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Comparison of outputs based on three different modelling approaches for the response of an intertidal ecosystem to climate change.

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Abstract: Three simple ecosystem models were developed to provide an understanding of how the choice of ecosystem modelling approach influences conclusions. The first ecosystem model is based on functional (biomass-flux) interactions, the second ecosystem model is based on Lotka-Volterra interactions and the third ecosystem model is based on a goal-orientated approach. All modelled the response of a rocky intertidal ecosystem to climate change. Each type of model has been shown to lead to different conclusions when considering change in the abiotic environment. This highlights the importance of using models based on different perspectives to gain a more complete insight in to the response of ecosystems to climate change.

Keywords: ecosystem model comparison intertidal climate change

1 Introduction

An ecosystem is never fully represented in a model. Each modelling approach has particular phenomena that it describes well. For example when a process based modelling approach is used to model an ecosystem it usually focuses on the flow of individuals or biomass from one state variable to the next. This is convenient when the individuals of the species being modelled are of commercial interest (Bald, 2006; Bald 2009) or the biomass represents an environmentally important element that needs to be tracked through the system. Instead of focusing on the flow of material from one state variable to another, Lotka-Volterra models focus on how each state variable influences each other by strength of interaction (Emmerson and Raffaelli, 2004), although this interaction in some models may represent implicitly flow of material, it does not account fully for the loss of material from one state variable to another (Jørgensen and Bendoricchio, 2001). A more novel modelling approach focuses on modelling ecosystem properties to project the future state of an ecosystem undergoing change. The most obvious properties are acclimatization, adaptation and succession. Such properties are usually modelled by using a goal-orientated approach, in which the goal is to choose the best model structure or parameter values for the prevailing environmental conditions. This approach is detailed in Jørgensen (1992).

Climate change is causing changes in many environmental variables that influence the dynamics of the intertidal zone. Changes in environmental variables such as temperature (Poloczanska et al., 2008; Menge et al., 2008; Hiscock et al., 2004), storminess (Hawkins et al., 2009; Poloczanska et al., 2008 Kendall et al., 2004),

salinity (Przeslawski et al., 2005) and pH (Guinotte and Fabry, 2008; Harley, 2006) impact directly on individuals of a species and therefore on their role in ecosystem processes. To contemplate the importance of which modelling approach to use to study the response of the rocky intertidal ecosystem to climate change, separate ecosystem models were developed based on each and the outputs compared.

2 Method and Models

2.1 Method

The outputs from the models were compared with intertidal data from Bishop (2003), and for this comparison to be valid the model output had to be representative of the same intertidal area as was monitored by Bishop. Bishop's data are from the area on the intertidal zone between mean high-water-neap-tide level to the mean low-water-neap-tide level. This meant that the state variables of the model needed to output values that reflect the average spatial ecosystem state of this area. The influence of climate change on the ecosystem was represented via forcing functions in the model. The environmental and physiological attributes of each functional group were represented by the most well known species of each functional group. The most well known species are those of the functional group that have the most information (available from www.marlin.ac.uk/biotic/) to describe the population dynamics and the environmental attributes of the species.

To check each model approach the output was verified against Bishop's data. The state variables represent the community structure of the rocky intertidal ecosystem. This required generalizing the amount of species on the rocky intertidal zone in to functional groups. According to Jax (2010) sorting the multitude of species into functional groups provides adequate resolution to model functional responses and is also a way to reduce the number of state variables that would be needed to be described if considering individual species. The rocky intertidal community may be categorized in to four functional groups: *plant* (primary producer), *grazer* (primary consumer), *predator* (secondary consumer) and *filter feeder* (decomposer/primary consumer) (Bishop, 2003; Boaventura et al., 1999; Little and Kitching, 1996).

Each model was verified by running the model under conditions where the response is known. The sensitivity of the model was determined by quantifying the change caused in the state variables due to changes in each of its parameters and initial values and environmental variables. The parameter sensitivity is defined as the percentage changed of the state variable (ΔS) with respect to the percentage change of the parameter (ΔP).

$$\text{parameter sensitivity} = \frac{\Delta S}{\Delta P} \quad (\text{Jørgensen and Bendoricchio, 2001})$$

The time-step for the model was chosen as one day, which initially appears very small considering that the influence of climate change is a long term process. A time-step of a year or a month was considered, but the problem with this, is that it failed to capture the variability of the weather from day to day, when daily maxima and minima can have a significant influence on living organisms. It is important to capture this daily variability and for this reason a time-step of one day was chosen. The simulations were numerically solved in Matlab using Runge-kutta 4 (ode23 method in Matlab). There simulations were run for each model described. The first simulation was forced by temperature, the second simulation was forced by storminess and the third simulation was forced by both temperature and storminess combined.

2.2 Models

Model 1 (Biomass-flux model)

In the first model the interaction between functional groups was represented by biomass-flux interactions. A biomass-flux interaction is the flow of biomass from

conditions as demonstrated by evolution. The goal function allows parameters, which describe environmental physiological attributes, to vary. The parameter which varies due to the goal function in our model is the growth rate of each functional group via the assimilation efficiency.

2.3 Simulations

Temperature

The first simulation run for each model was forced by temperature. Temperature has an optimum influence. An increase in temperature will increase the growth rate due to higher metabolism but once the temperature goes past a certain value any increase will decrease the growth rate due to temperature stress. The influence of temperature is defined by an optimum function described in Jorgensen and Bendricchio (2001) as;

$$f(T) = \exp\left(-2.3 \times \frac{T - \text{opt}T}{T_x - \text{opt}T}\right)^2 \quad (2)$$

where T is air temperature, optT is the optimum air temperature for growth, Tx is the minimum air temperature in which growth can occur if T is less than optT otherwise Tx is the maximum air temperature in which growth can occur. To estimate the value of these parameters, the geographical distribution of the representative species of each functional group was used. According to Southward (1958) the sensitivity of a species to temperature change is related to the geographical distribution. Here, the geographical distribution is the area of the western European coast in which the species can be found. The geographical distribution covers the range from the warmest to the coldest places where the species occurs. It is assumed that the average air temperature of the northern extent of the geographical distribution is the value of the parameter, maximum air temperature, used in the temperature function. It is also assumed that the average air temperature of the southern extent of the geographical distribution is the value of the parameter, minimum air temperature, used in the temperature function.

Storminess

The second simulation run for each model was forced by storminess. Waves move at about the same speed as the wind which creates them (Mollison, 1985), so it was assumed that the wave speed is equal to the wind speed. Wind speed was used then to represent the increase in storminess predicted as a result of climate change. Each functional group can withstand a certain velocity of wave speed which in the model requires a parameter to describe the wind speed at which the functional group begins to loose biomass. In the model an increase in wind speed causes a reduction in growth. The storminess parameters were deduced for each functional group from the preferred range of water flow speed conditions outlined in www.marlin.ac.uk/biotic/.

Combined influence of environmental variables

The third simulation run for each model was forced by both temperature and storminess. The combined influence is an average of both.

3 Results

For Model 1, the outputs showed a decrease in the *filter* feeding functional group over 100 years with increased temperature, where as with increased storminess there is a decrease in the *plant* functional group. As shown in Figure 3, when change in both environmental variables are considered all functional groups collapse during the 100 year simulation runs.

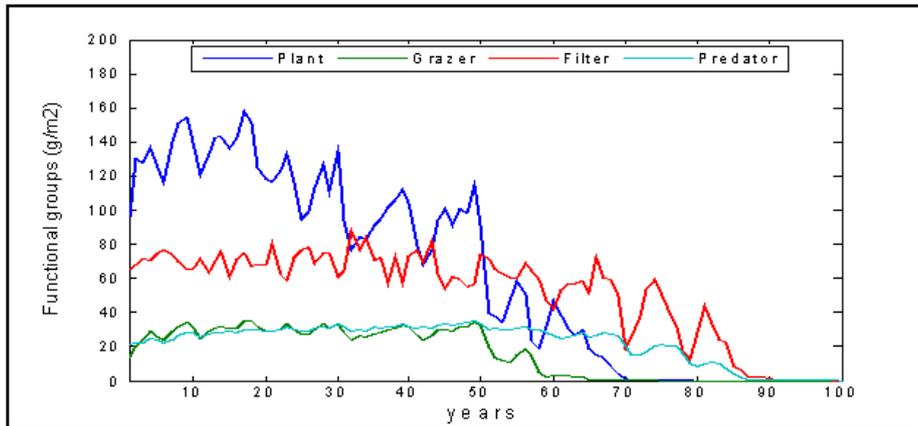


Figure 3. Output of Model 1 with the influence of temperature and storminess.

For Model 2, the output was similar to Model 1 for temperature and storminess in isolation. But Figure 4 shows when both environmental variables are combined the functional groups did not collapse completely as in Model 1 but were significantly reduced. This means that the inclusion of inhibition and facilitation interactions gives stability when the biomass densities are low.

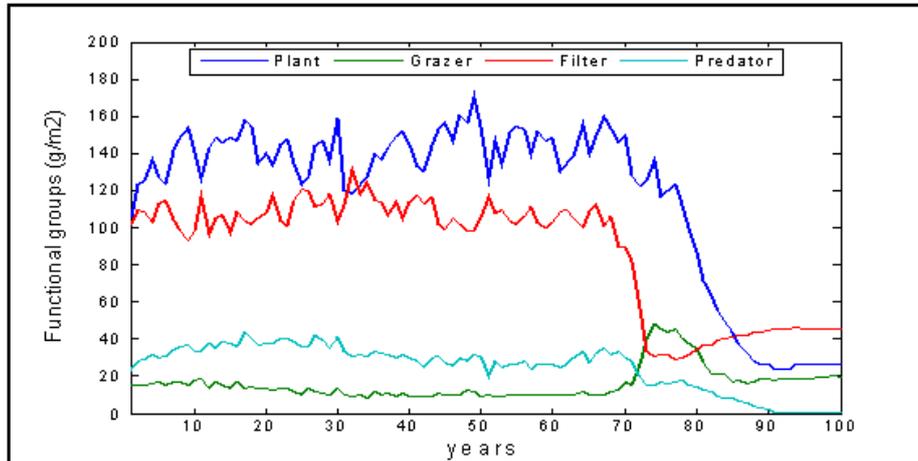


Figure 4. Output of Model 2 with the influence of temperature and storminess.

For Model 3, the output was similar to Model 1 and Model 2 for temperature and storminess in isolation. But Figure 5 shows when both environmental variables are combined the functional groups do not decrease as in Model 1 and Model 2, but instead the biomass densities of the functional groups remain relatively constant. This means that the inclusion of adaptation in the model gives greater stability of all functional groups.

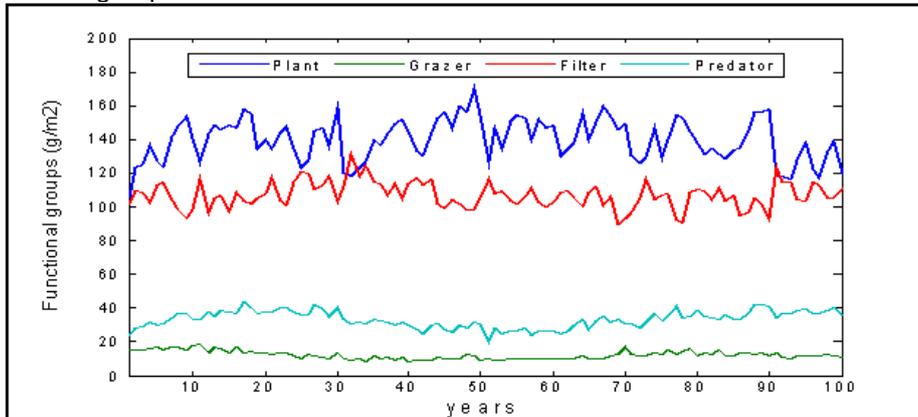


Figure 5. Output of Model 3 with the influence of temperature and storminess.

4 Discussion

In modeling today there are many modeling approaches and models to choose for any ecosystem modelling task. Jorgensen et al. (2010) describe 16 different modelling approaches. Increase in computer speed and memory is a factor in the amount of modeling approaches available in recent years. Before the availability of computer power, modeling in ecology was mainly concerned with interactions between a few species or the distribution of species within a community as discussed by Giller (1984). The aim of this paper was to see how taking different approaches influences the conclusions reached.

Three simulations were run for each model described. The outputs from the temperature and the storminess simulation were similar for all three models. It was when the combined influence of temperature and storminess was considered that the models gave different outputs. As shown in Figure 3, when change in both environmental variables are run in Model 1 all functional groups collapse during the 100 year simulation runs. As shown in Figure 4, when change in both environmental variables are run in Model 2 all functional groups are significantly reduced but did not collapse. And as shown in Figure 5 when change in both environmental variables are run in Model 3 the functional groups do not decrease as in Model 1 and Model 2, but instead the biomass densities of the functional groups remain relatively constant. This means that the inclusion of adaptation in the model gives greater stability to all functional groups and that the inhibition and facilitation interactions provide stability at low biomass densities which may be due a regulation affect reducing the cascade through the functional groups via the biomass flux interactions.

Adaptation allowed the ecosystem model to be more resilient by giving the ecosystem model the ability to find a solution to the environmental change. This suggests that adaptation may be a very influential stabilizing system behaviour when considering the influence of climate change. With adaptation our model suggests that the ecosystem is capable of remaining functionally intact in which the species composition of functional group changes but not the biomass density of the functional groups. The change in species composition within functional groups is reflected in Model 3 by the change in the values found for the growth rate parameter through the simulation runs. Change in species composition is the same conclusion as for the MarClim project (Miezkowska et al., 2006). The MarClim project investigated the effect of climate warming on the rocky intertidal ecosystem in the UK and Ireland. It provided evidence that recent warming resulted in changes in species composition (Miezkowska et al., 2006).

The mathematical equations used for the three models described are usually part of the modelling methodology where a generic form of the equations are fitted to the data and not inferred from the data. This is completely opposite to models developed from equations inferred from the data using automated techniques, as with artificial neural networks (Park et al., 2003). Such techniques may be more objective since preferred mathematical equations are not compulsory but have the disadvantage of requiring more detailed data.

Detailed data are not available for most ecosystems at present and to describe the dynamics of these ecosystems it is better to use the better known equations as in the models used for our comparison. Although there are some good time series data for components of ecosystems there is considerable gap in the ecological literature of how change in an environmental variable affects the performance of organisms. More empirical work is needed on how change in environmental variables affects the performance of an organism; such information would provide a valuable contribution to modelling how an ecosystem will respond to climate change.

The difference between Model 3 and Model 2 is that the growth rate parameter is constant in Model 2 where as it can change value in Model 3. The change in the value is dependent on the parameter set which provides the highest eco-exergy after 10 years, in which the highest eco-exergy is the goal of the goal function. By having a goal does not assume an ecosystem has an intrinsic purpose but it is a useful technique to model ecosystem adaptation. The change in parameter value may reflect acclimatization or adaptation of the functional group depending on the amount of change and the functional group considered. Model 1 has constant parameters for its biomass flux interactions. The biomass flux interactions means that change in biomass density of one functional group directly impacts functional groups it interacts with, such interactions are usually the mechanism of trophic cascades in ecosystems. Model 1 does not represent inhibition or facilitation interaction as in Model 2 or Model 3. These interactions have a regulatory affect because these have a significant impact at either very low or very high biomass densities and so encourage a low biomass density to increase or a high biomass density to decrease. Sometimes inhibition or facilitation interactions are not considered because it is difficult to find empirically values and therefore qualitative assumptions are needed.

5 Conclusions

Each type of model captures different processes of the ecosystem, which have been shown to lead to different model outputs when considering change in the abiotic environment due to climate change. This highlights the importance of choosing the appropriate type of model to capture the processes which are important and also highlights the importance of considering a number of modeling approaches to gain a deeper understanding to how ecosystems will respond when faced with change in the environment.

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