide response is, following some relatively big perturbation on a particular species.

We have used another version of I_H , named I_H^* , where we quantify the overall response of species i , following the perturbation of any of the species.

$$I_{H(i)}^* = \sum_{j=1}^{48} |P_i^j - P_i^*| \quad (4)$$

where P_i^* is the number of individuals of species i at the reference simulation (without perturbation), and P_i^j is the mean number of individuals of i based on 20 simulations when all species j were perturbed. We have excluded self-effects also here ($i \neq j$). This measure quantifies how sensitive species i is to perturbing any

Table 4

The rank of trophic groups based on stochastic dynamic sensitivity analysis. I_H and I_H^* quantify species importance based on effect on the variance of others population size and the effect of others on the variance of the studied groups population size, respectively.

	I_H		I_H^*
Nshore	332,9215	Halibut	5356,806
Herbizoo	218,7412	Seabird	417,1032
Sleepershark	208,7874	Deepepi	108,0029
Macroalge	202,7006	Shaligepi	100,3646
Nearherbizoo	198,4092	Capelin	81,57298
Pacificcod	195,6622	Juvherring	80,12305
Salmonshark	191,774	Spiny	56,47612
Offshorephyto	190,7102	Pacificcod	38,93173
Juvpollock	186,4349	Macroalge	37,53366
Pinniped	181,288	Octopod	36,24754
Deepdemfish	180,2726	Seaotter	35,26956
Adsalmon	176,1529	Pinniped	34,27198
Salmonfry	175,6586	Jellies	34,21654
Nearphyto	169,333	Lingcod	33,9076
Baleen	169,1709	Adsalmon	31,44734
Sablefish	166,4515	Nshore	28,9631
Adherring	165,5893	Nearherbizoo	27,9367
Resorca	164,802	Inverteat	27,69864
Seaotter	161,5243	Adpollock	26,43388
Adpollock	157,8397	Salmonshark	25,01807
Eulachon	157,6989	Nearomnizoo	19,39001
Lingcod	155,7288	Omnizoo	19,07195
Inverteat	155,2152	Sablefish	18,96375
Octopod	151,4581	Shalsmepi	18,15814
Omnizoo	151,2922	Avian	17,61466
Adarrowtooth	147,9595	Deepginf	17,21663
Avian	147,296	Offshorephyto	16,339
Shaliginf	147,2926	Deepsminf	16,2753
Nearomnizoo	144,4721	Eulachon	15,58031
Meiofauna	135,7082	Shaliginf	15,42056
Juvherring	132,9509	Sleepershark	15,03125
Deepginf	128,9505	Salmonfry	14,50267
Deepsminf	128,2209	Shalsminf	14,08329
Shalsminf	123,8591	Herbizoo	13,98601
Porpoise	118,5254	Baleen	13,49651
Transorca	112,7393	Nearphyto	13,43305
Spiny	112,2389	Rockfish	13,31296
Shalsmepi	106,4931	Meiofauna	12,39792
Deepepi	105,246	Juvatooth	12,27955
Capelin	104,2345	Adarrowtooth	12,21726
Shaligepi	95,27019	Adherring	10,03192
Squid	87,56856	Resorca	8,94861
Rockfish	85,72298	Juvpollock	4,810008
Sandlance	77,03046	Transorca	4,206301
Juvatooth	69,99225	Porpoise	3,992915
Jellies	35,67209	Squid	2,375242
Halibut	27,46907	Deepdemfish	0
Seabird	20,93072	Sandlance	0

other species in the ecosystem. In the matrix of $|P - P^*|$ response values (where perturbing in row x will result in a response in column y), I_H corresponds to row sums and I_H^* corresponds to column sums.

We also have calculated both I_H and I_H^* based on variance instead of mean. Here, we calculated the variance of the number of individuals of each species in the 20 runs of each situation (e.g. either reference run or a perturbation run with species i perturbed). Variance was divided by the mean values (used before) and the Hurlbert response measure was calculated for the coefficient of variation. Thus, the focus here is not on changed population size but, instead, on changed variability in population size (for several stochastic simulations). This variance-based approach may tell less about actual effects but more about control.

Other response measures have also been tested (e.g. considering $(P_i^j - P_j^*)/P_j^*$ but here we present only the Hurlbert response-based measures, for simplicity. In summary, I_H and I_H^* are used as stochastic dynamic sensitivity analysis-based importance measures of trophic groups in the studied ecosystem (Table 2). I_H is more like

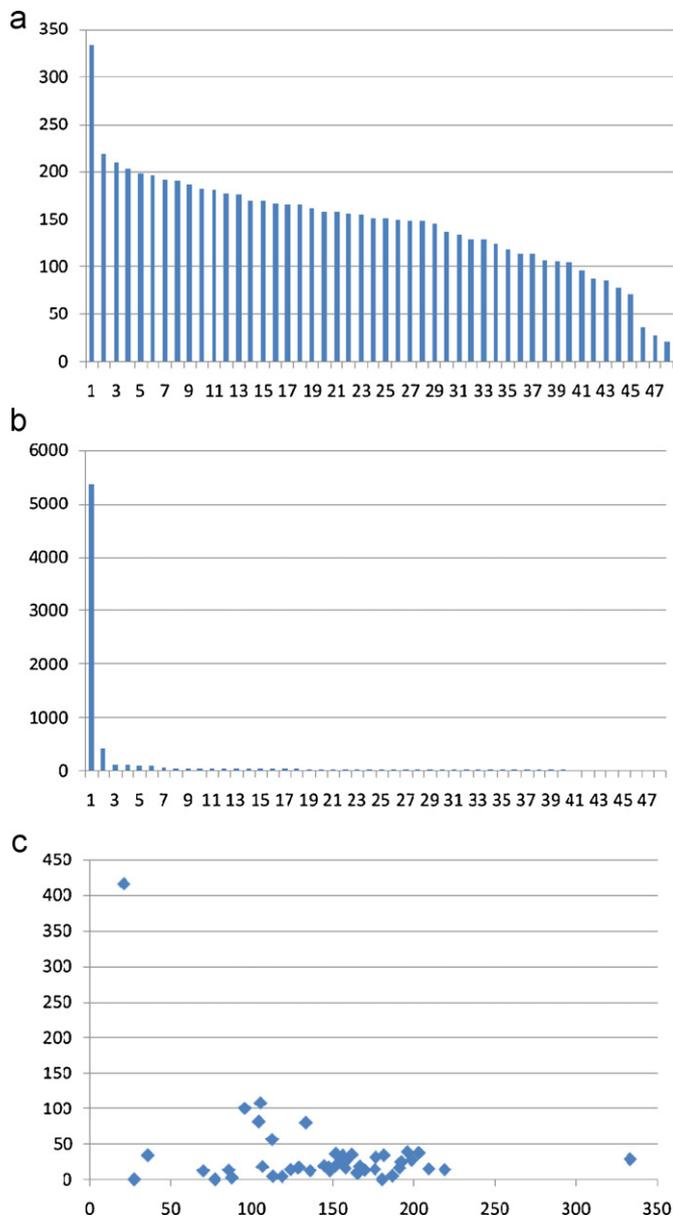


Fig. 5. The variance-based species importance quantified as the effect on other species (I_H , a), the effects of other species on the studied species (I_H^* , b), and their relationship (c). The distribution is unimodal in (a) and shows a strong keystone pattern-like distribution in (b).

a global response to a local change, while I_H^* is more like a local response to global changes.

2.5. Other measures of importance

2.5.1. Topology

One of our goals is to study the topological position of trophic groups most important in stochastic sensitivity analysis. For simplicity, we use only three indices here (Table 2). Node degree (D) is the number of direct interacting partners: in a food web, this is the sum of preys and predators. Weighted node degree (wD) is the sum of carbon flows coming from preys and going to predators (i.e. the sum of weights on incoming and outgoing links in the network). Finally, betweenness centrality (BC; see Wassermann and Faust, 1994) measures how frequently a node i is incident to all shortest

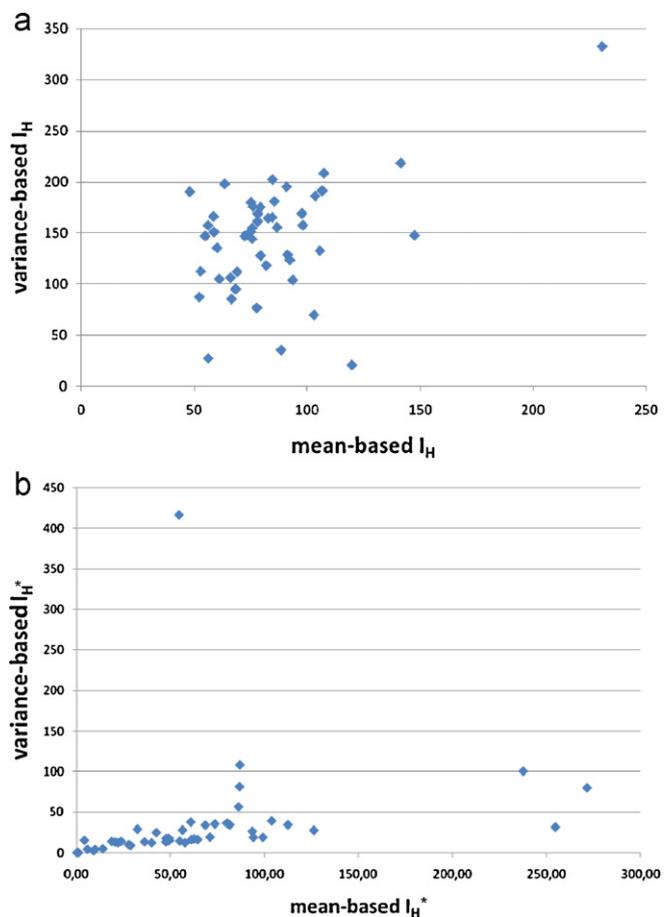


Fig. 6. The relationship between the mean-based and the variance-based importance of species, for I_H (a) and I_H^* (b). Note that halibut (#5) is not shown in (b) for clarity.

paths between two other nodes in the same network:

$$BC_i = \sum_{i>k} \frac{g_{jk}(i)}{g_{jk}} \quad (5)$$

where $i \neq j, k$, g_{jk} is the number of equally shortest paths between nodes j and k , and $g_{jk}(i)$ is the number of these shortest paths to which node i is incident.

D is studied, because it is the simplest measure of positional importance. Earlier studies have shown that wD fits well to simulated behaviour (Jordán et al., 2008), thus our use of it here. Finally, BC characterizes a fairly different aspect of centrality, apart from the number of neighbours (Jordán et al., 2007), so it was chosen to quantify other kinds of key nodes. Apart of these centrality indices, we have also studied the relationship between dynamic importance and trophic level (TL, that equals one plus the distance from producers in a food web digraph), with $TL = 1$ for producers and $TL = 5.41$ for the highest top predator (transient orca, #1).

2.5.2. EwE dynamics

Here we only use the interaction strength index (ISI, Table 2), as this is the most similar one to the Hurlbert response measure we use in stochastic simulations. We have also calculated community importance (CI), community longevity support (CLS), and the keystone index of Okey (KI) (Okey, 2004) and the keystone index of Libralato et al. (KN, Libralato et al., 2006), but they do not serve the present deterministic/stochastic comparison well.

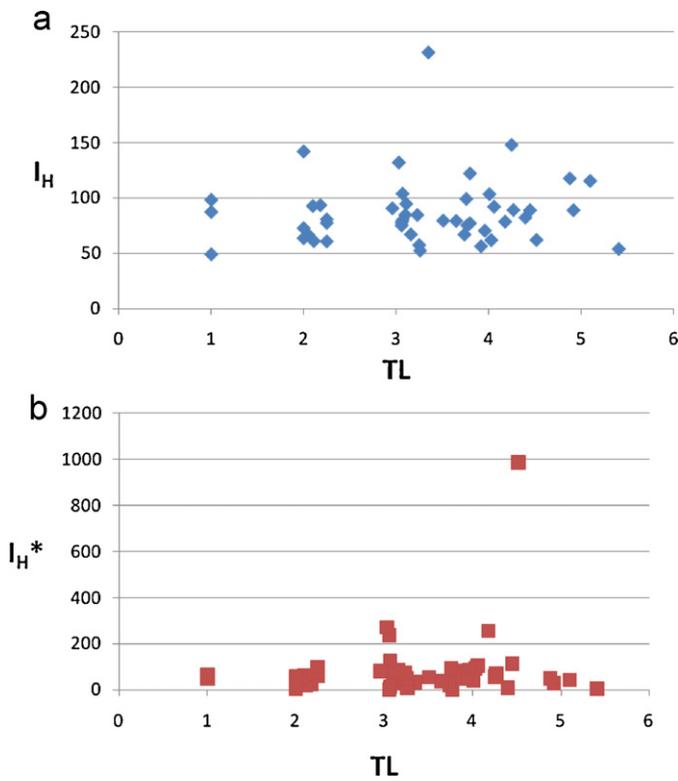


Fig. 7. The relationship between species importance (I_H in a, I_H^* in b) and trophic level (TL).

3. Results

The community remained close to equilibrium during the simulations, even if some minor extinction events occurred (just like in EwE models, see the extinction of pepino in Okey et al., 2004).

In Fig. 3, the size of graph nodes is proportional to their stochastic dynamic importance (measured as the effect on the mean population size of other species, i.e. mean-based I_H). Based on this sensitivity analysis, the importance rank of species is led by nearshore demersals (#23), followed by adult arrowtooth (#9) and herbivorous zooplankton (#45, see I_H in Table 3). Apart of this ranking, based on effects on others (I_H), we also provide the ranking of species based on how much they are influenced by disturbing other members of the community (I_H^*): here, halibut (#5) is of outstanding importance, followed by juvenile herring (#34) and adult salmon (#10) as the three most sensitive species (Table 3). The rank order of values is shown for both I_H (Fig. 4a) and I_H^* (Fig. 4b). The relationship between the two used stochastic dynamic importance measure is shown in Fig. 4c (see also Table 3). It seems like a hyperbolic curve, suggesting that a species has either a strong effect on others (large I_H) or is strongly influenced (I_H^*). The trophic group with relatively high index value in both is juvenile herring (#34).

Variance-based dynamic species importance measures suggest the same species in the first ranks (nearshore demersals, #23, for I_H and halibut, #5, for I_H^* , see Table 4) but somewhat different rank orders later (Table 4, Fig. 5a and b): followed by herbivorous zooplankton (#45) and sleepershark (#4) if being influenced in mean and followed by seabirds (#17) and epibenthos groups (#27 and #33) if being influenced in variance. The $I_H - I_H^*$ relationship is hyperbolic here too, and juvenile herring (#34) is one of the trophic groups of relatively large importance in both (Fig. 5c). Note that halibut (#5) and seabirds (#17) are the worst in the I_H rank but the leading groups in the I_H^* rank.

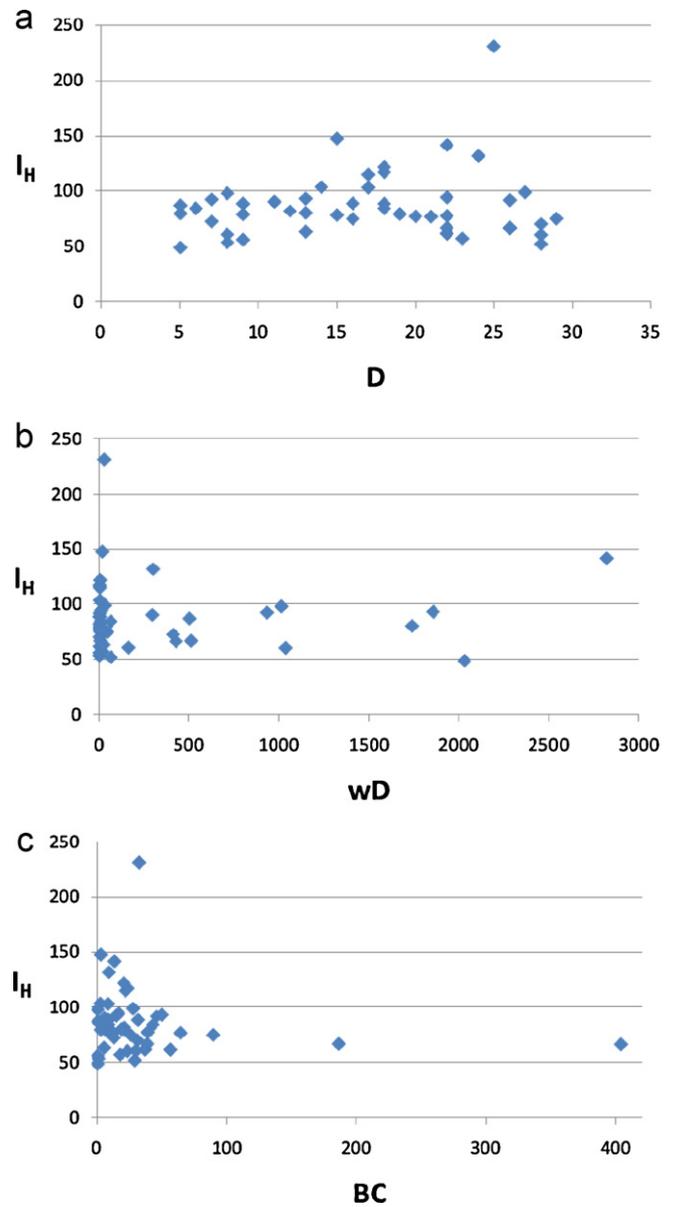


Fig. 8. The relationship between mean-based I_H and three topological indices, degree (D, a), weighted degree (wD, b) and betweenness (BC, c).

The correlation between effects (I_H) on the mean and effects on the variance of other species is seen in Fig. 6a, while the correlation between being influenced (I_H^*) in mean versus being influenced in variance is presented on Fig. 6b.

Different indices suggest somewhat different distributions for importance values of species (Mills et al., 1993). Fig. 4 shows that in some cases a keystone pattern-like distribution (i.e. a few species with outstanding importance values and the majority with much lower ones) appears (e.g. Fig. 4b), while in other cases the distribution is closer to uniform (Fig. 4a) or unimodal (see Fig. 5a below).

Both I_H and I_H^* are higher in the middle of the trophic scale (Fig. 7a and b). Note that in deterministic simulations either top-predators or phytoplankton seem to be of highest importance: transient orca (#1) by CI and KI (Okey, 2004), offshore phytoplankton (#47) by CLS and ISI (Okey, 2004) and orca followed by offshore phytoplankton by the keystone index of Libralato et al. (2006).

Fig. 8 shows the relationship between I_H and three topological indices. Dynamically important species have higher degree (Fig. 8a), high or low weighted degree (Fig. 8b) and low between-

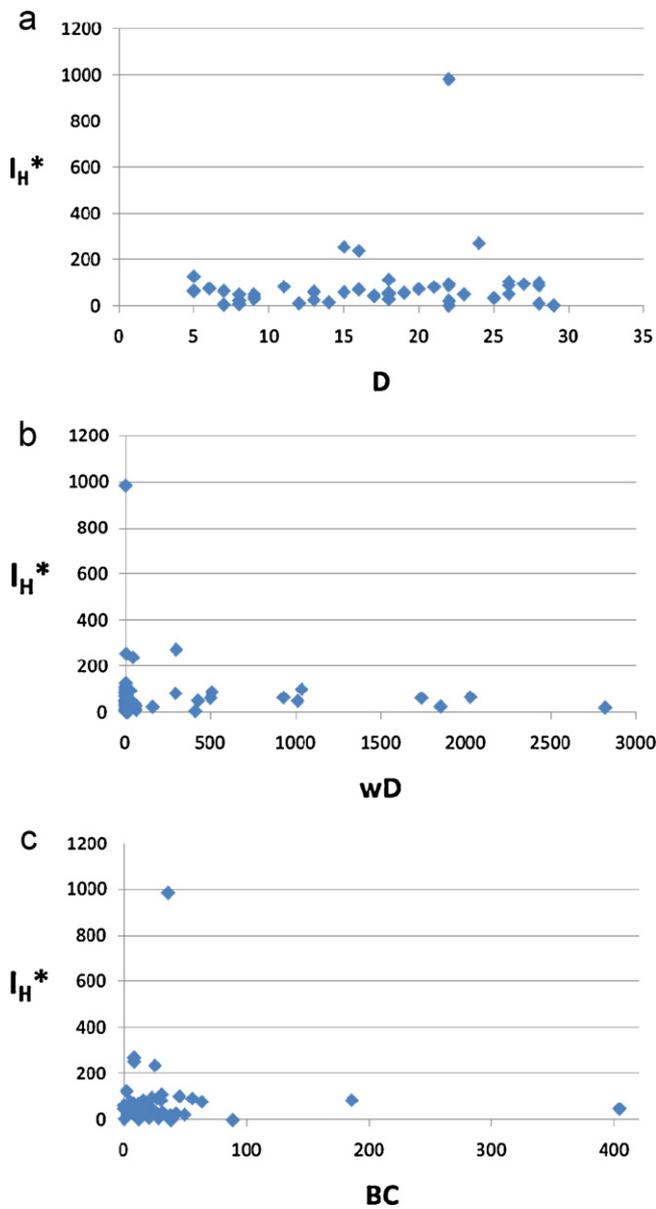


Fig. 9. The relationship between mean-based I_H^* and three topological indices, degree (D , a), weighted degree (wD , b) and betweenness (BC , c).

ness centrality values (Fig. 8c). Fig. 9 shows the same for I_H^* . For the mostly sensitive species, D is about the average and shows poor correlation (Fig. 9a), while wD and BC are small (Fig. 9b and c). The possibility of having a large effect on the community with only a few interacting partners is supported by other studies as well (see Montoya et al., 2009). Among the several deterministic dynamics-based importance indices, ISI is the most similar to our stochastic ones. Fig. 10 shows negative correlation for both I_H and I_H^* , stronger for the latter.

In this modelling exercise, deep demersal fish (#18) and sandlance (#32) frequently went extinct, but their survival depended on which other species were perturbed. For example, perturbing sablefish (#12), i.e. dividing its population size by two, does help deep demersals (#18) to survive (however their population size remains very small, see Fig. 11) but not sandlance (#32). Another particular interaction between jellies (#35) and juvenile pollock (#30) was also studied. The strength of mutual effects between them is around the average strength (but see Purcell et al., 2000).

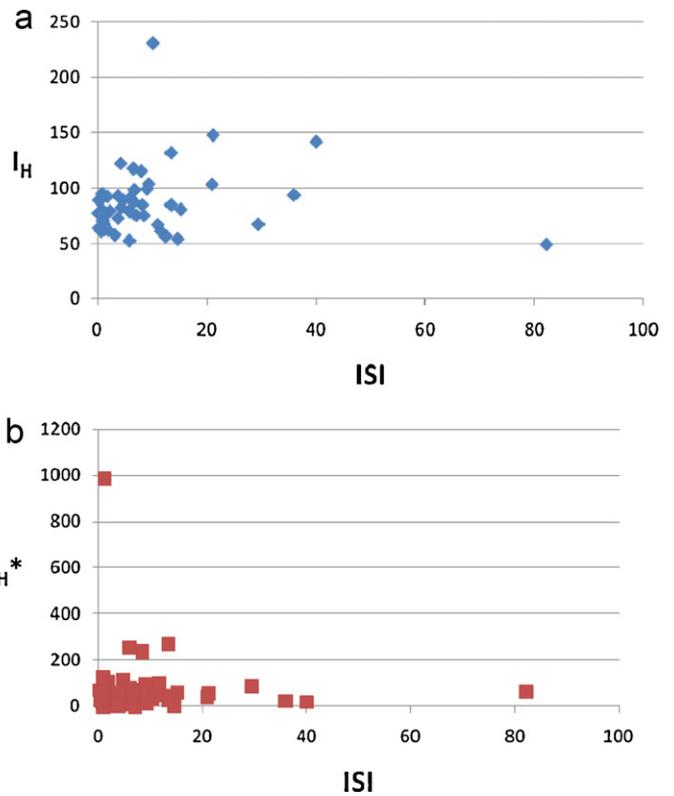


Fig. 10. The relationship between species importance (I_H in a, I_H^* in b) and the interaction strength index (ISI) based on deterministic dynamic simulations.

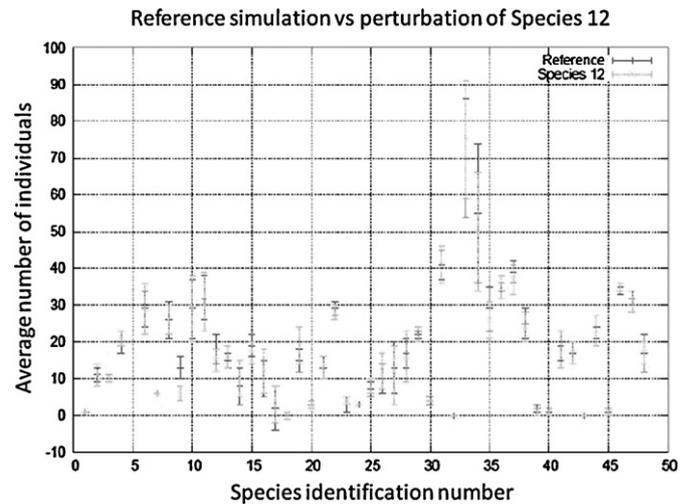


Fig. 11. Effect of disturbing sablefish (#12) on the mean population size of each other species (functional group) in the community (based on 20 runs). Light points show data for each species when sablefish was disturbed, while dark points show the reference simulation, when no species was disturbed. Their difference is the basis of the response measure (I_H).

4. Discussion

Stochastic processes and internal and external noise are important elements of biological systems, not just a sign of imperfection (cf. Simberloff, 1980). Dynamics of small populations can be noisy and their understanding frequently calls for individual-based models. Here, we presented an individual-based, stochastic, data-rich simulation of a large real ecosystem model.

Our approach, using a process algebra-based language is ecologically reasonable, as it can capture the inherent variability of

biological systems, as opposed to ODE-based simulations considering a homogeneous set of components. While the latter represents a view focusing on equations providing strong laws with some (mostly external) noise, the former describes a situation where variability is inherent and influential.

The sensitivity analysis performed in our simulation framework provides information on the behaviour and importance of individual species, pairwise interactions, and the whole community. Moreover, we have gained some insight also into the comparison of modelling techniques. For the distribution of relative importance values in the whole community, most indices show a keystone pattern-like distribution, while some support unimodal or close to uniform importance distributions. The identity of key species depends on the index chosen. Nearshore demersals (#23) seem to be the most important species in influencing others, both in mean population size and in its variance. The result is totally different if we quantify which species are most sensitive to changes in others. Halibut (#5) leads both lists, with huge advantage. The big difference between “influence others” and “being influenced” in the same simulations raises big questions about how to measure species importance and how to understand sensitivity (also in the context of environ analysis, Patten, 1981, 1991). The functional group that seems to be most important according to both approaches is juvenile herring (#34, being both effective and sensitive). The correlation between indices based on the mean and based on the variance of effect values is weak, i.e. if a species has a large effect on the mean population size of others, it does not guarantee that it will have a large effect also on the corresponding variances. Strongly interacting groups appear at each trophic level, mostly around the middle of the food web. This may refine the earliest paradigm (keystones are top predators) and support recent findings on species of high importance in the middle of the trophic scale (Cury et al., 2000; Stibor et al., 2004) or at least below the highest top-predators (like bonito, Coll et al., 2009). All deterministic dynamic importance indices suggest either top-predators or producers to be of highest importance (Okey, 2004; Libralato et al., 2006). Static topology was relatively poor in predicting the identity of dynamic key species in these simulations. Betweenness is negatively correlated with stochastic dynamic importance, while degree shows some weak positive correlation. Weighting the network by trophic flows is important, as weighted degree shows a correlation different from that of (binary) degree. Surprisingly, another kind of dynamic community importance index (ISI), based on deterministic modelling, shows a clear negative correlation to stochastic importance measures. Further research is needed here to clarify whether the difference is of technical or biological nature.

The effect of sablefish (#12) on deep demersals (#18) and sandlance (#32) can be explained by looking at the weights on network links: sablefish (#12) feeds on both preys to a different extent. Trophic flow from deep demersals (#18) to sablefish (#12) is 0.0903, while it is only 0.0019 to sandlance (#32; mass transfer data are expressed in t/km², Okey, 2004). Larger flows are responsible for stronger effects in this case. In case of the relationship between jellies (#35) and juvenile pollock (#30) their well-documented strong interaction is not seen in our simulation, probably because the dominant effect is of non-trophic or spatial nature (like amensalism or aggregation, see also Purcell et al., 2000).

Other directions of future research may focus on making the model more complete, as this is a first version. First of all, a hybrid model describing abundant species (zooplankton) in a deterministic and rare ones (orca) in a stochastic way would be logical. Other directions could be considering spatial dynamics (see Ciocchetta and Jordán, 2010), multiple interaction types (e.g. facilitation in signed graphs, see (Purcell et al., 2000), demographical details (cf. size-overfishing, Okey et al., 2004) and refining the basic structure of the model (in order to model diverse functional responses more

realistically). Finally, more research is needed on comparing the same simulation outcomes analysed by different response measures (see Harley, 2003). As a further complication, the effect of species *i* on the effect of species *j* on species *k* could also be analysed (see Yodzis, 2000).

Applications of stochastic, individual-based modelling seem to be helpful in situations where there are big differences between the behaviour of individuals, i.e. population dynamics are not homogeneous. An example is size-overfishing (e.g. “bacalao”, Okey et al., 2004), where a deterministic model of the homogeneous population can be misleading. Here, individual-based, stochastic models may eventually shed light on poorly understood findings. Generally, the very hottest problems of conservation practice call for individual-based, stochastic modelling (considering the rarity and noisy behaviour of the smallest populations to protect). Here, there is a need for better integrating theory and empirical data (Simberloff, 2003).

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