Potential role of predators on carbon dynamics of marine ecosystems as assessed by a Bayesian belief network

CrossMark

Elisabeth K.A. Spiers [a,1], Richard Stafford [a,b,*,1], Mery Ramirez [b], Douglas F. Vera Izurieta [b], Mariaherminia Cornejo [b], Johnny Chavarria [b]

[a] Centre for Conservation Ecology and Environmental Sustainability, Department of Life and Environmental Sciences, Bournemouth University, Fern Barrow, Poole, UK
[b] Facultad Ciencias del Mar, Universidad Estatal Penisula de Santa Elena, Avda. Principal La Libertad, Santa Elena, Ecuador

ARTICLE INFO

ABSTRACT

While the effects of climate change on top predators are well documented, the role of predation on ecosystem level carbon production is poorly developed, despite it being a logical consequence of trophic dynamics. Trophic cascade effects have shown predator mediated changes in primary production, but we predict that predators should lower the overall biomass capacity of any system with top down control. Through a simple Bayesian belief network model of a typical marine foodweb, we show that predator removal, as is common through activities such as fishing and shark finning, results in higher biomasses of lower trophic level fish and zooplankton, resulting in higher net carbon production by the system. In situations common throughout much of the ocean, where activities such as shark finning and over fishing reduce the highest tropic levels, the probability of net carbon production increasing in the model was ~60%, and unlike previous studies on simple food chains, trophic cascade effects were not present. While the results are preliminary, and sources of uncertainty in data and models are acknowledged, such results provide even more strength to the argument to protect open sea fish stocks, and particularly large predators such as sharks, cetaceans and game fish.

© 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Overfishing has drastically altered almost all marine ecosystems from coastal to open ocean (Darimont et al., 2015; McCauley et al., 2015; Myers and Worm, 2003). The most valuable and targeted fish tend to be highly predatory and of a high trophic level (e.g. tuna, swordfish and marlin), but also cod, haddock, bass and other well-known human food fish are high on the trophic scale (Myers and Worm, 2003). The increase in demand for shark fins has also decimated many species of elasmobranch, often apex predators in marine foodwebs (Ferretti et al., 2010; Stafford et al., 2016). Despite the general focus on high trophic level predators, in some ecosystems almost all fish are targeted (e.g. herring and even sandeel by industrial fisheries – Frederiksen et al., 2004).

Since biomass conversion between trophic levels is inefficient (Linderman, 1942; Pauly and Christensen, 1995), removal of higher trophic levels in a system exhibiting top down control, should logically result in higher levels of biomass at lower levels. Within a foodchain, or simple foodweb, this would lead to a trophic cascade effect (Paine, 1980). However, in more complex systems, where an organism may eat prey from a range of trophic levels, these cascades are not so obvious (Polis and Strong, 1996; Thompson et al., 2007). So, in general, we hypothesise that a removal of many predatory species, as occurs from overfishing, will simply mean an overall increase in prey and as such an overall increase in system biomass.

Given a typical trophic efficiency of 10% (Pauly and Christensen, 1995), this means that removal of a certain biomass of predators could equate to a biomass 10 times bigger than this removed at lower trophic levels. Such a severe level of increase is highly unlikely, because there is likely to be some degree of bottom up control of the foodweb (either ultimately from primary production limitations, or from food limiting population sizes at higher trophic levels) (Menge, 2000; Meserve et al., 2003;). However, there is potential for large increases in biomass of lower trophic levels as a result of predator removal, and overall, increases in biomass in the entire marine ecosystem. Biomass is directly proportional to respiration in a wide range of organisms (Moodley et al., 2008), therefore, increased biomass would lead to increased respiration and therefore increased carbon dioxide production of the oceans.

The ability of predators to influence the carbon production of entire ecosystems has been documented, although focussed on short food chain examples, where trophic cascades will ultimately increase or

* Corresponding author at: Centre for Conservation Ecology and Environmental Sustainability, Department of Life and Environmental Sciences, Bournemouth University, Fern Barrow, Poole, UK.
E-mail address: rstafford@bournemouth.ac.uk (R. Stafford).
[1] EKA Spiers and R Stafford have contributed equally to this manuscript and would like to be considered joint first authors.

decrease the amount of zooplankton and primary producers (Atwood et al., 2013; Estes et al., 2011; Strickland et al., 2013). The length of the foodchain is important in determining whether a net increase or decrease is occurring, with chains with an odd number of links demonstrating increases in predators result in decreases in net carbon production, and those with even links demonstrating increases in predators result in increased carbon production (Atwood et al., 2013). Quantification of the role of predators on carbon release due to prey bioturbating mangrove or salt-marsh sediments and hence releasing captured carbon has also been demonstrated as a secondary effect (Atwood et al., 2015). However, we do not believe that the role of marine predator removal, as per common fisheries practices, on the overall carbon cycle of a complex and interconnected foodweb has previously been examined.

In this study, we test the hypothesis that decreases in predator population sizes typical in most marine communities due to fisheries harvesting (food fish, industrial fish and shark finning) will result in net increases in overall carbon production by these ecosystems.

2. Methods

Estimating biomass in marine ecosystems, as well as size, growth and recruitment of open ocean populations is extremely challenging and full of uncertainty (Pikitch et al., 2004). Furthermore, trophic interactions are highly uncertain, and competitive interactions largely unexplored, other than in experiments on manipulatable systems such as rocky shores (reviewed by Raffaelli and Hawkins, 1996). As such, creating a model of a marine system to examine carbon dynamics must be considered as preliminary work, which will have many uncertainties. This study accepts these limitations, but aims to quantify uncertainty in the structure of the model by using Bayesian belief networks (BBNs). The basic concepts of BBNs are provided below; along with some modifications incorporated in the model used in this study to greater examine ecosystem dynamics effects. Before presenting the specific model used in this study, we also highlight some of the limitations of BBNs.

2.1. An overview of Bayesian belief networks

Bayesian belief networks (BBNs) consist of a series of connected nodes, which have a probability of existing in a number of fixed states. For example, a node could represent the population size of a species, and it could be in two fixed states: *Increasing* or *Decreasing*. The probabilities of both states would sum to 1. Prior probabilities of each state of each node can be defined, for example, if evidence suggested a species was likely to decrease (i.e. a fishery for that species was commencing) then it would be possible to set the prior values accordingly.

Nodes are interconnected by edges. Each edge indicates a certainty and direction that one node may affect another. For example, if species A was connected to species B then it could be specified that; If species A was increasing (with a probability of 1), then it is 80% certain that species B will decrease (probability of 0.8). As absolute certainty (probability of 1) is unlikely, the network uses Bayesian inference to calculate the probability of species B decreasing, given the calculated probability of species A increasing.

Each node in the network in the provided model can be assigned two probabilities. Firstly that the node (i.e. the population of top predators) is increasing, and secondly that it is decreasing. These two probabilities summed to 1. Unless otherwise stated, the prior values of each node were:

$$P_{increase} = P_{decrease} = 0.5 \tag{1}$$

Edges connecting the nodes specify the probability that node being affected by the edge will change with the probability of the edge, assuming the effecting node is increasing with probability of 1. To

determine actual posterior values the following Bayesian equation is applied to determine the probability of the node increasing:

$$P(X_i|Y) = [P(X_i|Y_i)^* \, P(Y_i) + P(X_i|Y_d)^* \, P(Y_d)] \tag{2}$$

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

2.2. Changes and updates to traditional BBNs to help model ecosystem dynamics

Modifications to traditional BBNs allow functionality important to ecosystem dynamics to be incorporated, including: 1) intuitive reciprocal interactions to be included in the network (i.e. as required by interspecific competition or both bottom up and top down tropic interactions). 2) reduced use of prior knowledge. This means only targeted species or groups need to have priors assigned. Non-targeted species, which may be indirectly affected by a change in management practice do not need priors assigned (or more accurately, priors can remain 0.5 for both increasing and decreasing). This avoids 'double accounting' presented in some BBNs, as the belief in what will happen to non-targeted species or nodes will already be incorporated in the probabilities of the network 'edges'. 3) Interactions are considered individually rather than collectively. For example, if both Species A and Species B predate on Species C, the model would only require estimates of Species A on Species C and Species B on Species C, rather than the combined effect of predation. This allows for easier parameterisation of the network from existing data, or less subjectivity if parameters are informed by expert opinion. 4) The BBN is presented in a simple user interface, using Microsoft Excel. Tests have shown that students entering university education are able to build and parameterise these networks using this interface with around 30 min training (Stafford and Williams, 2014). This means the model is transparent and user friendly, and parameters are easy modify for sensitivity analysis. The model (the Excel spreadsheet with underlying VBA code) is provided as supplementary material to this paper, and a fuller description of the mathematics of the changes and updates is given in Stafford et al. (2015).

2.3. Limitations of BBNs for ecosystem studies

The biggest single limitation of BBNs is that they do not readily specify the strength of an interaction. Only the direction of the interaction is specified, along with a probability that this direction is correct. The value of the probability does not correspond to the strength of the interaction, and care must be taken to avoid this interpretation. In this study, we have taken care to examine each possible interaction, and decide whether it is likely to be strong enough to have a direct effect on a neighbouring node. For example, we have taken the decision to remove links between the top three trophic levels of predators and overall respiration and decomposition of the ecosystem. This is despite the fact that these populations will respire and clearly produce CO_2. However, the amount of CO_2 (or the strength or magnitude of this interaction) will be far lower than for the other populations at lower trophic levels, due to the biomass and energy flow through these levels. With a BBN which describes only positive or negative interactions, it is not possible to include these higher tropic level contributions without greatly biasing the output of the model to lower population sizes.

2.4. The marine ecosystem BBN

A BBN of a general marine foodweb was constructed, rather than faithfully trying to replicate an exact system. Importantly, feeding occurred at more than one tropic level for most species (Oeky et al., 2004; Pauly and Christensen, 1995). Major causes of CO_2 production and uptake, including photosynthesis and decomposition were
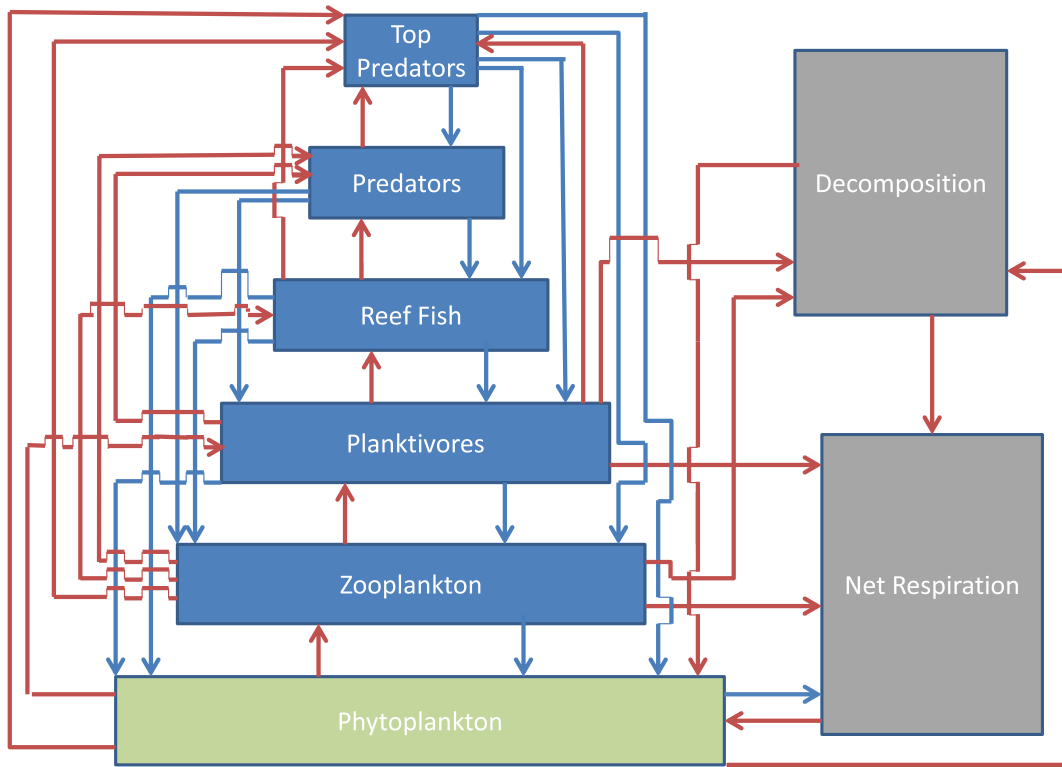
Fig. 1. Structure and interactions incorporated in the BBN. Red lines indicate a positive direct relationship between connected nodes (if the affecting node increases, it will increase the probability of the affected node increasing, and vice versa). Blue lines indicate negative direct relationships (if the affecting node increases, the affected node will decrease, and vice versa). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

included (Atwood et al., 2013; Moore et al., 2004). The structure of the BBN is presented in Fig. 1.

It was assumed that 'top predators' were those which were unlikely to be eaten by natural predators, consisting of larger sharks, game fish such as large tuna and marlin, large grouper and marine mammals, including baleen whales with largely plankton based diets. Predators would consist of could consist of gadoids (e.g. cod, haddock), bass and bream or large snappers and small groupers (depending on the exact geographic location of the ecosystem). Reef fish would comprise small snappers, invertivores, smaller wrasse, angel fish, or smaller demersals such as juvenile gadoids and benthic species such as flatfish. Planktivores would comprise smaller shoaling species such as chromids, or sardines or sandeels depending on the system. Decomposition was considered a process driven by microbes on waste and dead organisms,

and therefore a positive contributor to respiration (e.g. Heimann and Reichstein, 2008), and nutrient flow (Moore et al., 2004).

Parameterisation of the BBN was based in converting data and conclusions from previous research into probabilities. The data, literature and underlying processes used to justify the connections of the model and probabilities of interaction are provided in Appendix A.

To simulate fisheries scenarios, prior probabilities of top predators decreasing, predators decreasing and reef fish decreasing were all set to 0.9, for the different scenarios in the results.

Due to lower biomass, the top three trophic levels were assumed to contribute little to net respiration or decomposition (see limitations section above). Because of this limitation of BBNs to account for magnitude of interactions, they were not connected to the net respiration or decomposition nodes.

Table 1
Parameters of 'edges' in the BBN. The values are for probability the effecting node (indicated by the row of the table) causing an increase on the affected node (the column of the table), given that the node in the row is increasing with p = 1. For example, the first value in the first row is the probability of Predators increasing, given that Top Predators are increasing. The value of Predators decreasing given that Top Predators are increasing is given by p = 1–0.1 = 0.9. No interactions occur for shaded cells.

	Top predators	Predators	Reef fish	Planktivore	Zooplankton	Phytoplankton	Decomposition	Net respiration
Top predators		0.1	0.1	0.4	0.4	0.4		
Predators	0.8		0.1	0.1	0.2			
Reef fish	0.8	0.8		0.3	0.2	0.2		
Planktivore	0.6	0.8	0.8		0.2	0.1	0.6	0.7
Zooplankton	0.6	0.65	0.7	0.7		0.3	0.8	0.9
Phytoplankton	0.6		0.7	0.7	0.9		0.7	0.2
Decomposition						0.7		0.9
Net Respiration						0.6		

Table 2
Results of several fisheries scenarios removing top predators from a marine ecosystem. Red symbols mean that changes to prior values have been made to the BBN (i.e. in terms of different fisheries strategies). Black symbols indicate posterior calculations where prior values were neither likely to show increases or decreases (p = 0.5). Single symbols (+ or -) indicate likelihood of change >50% ≤ 60%. Double symbols (++ or - -) indicate likelihood of change >60% ≤ 70%. Triple symbols (+++ or - - -) indicate likelihood of change >70%. + indicates likelihood of increase, - indicates likelihood of decrease, 0 indicates equal probability of increasing and decreasing.

Scenario	Top predators	Predators	Reef fish	Planktivores	Zooplankton	Phytoplankton	Decomposition	Net respiration
Removal of top predators	---	+++	+++	+	+	+	+	+
Removal of predators	---	---	+++	+++	++	--	+	++
Removal of predators and top predators	---	---	+++	+++	++	+	+	+
Removal of top three trophic levels	---	---	---	+++	+++	++	+	+

3. Results

The BBN was interrogated with a range of typical fishing strategies. Firstly, the removal of predatory fish (i.e. those most commonly targeted for food fisheries) was conducted. Such a response resulted in a probable decline in top predators which relied on the previous trophic level for much of their food. It also resulted in a highly probable increase in the lower two trophic levels of reef fish and planktivores which formed the diet of the predatory and some of the reef fish (Table 2). Feeding on more than a single trophic level prevented clear trophic cascade effects forming, although the ability of some predatory fish to consume zooplankton, but not phytoplankton resulted in zooplankton increasing, and phytoplankton decreasing. Net respiration was likely to increase in this scenario as lower level respiring biomass increased, and photosynthesising biomass decreased. In the same manner, removing only the top predators from the system also demonstrated increased biomass at all other levels (including phytoplankton), and increased levels of decomposition. Again, the net effect was a probable increase in respiration (Table 2).

Scenarios involving removing top predators (i.e. tuna fisheries, shark finning) in addition to typical food fish predators again showed little evidence of simple tropic cascades (Table 2). Again, all lower trophic level groups increased under this scenario, and particularly increases in zooplankton and decomposition resulted in likely increased respiration rates. Similar responses were found using typical fisheries strategies removing reef fish in addition to the two higher tropic levels. In all four tested scenarios, removal of some or all of the higher trophic levels increased biomass at lower levels, and on balance, resulted in a probable outcome of increased respiration and hence CO$_2$ production (Table 2).

4. Discussion

Results support our hypothesis that predator removal (as per common fishing practices) results in higher levels of respiring biomass in the oceans, and ultimately higher levels of CO$_2$ production. The results of this model also show that within complex ecosystems, where species feed on more than one trophic level of prey (i.e. Thompson et al., 2007), trophic cascade effects are less apparent, and increases in one trophic level do not directly lead to decreases at a lower level (as per Polis and Strong, 1996; but see Pace et al., 1999 for alternative views).An example of this is the relationship between zooplankton and phytoplankton, whereby, although these are linked in a predator/prey manner, the results show likely increases or decreases of both simultaneously, with the exception of one scenario. This is most likely a result of the majority of plankton eating organisms eating both phyto- and zooplankton in the model.

The foodweb structure presented here is general for a number of marine ecosystems, and exact interactions may vary and be considerably more complex than depicted, or prey switching may occur if some trophic levels are fully fished. However, given the consistency of results between different fishing scenarios, we predict that predator removal, as is currently occurring in oceans worldwide, will result in an increase in net respiration, due to a higher overall capacity of respiring biomass. While the models do not provide unequivocal proof of increased carbon production, they do provide the foundations and illustrate the urgent need for further, more quantifiable, studies in this area, and certainly highlight previously unconsidered large scale ecosystem effects of human harvesting of marine resources.

While the basis of the theory applies equally to land predators, in the ocean top predators, such as sharks, are being removed at an alarming rate, ecosystems are generally more natural (i.e. much less area is cultivated for agriculture) and food chains are longer (Cohen, 1994).While testing net carbon production of an open ecological system such as a marine pelagic/benthic system would be difficult, the fundamental and well established ecological theory of trophic dynamics supports the hypothesis of carbon mediation by top predators, as presented in the Introduction. The models further support this previously overlooked, but potentially vital role of predators. Overall, this study adds further evidence to the need to conserve large areas of ocean from the effects of fisheries and other harmful activities such as shark finning, which generally target predatory species of fish.

Acknowledgements

Appendix A. Evidence for key interactions in the Bayesian belief network (BBN)

Knowledge of trophic interactions in the marine environment is limited, and despite the long standing acknowledgement of importance of such interactions (e.g. Andersen and Ursin, 1978; Pope, 1975; Pope, 1979). Fisheries science has generally relied on single species stock assessments rather than species interaction models (e.g. MSVPA, Magnusson, 1995; SMS; Lewy and Winther, 2004), despite the large effort of empirical data collection and modelling activities which have gone into their development. These models are also 'top down' approaches, whereby predators effect prey, but prey do not effect predators (i.e. through starvation if they are scarce or by increased growth

rates if they are abundant). The Ecopath modelling framework (Christensen and Pauly, 1992), does consider bottom up processes too. However, lack of direct knowledge on population sizes of fish/plankton, and the trophic relationships between them (see review in Harris et al., 2010) mean that models are 'thermodynamically balanced' either in terms of population sizes which can exist in the system, or in the strengths of interactions between species. While such models can perform well to investigate typical changes in management (for example, see ICES, 2015), large changes, such as large scale removal of predators, as considered in this study, and as has occurred over multiple years of over fishing, may affect the parameterisation and balance of the model cause unrealistic results resulting in systems crashing or behaving chaotically (Stafford and Spiers, 2015).

As such, the BBN approach is highly suited to this uncertain data. Essentially 'best guess' estimates can be used for BBNs with results mimicking both well researched and highly empirically based data and field results (see Stafford and Williams, 2014; Stafford et al., 2015). Although as discussed in the main paper, there are limitations of the BBN approach in understanding the magnitude of interactions and magnitudes of responses to changes.

The following is a review of ecological literature and data that we have used to develop the parameters of the BBN used in this study, and is broken up by the type of interaction.

Establishing trophic connections

Fishbase (Froese and Pauly, 2016) was used to help establish tropic connections in the BBN. From information about trophic levels, in the help file for the Ecology Tables, it stated that a trophic level of 2 was for a pure plant consumer, 3 would be first level animal consumers (i.e. planktivores feeding on zooplankton). Since most fish feed on multiple tropic levels, it is difficult to assign a simple trophic structure to the BBN model, however, Table A1 presents an overview of trophic interactions for a range of species which fit the taxonomic groupings shown in the BBN.

To establish trophic connections, five species thought to correspond to each of the categories provided in the BBN model were selected. The mean and SD were calculated from the information in the Ecology table for the species in Fishbase (back calculating from the SE provided by multiplying by the square root of the number of samples). It was assumed that trophic relationships would be strong within one standard deviation of the mean (although interactions with trophic levels higher or equal to the BBN category being considered were not mapped). Species were selected from a range of different types of marine ecosystem (e.g. open ocean, coastal, tropical, temperate). This table was then used to determine trophic connections in the BBN.

Top down effects of predation

Top down effects of predation result in predators reducing population sizes of prey. These are probably the most well studied and quantified interactions in the model (reviewed by Magnusson, 1995), and much work, especially in terms of consumption of non-plankton based food sources has been conducted using fish stomach analysis (ICES, 1987, 1992), and stable isotopes (Peterson and Fry, 1987). Where trophic connections were apparent (Table 1A), these links were added to the BBN using the following probabilities, whereby if the node was increasing in population size, the effected node would be likely to decrease with the probability defined.

Four or five example species in Table 1A eating a particular tropic level, 0.9, three example species = 0.8, two example species = 0.7, one example species = 0.6.

Bottom up effects of prey availability

As indicated above, far fewer studies have quantified the effects of bottom up production (essentially growth and survival of a population being food dependent). However, some studies have demonstrated the link can be extremely strong (e.g. Ware and Thomson, 2005). Frank et al. (2007) review the literature on bottom up control of marine ecosystems, and conclude that while it is likely to occur, the strength and importance is spatially and temporally variable. As such, we use the same trophic interactions, but apply slightly less confidence to the results, so for a prey node which is increasing, the probability of the predator node increasing would be:

Four or five example species in Table 1A feeding on a particular tropic level = 0.8, three example species = 0.7, two example species = 0.65, one example species = 0.6.

Plankton dynamics

Unlike other trophic dynamics discussed above, the linkage between zoo- and phytoplankton is more clear. Zooplankton generally feed exclusively on phytoplankton (and other zooplankton species), so the

Table A1

Trophic relationships between nodes in the BBN. Examples of each category of living organism in the BBN (excluding plankton) were selected from the Fishbase database. Crosses indicate which categories each species may consume, based on the mean ± one standard deviation. Only trophic relationships below the category under consideration are highlighted.

BBN category	Species	Trophic level	SD	Predators (4.5–5)	Reef_fish (4–4.5)	Plankti-vores (3.5–4)	Zoo-plankton (3–3.5)	Phyto-plankton (2–3)
Top predator	Great white shark	4.67	0.37	x	x			
Top predator	Tiger Shark	4.63	0.51	x	x			
Top predator	Blue fin tuna	4.50	0.63	x	x	x		
Top predator	Basking shark	3.20	0.3				x	x
Top Predator	Marlin	4.50	0.41	x	x			
Predator	Cod	4.10	0.40		x	x		
Predator	Skipjack tuna	4.43	0.40		x	x		
Predator	Red Snapper	4.48	0.76		x	x	x	
Predator	Whiting	4.36	0.70		x	x	x	
Predator	Nassau grouper	4.00	0.67		x	x	x	
Reef fish	Clownfish	3.03	0.45				x	x
Reef fish	Blue whiting	3.93	1.09			x	x	
Reef fish	Dusky Parrotfish	2.00	0.00					x
Reef fish	Angelfish	3.10	0.19				x	x
Reef fish	Flounder	3.50	0.37			x	x	
Planktivore	Chromis	2.50	0.16					x
Planktivore	Sandeel	3.01	0.10				x	x
Planktivore	Pilchard	3.06	0.10				x	x
Planktivore	Sprat	3.01	0.07				x	x
Planktivore	Sardine (tropical)	2.69	0.30					x

nature of the linkage is well established. However, the population level effects are less well documented, and have some debate in the literature (reviewed by Paerl and Justic, 2011). In general, bottom up effects are more accepted than top down grazing, although both are thought likely to occur in many situations. As such, an increase in phytoplankton will result in a 0.9 probability of an increase in zooplankton, but an increase in zooplankton will lead to a 0.3 probability of an increase in phytoplankton (or a 0.7 probability of a decrease in phytoplankton).

Decomposition

As living organisms die, they breakdown into organic matter, in a process controlled by various microbes and fungi (Heimann and Reichstein, 2008). This process results in respiration (Heimann and Reichstein, 2008), but also the recycling of organic matter into the system, especially important in the growth of primary producers (e.g. Moore et al., 2004). However, two factors preclude high certainty of these processes. Firstly, dead organisms can form a carbon sink, falling through the water column (in oceanic environments) to remain undecomposed in the deep benthos (ref). Secondly, events such as upwelling, or breakdown of thermo- or halo-clines can create nutrient rich waters, easily diluting any effects of nutrient availability through decomposition. As such, a 0.9 probability was assigned to increased respiration if decomposition increased, with 0.7, 0.8 and 0.6 probability of decomposition increasing defined to each of the trophic levels of phytoplankton, zooplankton and planktivores respectively,if their population sizes increased. These lower and differing probabilities account for potential uncertainty in the fate of the organic material and the different standing biomasses of the trophic levels (with zooplankton having the highest standing biomass (Gasol et al., 1997) - see also main paper for justification of removing higher trophic level links to decomposition from the BBN). The connection between decomposition (increasing) and phytoplankton (increasing) was defined as 0.7, to account for seasonal, weather and upwelling processes, which would mask the effects of decomposition.

Net respiration

There are four inputs to net respiration in the model – from the lower three trophic nodes, and from decomposition (described above and probability assigned). The higher levels are not connected to the respiration node, as the lower biomass would increase uncertainty over what might happen in the model (see main paper). Other than decomposing, phytoplankton, during daylight, photosynthesise and reduce CO_2 levels. Zooplankton and planktivores respire and release CO_2. Respiration is proportional to biomass (Moodley et al., 2008), and as such, probabilities are allocated in the same way. The following probabilities account for differences in biomass of each level, and if the trophic level increases, the probability of respiration increasing is 0.2, 0.9 and 0.7 respectively for phytoplankton (which will reduce CO_2), zooplankton (the highest standing stock level - Gasol et al., 1997), and planktivores respectively.

Appendix B. Supplementary data

A Microsoft Excel file containing the full working Bayesian belief network described in this study, including all parameter values used and all VBA source code (as a macro for the 'calculate' button). Supplementary data to this article can be found online at doi:10.1016/j.ecoinf.2016.10.003.

References

Andersen, K.P., Ursin, E., 1978. A multispecies analysis of the effects of variations of effort upon stock composition of eleven North Sea fish stocks. Rapports et Procés-Verbaux des Réunions, Conseil International pour l'Exploration de la Mer 172, 286–291.

Atwood, T.B., Hammill, E., Greig, H.S., Kratina, P., Shurin, J.B., Srivastava, D.S., Richardson, J.S., 2013. Predator-induced reduction of freshwater carbon dioxide emissions. Nat. Geosci. 6, 191–194.

Atwood, T.B., Connolly, R.M., Ritchie, E.G., Lovelock, C.E., Heithaus, M.R., Hays, G.C., et al., 2015. Predators help protect carbon stocks in blue carbon ecosystems. Nat. Clim. Chang. 5, 1038–1045.

Christensen, V., Pauly, D., 1992. Ecopath II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169–185.

Cohen, J.E., 1994. Marine and continental food webs: three paradoxes? Philos. Trans. R. Soc. B 343, 57–69.

Darimont, C.T., Fox, C.M., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. Science 349, 858–860.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., et al., 2011. Trophic downgrading of planet earth. Science 333, 301–306.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol. Lett. 13, 1055–1071.

Frank, K.T., Petrie, B., Shackell, N.L., 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends Ecol. Evol. 22, 236–242.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P., Wilson, L.J., 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J. Appl. Ecol. 41, 1129–1139.

Froese, R. and Pauly D. 2016. FishBase. Version (06/2016). www.fishbase.org

Gasol, J.M., del Giorgio, P.A., Duarte, C.M., 1997. Biomass distribution in marine planktonic communities. Limnol. Oceanogr. 42, 1353–1363.

Harris, R.P., Buckley, L.J., Campbell, R., et al., 2010. Dynamics of marine ecosystems: observation and experimentation. In: Barange, M., Field, J., Harris, R., Hofmann, E., Perry, R.I., Werner, F. (Eds.), Marine Ecosystems and Global Change. Oxford University Press, Oxford, pp. 129–178.

Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451, 289–292.

ICES, 1987. Report of the ICES Advisory Committee on Marine Pollution, 1986. Cooperative Research Report, International Council for the Exploration of the Sea, 142. ICES, Copenhagen.

ICES, 1992. Report of the ICES Advisory Committee on Marine Pollution, 1992. ICES Cooperative Research Report, 190. ICES, Copenhagen.

ICES, 2015. Report of the Working Group on Multispecies Assessment Methods (WGSAM). ICES CM 2015/SSGEPI:20. ICES, Copenhagen.

Lewy, P., Winther, M., 2004. Modelling stochastic age-length-structured multi-species stock dynamics. ICES C.M. 2004 FF:20. ICES, Copenhagen.

Linderman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.

Magnusson, K.G., 1995. An overview of the multispecies VPA – theory and applications. Rev. Fish Biol. Fish. 5, 195–212.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. Science 347, 247–255.

Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. J. Exp. Mar. Biol. Ecol. 250, 257–289.

Meserve, P.L., Kelt, D.A., Milstead, W.B., Gutierrez, J.R., 2003. Thirteen years of shifting top-down and bottom-up control. Bioscience 53, 633–646.

Moodley, L., Steyaert, M., Epping, E., Middelburg, J.J., Vincx, M., van Avesaath, P., et al., 2008. Biomass-specific respiration rates of benthic meiofauna: demonstrating a novel oxygen micro-respiration system. J. Exp. Mar. Biol. Ecol. 357, 41–47.

Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C., Dong, Q., Hastings, A., et al., 2004. Detritus, trophic dynamics and biodiversity. Ecol. Lett. 7, 584–600.

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423, 280–283.

Oeky, T.A., Banks, S., Born, A.F., Bustamante, R.H., Clavopina, M., Edgar, G.J., et al., 2004. A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol. Model. 172, 383–401.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades relieved in diverse ecosystems. Trends Ecol. Evol. 14, 483–488.

Paerl, H.W., Justic, D., 2011. Primary producers: phytoplankton ecology and trophic dynamics in coastal waters. Treatise on Estuarine and Coastal Science 6, 23–42.

Paine, R.T., 1980. Food webs: linkage, interaction strength, and community infrastructure. J. Anim. Ecol. 49, 667–685.

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320.

Pikitch, E., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., et al., 2004. Ecosystem-based fishery management. Science 305, 346–347.

Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. Am. Nat. 147, 813–846.

Pope, J.G., 1975. The effect of biological interaction on the theory of mixed fisheries. International Commission Northwest Atlantic Fisheries Selected Papers 1975, 157–162.

Pope, J.G., 1979. A modified cohort analysis in which constant mortality is replaced by estimates of predation levels. ICES CM 1979/H:16. ICES, Copenhagen.

Raffaelli, D., Hawkins, S.J., 1996. Intertidal Ecology. Springer, Berlin.

Stafford, R., Spiers, E.K.A., 2015. Predators reduce carbon production in multi-trophic level marine ecosystems. British Ecological Society Annual Meeting, Edinburgh.

Stafford, R., Williams, R.L., 2014. Teaching basic numeracy, predictive models and socio-economics to marine ecologists through Bayesian belief networks. F1000Research 3, 312.

Stafford, R., Williams, R.L., Herbert, R.J.H., 2015. Simple, policy friendly, ecological interaction models from uncertain data and expert opinion. Ocean Coast. Manag. 118, 88–96.

Stafford, R., Clitherow, T.J., Howlett, S.J., Spiers, E.K.A., Williams, R.L., Yaselga, B., Zeas, V.S., Vera Izurieta, D.F., Cornejo, M., 2016. An integrated evaluation of potential

management processes on marine reserves in continental Ecuador based on a Bayesian belief network model. Ocean Coast. Manag. 121, 60–69.

Strickland, M.S., Hawlena, D., Reese, A., Bradford, M.A., Schmitz, O.J., 2013. Trophic cascade alters ecosystem carbon exchange. Proc. Natl. Acad. Sci. 110, 11035–11038.

Thompson, R.M., Hemberg, M., Starzomski, B.M., Shurin, J.B., 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88, 612–617.

Ware, D.M., Thomson, R.E., 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science 308, 1280–1284.