

## Simple, policy friendly, ecological interaction models from uncertain data and expert opinion

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**Abstract**

In the marine environment, humans exploit natural ecosystems for food and economic benefit. Challenging policy goals have been set to protect resources, species, communities and habitats, yet ecologists often have sparse data on interactions occurring in the system to assess policy outcomes. This paper presents a technique, loosely based on Bayesian Belief Networks, to create simple models which 1) predict whether individual species within a community will decline or increase in population size, 2) encapsulate uncertainty in the predictions in an intuitive manner and 3) require limited knowledge of the ecosystem and functional parameters required to model it. We develop our model for a UK rocky shore community, to utilise existing knowledge of species interactions for model validation purposes. However, we also test the role of expert opinion, without full scientific knowledge of species interactions, by asking non-UK based marine scientists to derive parameters for the model (non-UK scientists are not familiar with the exact communities being described and will need to extrapolate from existing knowledge in a similar manner to model a poorly studied system). We find these differ little from the parameters derived by ourselves and make little difference to the final model predictions. We also test our model against simple experimental manipulations, and find that the most important changes in community structure as a result of manipulations correspond well to the model predictions with both our, and non-UK expert parameterisation. The simplicity of the model, nature of the outputs, and the user-friendly interface makes it potentially suitable for policy, conservation and management work on multispecies interactions in a wide range of marine ecosystems.

**Key Words:** Rocky Shore, Predictive Model, Sparse Data, Marine Management, Fisheries, Bayesian Belief Network, Conservation

## 1 **1. Introduction**

2 The marine environment and its ecosystems present major challenges for management (see reviews  
3 by Islam and Tanaka, 2004; Cicin-Sain and Belfiore, 2005; Ehler, 2005; deYoung et al., 2008;  
4 Zacharias, 2014). For example, in much of the marine environment, determining population sizes  
5 cannot be achieved by simple counts, but require mathematical models with inherent uncertainty  
6 (Hilborn and Walters, 1992). Ecological interactions are also uncertain. For example, in fisheries, top  
7 down tropic interactions have been extensively studied but data are highly variable in nature and  
8 patchy in time, space and for different species (Pope, 1991; Magnusson, 1995; Livingston and  
9 Jurado-Molina, 2000; Pinnegar and Stafford, 2007; Pinnegar, 2014). Knowledge of bottom up  
10 interactions is largely non-existent in many systems, and rarely incorporated in predictive models  
11 (see Engelhard et al., 2013 for ecological importance of bottom up effects; and Christensen and  
12 Pauly, 1992 for details of the Ecopath model, which considers biomass consumption in a bottom up  
13 context). Competition is very rarely included in species interaction models (despite initial predictions  
14 by May et al., 1979 of its potential importance).

15 Marine ecosystems differ from many terrestrial systems in being largely 'natural'; albeit highly  
16 disturbed by anthropogenic activity. Food production on land, for example, is largely through  
17 agriculture, yet, despite increases in aquaculture, most marine fish are natural resources harvested  
18 directly from a natural system (World Bank, 2013). As such, predictive community based models  
19 might be more useful in marine environments than in terrestrial environments.

20 Protecting the marine environment is of paramount concern to environmental policy makers  
21 (Hallwood, 2014; Zacharias, 2014). The marine environment provides economic income through  
22 fisheries, as well as a range of other ecosystem services (Hallwood, 2014). Under international  
23 agreements such as the Convention on Biological Diversity ([www.cbd.net](http://www.cbd.net)), detailed policy  
24 documents have recently been produced by many governments to protect marine resources. For  
25 example in the North-East Atlantic, fifteen governments are contracted to establish a network of  
26 marine protected areas (OSPAR Commission, 2013). Under the European Union (EU) Marine Strategy  
27 Framework Directive (MSFD), member states aim to achieve good environmental status across  
28 European seas by 2020. To meet commitments under MSFD the UK is committed to contributing to a  
29 network of marine protected areas (JNCC, 2014). Policy documentation from the UK government on  
30 implementation of MSFD provides a wide range of targets, which for many named species or  
31 taxonomic groups indicate population level targets of 'no decrease on current levels' (DEFRA, 2012).  
32 Similarly, population management targets of 'maintain or 'recover' have been assigned to particular  
33 species within designated Marine Conservation Zones in England (Natural England, 2014). As an

1 example, the ministerial order (second level legislation) for the MCZ in the Tamar Estuary in SW  
2 England reads: “(1) The conservation objective of each of the Zones is that the protected features—  
3 (a) so far as already in favourable condition, remain in such condition; and (b) so far as not already in  
4 favourable condition, be brought into such condition, and remain in such condition. (2) In paragraph  
5 (1), —favourable condition — (a) with respect to a broadscale marine habitat or a marine habitat  
6 within a Zone, means that— (i) its extent is stable or increasing; and (ii) its structures and functions,  
7 its quality, and the composition of its characteristic biological communities are such as to ensure  
8 that it remains in a condition which is healthy and not deteriorating;” (Tamar Estuary Marine  
9 Conservation Zones Designation Order, 2013). While specific species are mentioned in many MCZ  
10 ministerial orders, the idea of habitats improving or deteriorating and populations increasing and  
11 decreasing are common throughout.

12 Even in states where marine protected areas have a longer history, the fundamental principles of  
13 systems recovering or not degrading are entrenched in their policy documentation. For example,  
14 New Zealand’s policy and implementation plan for marine protected areas has the following  
15 “desired outcomes for Coastal and Marine Biodiversity in 2020”:

16 “a) New Zealand’s natural marine habitats and ecosystems are maintained in a healthy functioning  
17 state. Degraded marine habitats are recovering. A full range of marine habitats and ecosystems  
18 representative of New Zealand’s marine biodiversity is protected. b) No human-induced extinctions  
19 of marine species within New Zealand’s marine environment have occurred. Rare or threatened  
20 marine species are adequately protected from harvesting and other human threats, enabling them  
21 to recover. c) Marine biodiversity is appreciated, and any harvesting or marine development is done  
22 in an informed, controlled and ecologically sustainable manner. d) No new undesirable introduced  
23 species are established, and threats to indigenous biodiversity from established exotic organisms are  
24 being reduced and controlled” (Department of Conservation and Ministry of Fisheries, 2005).

25 Indeed, while there is much more detail on the comprehensive benefits of networks of MPAs in New  
26 Zealand, the overall goals are still expressed in terms of population increases and decreases.

27 Given the uncertainty in knowledge of marine ecosystems, and the need to adhere to what could be  
28 perceived as ‘crude’ policy and legislation measures, simple predictive models, with an ability to  
29 cope with sparse data and uncertainty are required (Stafford and Gardner, 2013). However, the  
30 predictions of these models can also be modest and still be fit for purpose (for example, predicting  
31 increase or decrease of population sizes). Bayesian Belief Networks are an example of such models,  
32 and have had considerable use in ecological management and in linking ecological and  
33 socioeconomical outcomes (Marcot et al., 2001; McCann et al., 2007; Langmead et al., 2009).

1 It should be noted that nomenclature surrounding Bayesian networks in general is not consistent  
2 between authors. Many Bayesian networks are complex, requiring much data in the form of  
3 parameter distributions for use (Uusitalo, 2007). Classes of Dynamic Bayesian Networks (DBNs) can  
4 use intensive time series data to 'learn' interactions between nodes (or species, in an ecological  
5 context), and cope with feedback loops (e.g. Aderhold et al. 2012; Grzegorzczuk & Husmeier 2013). In  
6 this study we define Bayesian Belief Networks (BBNs) as static networks, which require point  
7 estimates of probabilities, such as those modelled by software such as JavaBayes or Netica. The  
8 advantage of such networks is that expert opinion, especially in the environmental sector, can be  
9 obtained by such point estimates (i.e. a 90% probability of an event happening), but is not easily  
10 obtainable in terms of more abstract 'population distributions' required by many more advanced  
11 Bayesian networks (Uusitalo, 2007). However, such BBNs cannot intuitively account for two way  
12 interactions between species (as may occur from competition, for example; Uusitalo, 2007; Norsys  
13 Software, 2015) reducing their practical value in modelling ecosystem community dynamics (Stafford  
14 et al., 2013; but see Hammond and O'Brian, 2001; Hammond and Ellis, 2002 for examples of top-  
15 down trophic dynamics). While there are often workarounds for incorporating two way interactions  
16 between competing species, these are not intuitive and not generally in common use (see reviews  
17 by Campbell et al. 2012; and Schuchert et al. 2012, for further discussion of these points). Indeed, to  
18 the authors' knowledge, no ecological studies using static Bayesian belief networks (rather than  
19 DBNs) have incorporated feedback loops or interactions between species, and most focus on the  
20 links between community state (as a node) and various socio-economic factors (Campbell et al.,  
21 2012). Where various species or taxonomic or functional groups have been modelled, interactions  
22 between species have not been included explicitly in the model (e.g. Langmead et al., 2009; Allen et  
23 al. 2012).

24 Given the importance of species interactions in creating stable and diverse communities, it is  
25 necessary to consider these interactions when modelling the fate of any given population. In this  
26 study, we present a modified belief network model, based on simple BBNs, and encapsulating much  
27 of the usability of the technique (e.g. point estimates), but capable of simulating trophic and  
28 competitive interactions in ecological communities (by implementing mechanisms for reciprocal  
29 feedback between nodes of the network). Within this study we refer to these models as 'Belief  
30 Networks', as they capture the concept of belief of processes, but are not based solely on Bayesian  
31 inference.

32 The primary objective of this research is to investigate whether the simple belief networks we have  
33 developed can be useful in predicting community dynamics at a level appropriate for

1 implementation as a policy instrument (i.e. indicating the certainty in which simple changes, such as  
2 increase or decrease, in different populations will occur as a result of an intervention). As a  
3 secondary objective, we also examine whether expert opinion can be incorporated in the network,  
4 and determine the significance of 'best guess' expert opinion on the final model predictions.

5 For ease of validation of results, we base our belief network on a rocky shore community in the UK.  
6 We parameterise the network based on estimates of parameters, from our knowledge of the system  
7 and peer-reviewed literature. We also compare many of these estimates to knowledge from marine  
8 ecologists who have not worked in the UK to best replicate knowledge experts may obtain from  
9 similar species in other parts of the world, as may be the case in many poorly studied regions and  
10 marine systems. Finally, we compare the model results to experimentally derived data from real  
11 rocky shores. The results indicate that these belief networks make accurate predictions, and they  
12 naturally and intuitively encapsulate uncertainty in predictions.

## 13 **2. Methods**

### 14 *2.1 Study system*

15 Boulders situated in the mid-intertidal zone (0.7 m to 0.9 m + CD) at Osmington Mill in Dorset UK  
16 (50.636 N, 2.374 W) were selected for the study. A preliminary search of the shore at this tidal level  
17 had indicated the main species present, consisting of primary producers, grazers, filter feeding  
18 barnacles and predatory molluscs (see Table 1 for species considered in this study). Fifteen boulders  
19 of dimensions  $\sim 0.75 \times 0.75 \times 0.75$  m were haphazardly selected at this tidal level. Percentage cover  
20 of live and dead barnacles (dead were determined by presence of empty shells) and seaweeds were  
21 recorded over the entire surface area of the boulder accessible (i.e. the exact area where the  
22 boulders were in physical contact with surrounding rock or sand was not recorded). Numbers of  
23 grazers and predatory dogwhelks were also recorded per boulder.

24 Grazer density was artificially modified on five of the boulders by collecting *Littorina littorea* from a  
25 section of shore > 200 m away from the boulders. Ten *L. littorea* were placed on each of the five  
26 rocks, and sprayed with seawater until crawling on the rock surface (as per Stafford and Davies,  
27 2005). The same procedure was conducted on another five boulders, but by collecting the dogwhelk  
28 *Nucella lapillus* to increase predator density.

29 Rocks were left for 25 days, during April 2014, before revisiting and remeasuring percentage cover  
30 or number of each species present. An increase or decrease in population was determined to occur if  
31 the mean value for each experimental treatment (across all five boulders) had altered by more than  
32 10% from the original value *and* differed by more than 10% over mean changes to control

1 treatments. Unless both of these criteria were fulfilled, we assumed no change in population size of  
2 the species. The value of 10% was based on our evaluation of an important difference in community  
3 structure and for most species corresponded to a 'moderate effect size' based on power calculations  
4 of Cohen (1988), however, the power to detect differences in furoid and *Ulva* cover were slightly  
5 lower than this (Cohen's 'small effect size') due to the high variance of these algae between  
6 boulders.

## 7 *2.2 Belief Network Model*

8 The network is based on Bayesian Belief Networks (reviewed by Grover, 2013; see Hammond and  
9 Ellis, 2002 for an ecological example applied to species interactions), but with several important  
10 differences making the application of the networks much more intuitive for application to species  
11 interactions, especially for the roles of competition and 'bottom up' trophic interactions. Since only  
12 some aspects of the described networks are based on Bayesian inference, the models are referred to  
13 herein as simply belief networks.

14 We implemented the belief network model using Microsoft Excel 2010, with the use of VBA  
15 programming to perform many of the calculations (see supplementary material for the full working  
16 example and details of how to use the network). For each species a 'prior' value between 0 and 1 is  
17 given to indicate the belief that a given species may increase or decrease [ $P(X_i)$  and  $P(X_d)$   
18 respectively]. A species is only ever considered as increasing or decreasing in population size, and  
19 the probability gives a clear indication of the likelihood of this. In this belief network, the sum of the  
20 probability of a species increasing and decreasing must equal 1. Furthermore, if there is no reason to  
21 assume a species will increase (i.e. it was not specifically manipulated in this study - see above), then  
22 the prior probability of increasing equals the prior probability of decreasing, both set at 0.5.

23 The parameters of species interactions are provided in a series of interrelated matrices (see Figure 1  
24 for overview of interactions considered in this study and Table 1 for details of parameters used in  
25 model). Each interaction is independent of any others. For example, top down predation can be  
26 indicated, but bottom up interactions are not automatically required. This use of only top-down  
27 trophic interactions is used in the described simulation, due to predictions being made over a short  
28 time scale of a few weeks, and lack of food is not likely to lead to starvation (e.g. Emerson and Duerr,  
29 1967 only found physiological effects of starvation after 70 days in an intertidal gastropod, not  
30 mortality). However, competitive interactions are two way processes, with reciprocal relationships  
31 between competing species (although these relationships are not always equally weighted, see  
32 below; Figure 1).

1 Each interaction is considered independently of any others (for example, the effect on biofilm of  
2 increased limpet populations is considered independently of the effect on biofilm of increased  
3 periwinkle populations), and complex community interactions or trophic cascade effects are only  
4 emergent properties of the belief network. The belief network draws on four sets of parameters for  
5 each species interaction. The most intuitive beliefs regarding species interactions are shown in Table  
6 1, demonstrating the probability of a species decreasing in population size, given that an interacting  
7 species is increasing in population size. However, the equations used to model species interactions  
8 (see below) require knowledge of:

- 9 1. Probability of species b decreasing, given species a is increasing (parameters in Table 1)
- 10 2. Probability of species b increasing, given species a is increasing
- 11 3. Probability of species b increasing, given species a is decreasing
- 12 4. Probability of species b decreasing, given species a is decreasing

13 In most cases, these are highly related parameters. For example, topshells (*Osilinus lineatus*) have a  
14 probability of decreasing of 0.7, if dogwhelks (*Nucella lapillus*) increase (Table 1). As such, the  
15 probabilities for beliefs relating to this interaction for situations 2,3 and 4 above are 0.3, 0.7 and 0.3  
16 respectively. This may not always be the case, however. For example in the current study, the  
17 authors assumed that an increase in green algae could reduce the coverage of coralline red algae  
18 (probability of coralline algae increasing given green algae is increasing = 0.2; probability of coralline  
19 algae decreasing given green algae is increasing = 0.8), however, if green algae would decrease, then  
20 the slow growing coralline algae would be unlikely to increase over this time scale (probability of  
21 coralline algae increasing with green algae decreasing = 0.5; probability of coralline algae decreasing  
22 with green algae decreasing = 0.5).

23 Given these parameters, intermediate probabilities of each species *increasing* given species  
24 interactions are calculated using the following Bayesian equation:

$$25 \quad P(X_i|Y)=[P(X_i|Y_i)* P(Y_i) + P(X_i|Y_d)* P(Y_d)] \quad ,$$

26 where X is the species under consideration, and Y are the interacting species, subscripts i and d  
27 indicate increasing or decreasing respectively for the species. These values are calculated for each  
28 interacting species.

29 Where there is no knowledge of a change in population of species Y (i.e. the prior probability of  
30 change is 0.5) then this species is not included in the above equation (however, such inclusion might  
31 occur in the second iteration of the model, see below for details).



1 At this point, no 'prior' information on species X is included in the calculation. In traditional Bayesian  
2 belief networks a lack of prior information on any species (or node) results in greater uncertainty  
3 propagating through the network, however, as described in the introduction, for species  
4 interactions, it is often not appropriate for ecologists to predict what will happen to 'un-  
5 manipulated' species, as beliefs about what would be likely to happen are already encapsulated in  
6 the interaction terms of the model. To ensure any prior knowledge available is maintained in the  
7 network, the overall posterior probability for each species is calculated in two ways, the first  
8 ensuring that additional information on species interactions add to the certainty provided by the  
9 prior, the second will ignore prior values, if information on species interactions provide more certain  
10 information than the prior:

11  $1) \text{Post}(X_i) = P(X_i) + |1 - P(X_i)| * [\sum_{1-n} (P(X_i) * (P(X_i|Y)-0.5)) / n] ,$

12 and

13  $2) \text{Post}(X_i) = [\sum_{1-n}(P(X_i|Y))] / n ,$

14 where n is the number of interactions with species X. The final value of Post(X<sub>i</sub>) is given by the value  
15 displaying the most certainty (i.e. furthest in magnitude from 0.5). The model is then repeated for a  
16 second iteration, but with updated prior probabilities such that:

17  $P(X_i) = \text{Post}(X_i) ,$

18 Two iterations of the model are sufficient in this case, since there the maximum number of  
19 connections in the longest food (or other interaction) chain is 2 (a grazer eats a producer, a predator  
20 eats a grazer), but needs to be set to equal this maximum food chain length to account for trophic  
21 cascades.

22 For the current simulation, where an experimental manipulation occurred (increasing the density of  
23 *Littorina littorea* or *Nucella lapillus*), the prior probability of these species increasing was set at 0.9,  
24 and 0.1 for decreasing.

25 Full details of the author generated interactions and interaction strengths used in this study are  
26 provided as supplementary material, as part of the working Excel model. The full VBA code can also  
27 be accessed through this Excel file.

### 28 2.3 Expert Survey

1 A series of questions was presented to marine scientists working in Asian marine science  
2 laboratories, via a web-based questionnaire. Ten participants responded and all worked in marine  
3 ecology, and some on rocky shores, but had no direct experience of working on UK shores, all were  
4 either PhD or postdoctoral researchers (although the targeted audience was not restricted to this  
5 level of experience). The species utilised in this study were shown in photographs but not identified  
6 (i.e. only identified as mollusc 1, seaweed 1 or barnacles). Participants were asked not to identify  
7 species (unless already known) and not to research interactions, but just to use knowledge of similar  
8 organisms to make predictions of what might occur. They were asked to answer a series of  
9 questions following the form of:

10 *The population of Mollusc 1 increases. What will be the direct effect on Seaweed 1?*

11 With multiple choice answers of:

12 Very certain it will increase; Quite certain it will increase; I don't know if it will increase or decrease,  
13 but there will be an interaction; Quite certain it will decrease; Very certain it will decrease; and  
14 There will be no direct interaction between these species.

15 It was clearly specified in the instructions that they should only consider direct (i.e. excluding trophic  
16 cascade effects) and short term (i.e. over 1 month maximum) consequences of the changes  
17 indicated, both from trophic interactions and competition.

18 Due to consideration of survey length, and associated completion rates of surveys (Williams et al.,  
19 2014), not all possible interactions were asked in the survey. However, sub-samples of grazing,  
20 predatory and top-down and bottom up interactions were all considered (Table 1).

21 Answers were converted to interaction strengths using the simple formula of 0.9 for a very certain to  
22 increase response, 0.7 for a quite certain to increase response, 0.5 for a 'don't know' response, 0.3  
23 for a quite certain to decrease response and 0.1 for a very certain to decrease response. If a 'no  
24 interaction' response was given, then it was considered there was no interaction between the  
25 species in the model. Reciprocal arrangements were also assumed – so if a probability of an increase  
26 in a species was 0.1, then the probability of a decrease would be 0.9.

27 The full (deactivated) survey is available at:

28 [http://rickstafford.com/expert\\_survey.html](http://rickstafford.com/expert_survey.html)

### 29 **3. Results**

#### 30 *3.1 Study system*

1 Barnacle, limpet, topshell and seaweed cover were all high on the boulders studied, but with  
2 relatively low populations of dogwhelks and periwinkles (Figure 2). As such, manipulations of these  
3 species greatly increased the percentage of them present in the respective treatments, although it  
4 should be noted that periwinkle abundance was between 20 and 80 % lower on the periwinkle  
5 manipulation treatment boulders after the 25 day period than immediately after the snails had been  
6 added to the boulders (i.e. many had either dislodged or had moved to other boulders). Similarly  
7 while on one boulder all the additional dogwhelks appeared to remain, on some boulders in this  
8 treatment only 4 of the initial 10 dogwhelks could be found (note – dogwhelks and periwinkles were  
9 not marked, so not only density can be measured, not site fidelity of individuals).

10 Nevertheless, density of the manipulated species has clearly increased over control levels (as  
11 defined by the 10% greater than start conditions *and* 10% greater than the end control levels rule  
12 given above). Sites with increased predation (dogwhelk manipulations) showed higher levels of  
13 green seaweeds and lower levels of barnacles, limpets, topshells and coralline algae (Figure 4). Sites  
14 with increased grazing (periwinkle manipulations) showed reduced levels of green seaweeds and of  
15 topshells (Figure 3), using the rule described above. Furoid algae appear to increase in the presence  
16 of dogwhelks, however the percentage increase is small (Figure 3), and although this test had less  
17 power than for other species (see methods), the increase appeared to be largely down to a  
18 measured increase on a single boulder which already demonstrated a high percentage cover of  
19 furoids (a change from 30% to 35%).

### 20 3.2 Expert Survey

21 Four participants from the survey were rocky shore ecologists with experience on Asian shores, but  
22 no direct work on UK shores. The remaining six worked on other aspects of marine ecology, again  
23 with experience outside of Europe and no direct work on UK rocky shores.

24 Data for each question were averaged across all participants (calculation of the mean value).  
25 However, if the majority of responses (the modal average) indicated no interaction between the two  
26 species then this was considered the majority verdict and no interaction was recorded in the model  
27 (Figure 4). Where there were clear 'outliers' in the responses to a question (i.e. the majority had  
28 indicated weak probability but one individual had indicated a very strong probability) these were  
29 removed (corrected data in Figure 4). Outliers in this case consisted of a single response greater than  
30 5 points (on the 1-10 scale) away from the remainder of responses, and were considered to be based  
31 on an incorrect reading of the question, rather than a difference in belief about how the system  
32 worked. The corrected data was in many cases similar to the authors predictions, although generally

1 the survey data were closer to 0.5 than the authors' data were. The major discrepancies were for  
2 questions where the authors felt that given the short time scale, there would be likely to be no  
3 interaction (for example, limpets will only affect barnacle recruitment and are unlikely to have an  
4 effect over the time of the study, or limpet abundance will not affect dogwhelk abundance in the  
5 short term, as it is a bottom up effect). Mean corrected values were subsequently used as some of  
6 the parameters in the belief network.

### 7 *3.3 Belief Network Model*

8 The predictions of the model, using both author derived beliefs and expert survey data, match the  
9 predictions of the experimental manipulations well (Figure 5). The only prediction which was not  
10 broadly correct was that of *Littorina littorea* in the predator increase model, where a decrease in  
11 population size was expected, but an increase was found. However, given the low initial density of *L.*  
12 *littorea* (Figure 3), minor changes in density would cause high percentage changes in population size,  
13 hence this increase could be largely a result of stochastic movement of just a few individuals.

14 The direction of change (increasing or decreasing population size) was largely predicted by the  
15 model, however, the certainty of the predictions (values furthest from 0.5) was highest for trophic  
16 relationships (i.e. greater consumption of green algae with increased grazer density, or consumption  
17 of limpets and barnacles with more predation pressure) than for competitive interactions (Figure 5).  
18 These trophic interactions also displayed the biggest changes in population size in the experimental  
19 data (Figure 3). Hence, certainty of grazing or predatory interactions with probabilities of > 80% from  
20 the simulation (> 0.8 or < 0.2) are the biggest changes which occur in reality.

## 21 **4. Discussion**

22 The belief networks developed make accurate broad scale predictions of community structure, even  
23 when knowledge of the exact interactions between species is uncertain. The encapsulation of  
24 'probability' in the models is also highly intuitive, offering a direct measure of certainty in the  
25 predictions. The models, however, do not make predictions of population size. As such, they could  
26 play an important role in community level management, but would be unsuitable for calculation of  
27 sustainable yields, for example.

28 The strength of a 'belief network' approach is in the intuitive parameterisation. Rather than drawing  
29 directly on hard data, this approach draws on researchers' beliefs (and/or knowledge) about  
30 underlying processes. Researcher's beliefs can be especially important in areas such as species  
31 interactions, where many interactions are known to occur, but are poorly reported in literature. An  
32 example of commonly understood but poorly reported interactions is dogwhelks predating limpets,

1 where such interactions are known and acknowledged to occur (mentioned on numerous websites  
2 and alluded to in published research – e.g. Silva et al., 2008) but rarely quantified (but see Yanes and  
3 Tyler, 2009, who demonstrate that examining drill holes in limpet shells can provide some  
4 quantitative evidence). Competition is another example where researcher’s beliefs are important.  
5 Exact parameters to quantify competition are difficult to articulate mathematically (see example of a  
6 two species biofilm model in Muhammad and Eberl, 2011), but knowledge of the occurrence of  
7 competition on rocky shores is common through manipulative exclusion experiments (e.g. Connell,  
8 1961; 1972; reviewed by Little et al., 2009). However, knowledge of competition in other marine  
9 systems, such as pelagic or demersal fish, is much more difficult to ascertain (e.g. Hixon, 1991;  
10 Jackson et al., 2001), and the application of expert opinion may well be a suitable method for  
11 determining this.

12 While it can be argued that expert opinion can be subjective, this study indicates that opinion is  
13 largely consistent between individuals, and that when averaged with outliers excluded, produce  
14 similar results to values derived from literature (albeit with some subjective interpretation to  
15 convert literature results to ‘parameters’). Furthermore, in our study, participants responded  
16 individually to surveys, where as if they were part of a focus group, it is likely that less divergence in  
17 a set of parameters would be reached (Krueger, 1997; Kidd and Parshall, 2000). Certainly increased  
18 variability in responses through misunderstanding of questions could be eliminated, and discussion  
19 over the exact parameters needed could be further discussed (i.e. in relation to the length of time  
20 the predictions needed to account for, and thus the importance of bottom up effects, which was the  
21 major discrepancy in this study).

22 Even when minor differences occur in parameter values, the overall difference to the most certain  
23 aspects of models are largely unchanged (although not all parameters were defined by the ‘expert’  
24 groups in this study, as participation rates for surveys reduce rapidly with the number of questions  
25 asked). Using the arbitrary 75% confidence level in this study, only the confidence in reduction of  
26 limpets in the presence of dogwhelks differed between the authors’ parameterised model and the  
27 survey data model. One difference, however, was that the average parameter values from the  
28 survey data tended to be closer to 0.5 than the author parameterised models, perhaps indicating the  
29 need for scientists to display more conviction in their beliefs. In this case, participants did not know  
30 exactly how their responses to the questionnaire would be used, and were less familiar with the  
31 community structure than the authors were. However, there is a general, if understudied, consensus  
32 that predictions by scientists tend to be conservative. In statistical terminology, scientists would  
33 rather make predictions resulting in a type 2 error than a type 1 error (Ziliak and McCloskey, 2008;

1 Oreskes and Conway, 2010; Brysse et al., 2013). Considerations around certainty of scientists'  
2 predictions need to be addressed alongside accuracy of predictions if approaches such as belief  
3 networks are to successfully inform policy; indeed, generally scientists can be more confident in  
4 their informed predictions than they are often willing to be (see discussion regarding climate change  
5 in Brysse et al., 2013).

6 The predictions (both by the authors and expert group parameterisations) are also broadly  
7 consistent with observed experimental results. Manipulations of two species (a grazer and a  
8 predator) result in changes occurring over a short time frame (3 weeks) on real shores. A possible  
9 weakness of the experimental results is that the cause of changes (for example, to limpet density, by  
10 increasing competition or predation), cannot be ascertained. For example, limpets may have been  
11 eaten by increased numbers of dogwhelks, or may have moved to neighbouring rocks in response to  
12 greater numbers of predators. However, knowledge of the ultimate cause of population decline or  
13 increase, although preferable, may not be necessary for management of, for example, a marine  
14 protected area. Knowing that an intervention may either increase or decrease a population in the  
15 local area may be enough for successful management. Longer term studies over larger areas than  
16 the 'individual boulder' would also help attribute cause to changes more clearly.

17 The simplicity of the belief network technique, ease of use of the user interface, ability to  
18 encapsulate knowledge from many sources and (at least in this study) reliability of outputs, make it a  
19 useful modelling tool for marine policy decision making, where direct knowledge of population sizes  
20 are not always known or required. The technique is also more intuitive for modelling ecological  
21 community interactions than existing Bayesian Belief Networks (e.g. JavaBayes, see Cozman, 2000),  
22 and the combination of this technique, with further computational methods, may allow for more  
23 complex, finer detail, models of population size to be developed (e.g. Stafford et al., 2013).

24 The study has demonstrated that species interactions can be incorporated easily in these modified  
25 networks, and that parameterisation is relatively easy and differs little between individuals.  
26 However, these results have been verified over small temporal and spatial scales, in a system with  
27 less management concerns than many others. Traditional Bayesian belief networks have been used  
28 successfully to inform policy and management scenarios; for example, the effects of multiple  
29 stressors on the benthic community in the Black Sea (Langmead et al., 2009), or on US freshwater  
30 systems (Allen et al., 2012). However, the ability to incorporate species interactions could be of  
31 value when considering many such scenarios. For example, considerable effort has been put into  
32 developing multispecies fisheries models (MSVPA, SMS, REFS) which are based on trophic  
33 interactions. While such models are not used directly in stock assessments, they can inform fisheries

1 management. The models, however, are data intensive, and have been based on intensive stomach  
2 sampling of commercial fish (Pope, 1991; Magnusson, 1995; Pinnegar and Stafford, 2007). An  
3 approach such as the belief networks identified here would be capable of providing some of the  
4 insights of species interactions in areas where such intensive study has not been undertaken.

5 The real strength of this study, however, is to be able to integrate two way interactions (such as, but  
6 not limited to between species interactions) into a framework which can address wider  
7 management issues. For example, Langmead et al. (2009) provide a Bayesian belief network of  
8 multiple drivers (from pollution to climate change) on the ecosystem health of the Black Sea. The  
9 output of the model is the effect of these drivers on specific functional groups of species (e.g.  
10 phytoplankton, demersal fish). Implementing the techniques proposed in this paper would also  
11 allow for an understanding of how these different functional groups could interact trophically (in both  
12 a top-down and bottom-up manner) or competitively, providing further biological realism to the  
13 model. Equally, simple ecosystem functions (such as fish landed) could be linked to community  
14 models (Stafford and Williams, 2014), where belief networks with reciprocal species interactions  
15 provide the details which ultimately feed into the details of ecosystem services.

16 Currently, policy driven research into conceptual models that link global drivers to specific  
17 ecosystems and then the ecosystems to ecosystem function are being conducted for a number of  
18 different habitat types in the UK marine environment (e.g. Alexander et al. 2014). While traditional  
19 Bayesian belief networks could be used to provide confidence of different effects of drivers, such  
20 models do not explicably demonstrate the details of species interactions. Again, the new technique  
21 makes the incorporation of such biological realism possible, and this may prove to be important on  
22 hard substrate habitat types, where competition for space is known to be strong. Overall, the study  
23 demonstrates that it is possible to provide further biological realism in belief network models, which  
24 can only improve their applicability to management scenarios.

25

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- 7

1

2 Figure 1. Species interaction web. Blue boxes are 'space occupying organisms', red boxes are grazers  
3 and green are predators. Blue arrows represent predatory interactions and green represent grazing  
4 interactions (not one way direction of these interactions creating only top down trophic  
5 interactions). Red arrows represent potential competitive interactions and are bi-directional  
6 (although not necessarily of equal strength).

7 Figure 2. Mean ( $\pm$  S.E.  $n = 15$ ) percentage cover (algae and barnacles) and number of molluscs per  
8 boulder before manipulations.

9 Figure 3. Mean ( $\pm$  S.D.) percentage change in cover (algae and barnacles) and number of molluscs 25  
10 days after manipulations. Horizontal line indicates no change. \* indicates that these are classified as  
11 important differences ( $> 10\%$  change on initial level and on final control level).

12 Figure 4. Interaction strengths as determined collectively by authors, averaged (mean  $\pm$  S.D.) from  
13 online survey, and averaged (mean  $\pm$  S.D.) with outliers removed from online survey.

14 Figure 5. Posterior probabilities of species increasing following the two experimental scenarios of  
15 increasing dogwhelks and littorinids and simulations of these scenarios with author parameterised  
16 models and partially expert survey parameterised models. If experimental values showed  $> 10\%$   
17 increase (as indicated in methods) they are shown with 75% probability of increase and if  $> 10\%$   
18 decrease they are shown as 25% probability of increase to indicate direction of change. Horizontal  
19 lines indicate 75% likelihood of increasing and 25% chance of increasing (or 75% chance of  
20 decreasing).

21

22

1 Table 1. Details of species interactions included in the author parameterised model. Cells with numbers indicate an interaction between the column and  
 2 associated row, grey shaded cells indicate no interaction over the time scale considered. Numbers refer to the probability of the species in the column  
 3 decreasing, given that the species in the row is increasing. For example, the interaction between *Nucella lapillus* and *Osilinus lineatus* indicated in bold  
 4 means that there is a probability of 0.7 that population sizes of *Osilinus* will decrease given that the population size of *Nucella* will increase. Cells with  
 5 asterisks indicate this specific interaction was examined in the expert survey.

6

	<i>Nucella lapillus</i>	<i>Osilinus lineatus</i>	<i>Patella vulgata</i>	<i>Littorina littorea</i>	<i>Chthamalus</i> and <i>Semibalanus</i>	<i>Ulva</i> spp.	Biofilm	<i>Corallina officinalis</i>	<i>Fucus vesiculosus</i>
<i>Nucella lapillus</i>		<b>* 0.7</b>	0.8	0.8	0.9	*			
<i>Osilinus lineatus</i>			0.6	0.6		0.8	0.8		
<i>Patella vulgata</i>	*	* 0.7		* 0.7	*	* 0.9	* 0.9	*	*
<i>Littorina littorea</i>		0.6	0.6			0.9	0.9		
<i>Chthamalus</i> and <i>Semibalanus</i>									
<i>Ulva</i> spp.		*					0.8	0.8	* 0.6
Biofilm									
<i>Corallina officinalis</i>									
<i>Fucus vesiculosus</i>									

7

8

1 Supplementary Material: Microsoft Excel file containing working implementation of the model  
2 described in this paper. The first worksheet – entitled ‘read me’ provides instruction on how the  
3 model works. Note, the model contains VBA code and requires that macros are enabled for it to  
4 perform calculations.

5

Figure1

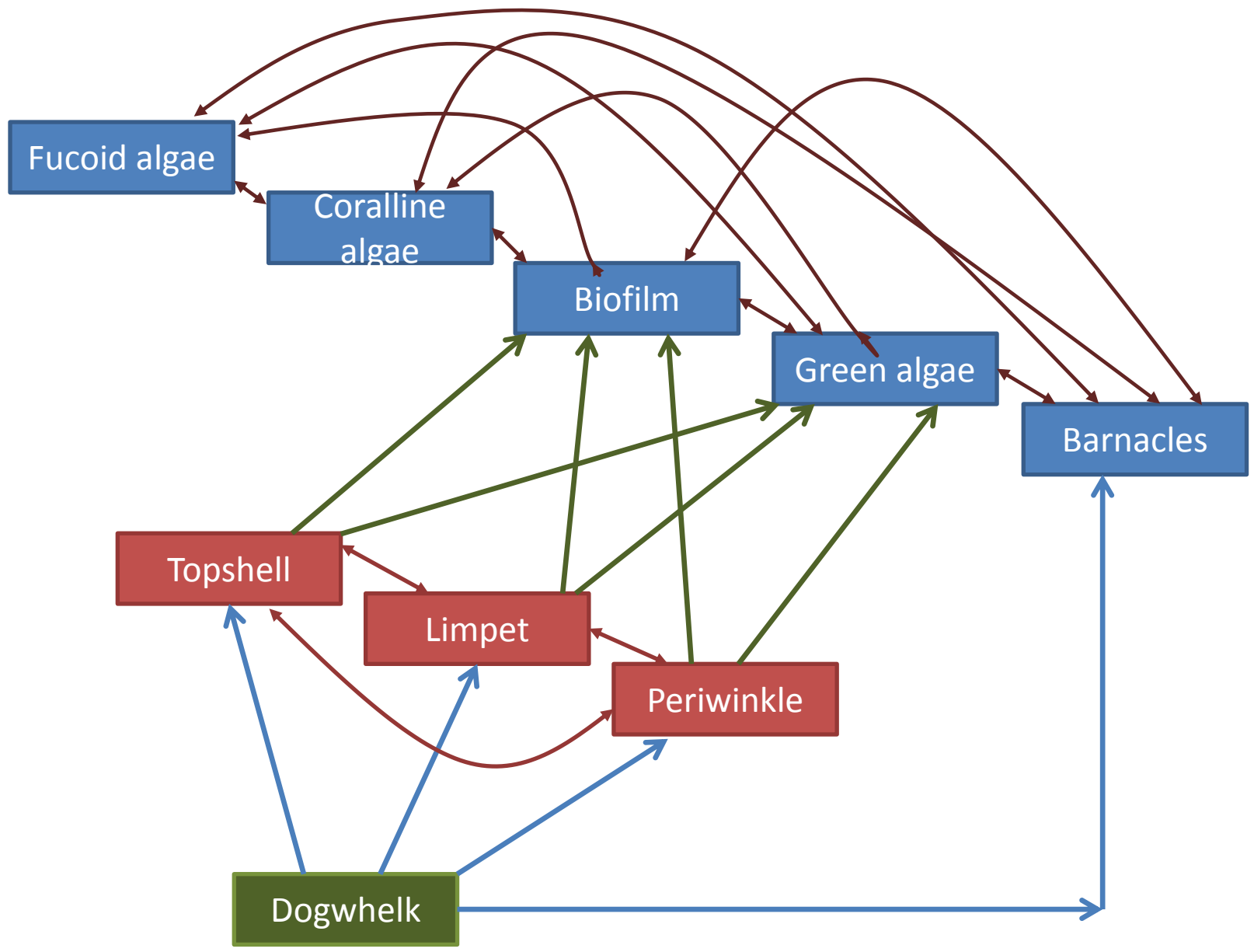




Figure2

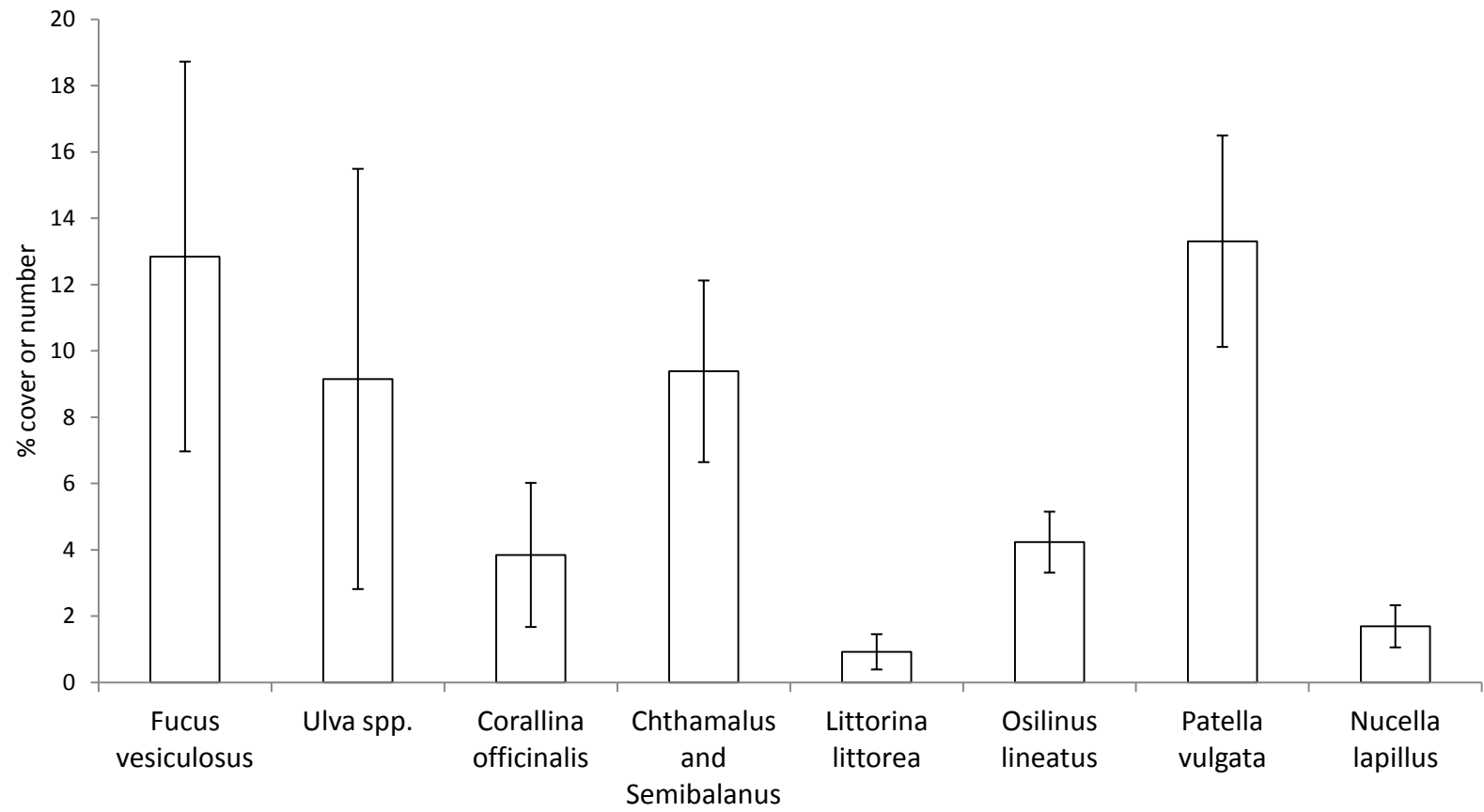


Figure3

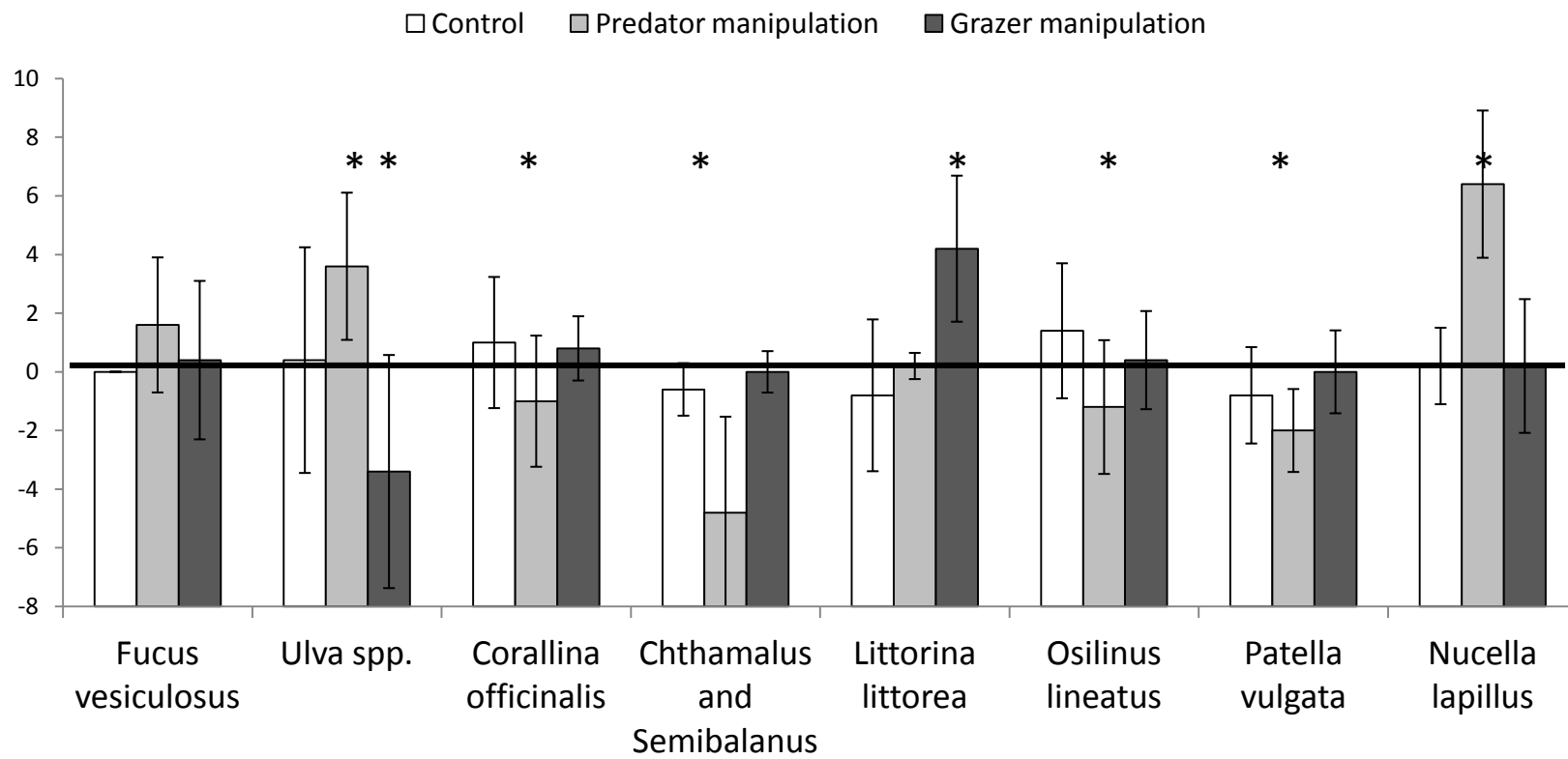
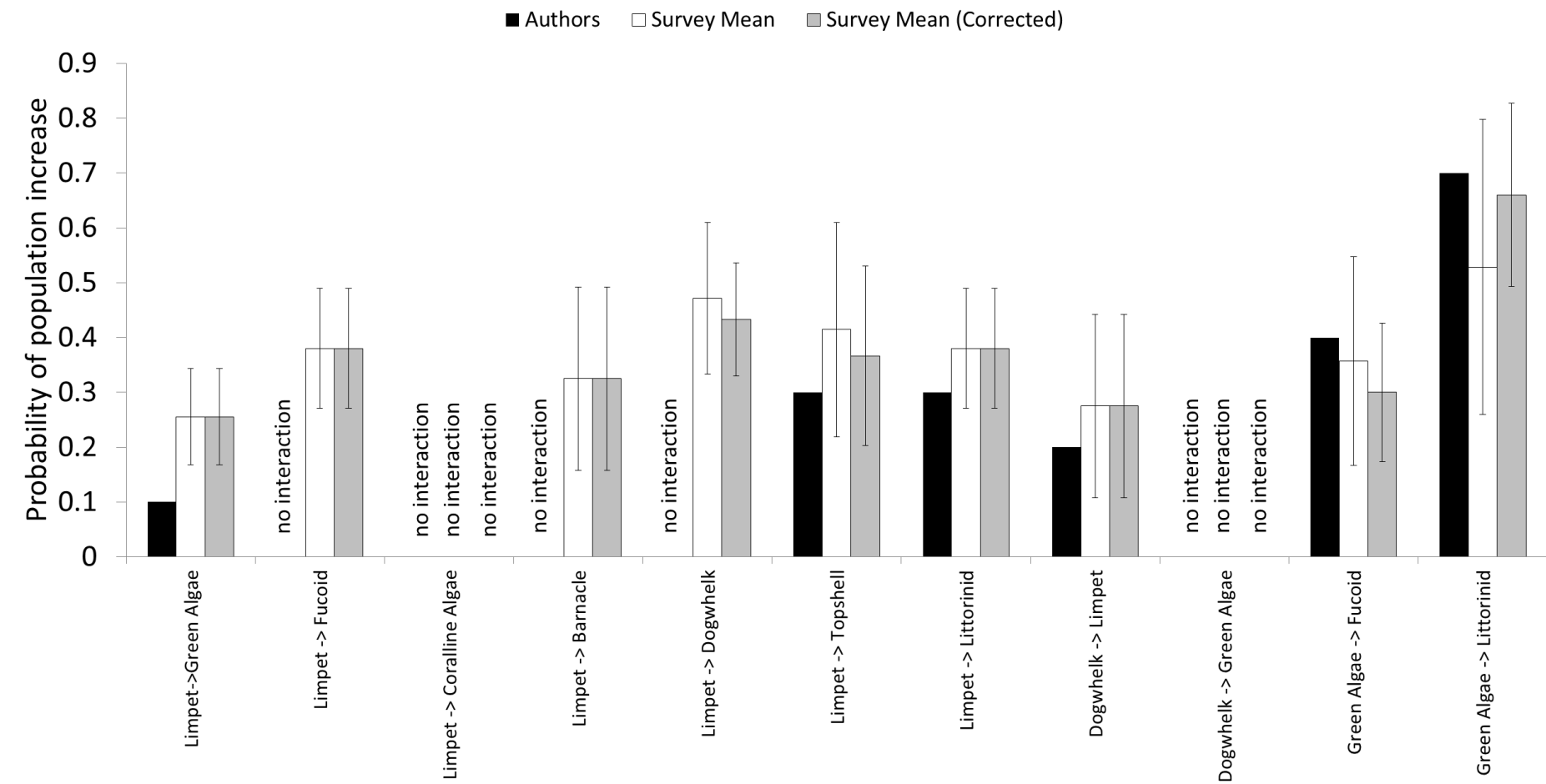
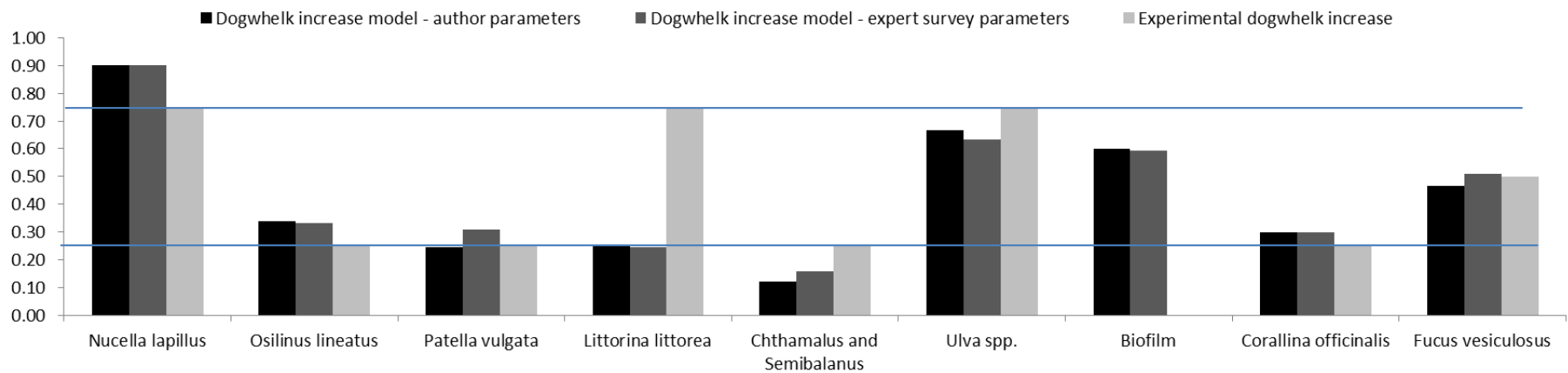


Figure4



**Figure5**

a)



b)

