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

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A B S T R A C T

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.

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

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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:

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

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 ofthe 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 highertropic 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