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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 et al., 2006; Bald et al., 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 Raffaeli, 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) [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). Three simulations were run for each model described. The first simulation was forced by temperature, the second simulation was forced be storminess and the third simulation was forced by both temperature and storminess combined.

2.2 Models

Model 1: 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 one functional group to another. The biomass-flux interaction between functional groups have the general mathematical expression:

$$\text{Biomass flux} = \text{state variable} \times \text{average flux rate} \times f(\text{environment}) \tag{1}$$

where f(environment) represents a function to determine how change in environmental variable values will influence the average flux rate.

Model 2: The second model represented inhibition and facilitation interactions in addition to biomass flux interactions described by Model 1. The inhibition interactions described are; the competition for space between sessile functional groups, inhibition to grazing caused by high biomass density of the *filter*, the removal of the *filter* due to swaying fronds of the *plant*. The facilitation interactions are; the shading benefit of the *plant* to the *grazer* and the the shading benefit of the *plant* to the *predator.*

Model 3: Ecosystem adaptation is represented in Model 3 in addition to the inhibition and facilitation interactions described by Model 2 and the biomass flux interactions described by Model 1. To represent ecosystem adaptation (acclimatization, adaptation, succession) a goal function algorithm is used. Maximum eco-exergy [Jørgensen, 1992] is the goal function used in our model iterations because it not only considers the maximum biomass but also the complexity of the organisms, which makes sense since increased complexity is a natural result of changing environmental conditions as demonstrated by evolution. The model allows parameters of each functional group to vary, so that the goal function can find the set of parameters which provide the highest eco-exergy. The parameters that are allowed to vary are those which describe environmental attributes of each functional group.

2.3 Simulations

Simulation one: 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 Jørgensen and Bendoricchio [2001] as;

$$f(T) = \exp\left(-2.3 \times \frac{T - optT}{T_x - optT}\right)^2 \tag{2}$$

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. The geographical distribution covers the range from the warmest to the coldest places where the species occurs along the western European coast. 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.

Simulation two: 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 the biotic website [www.marlin.ac.uk/biotic/].

Simulation three: 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 for simulation one, whereas for simulation two there is a decrease in the *plant* functional group. As shown in Figure 1, for simulation three, all functional groups collapse before the end of the 100 year simulation.

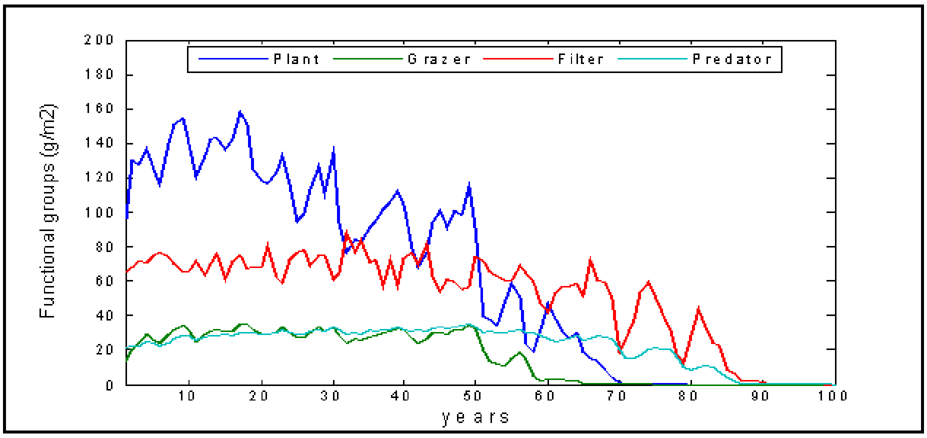

Figure 1. Output of simulation three by Model 1.

For Model 2, the output was similar to Model 1 for simulations one and two, in which the outputs showed a decrease in the *filter* feeding functional group for simulation one, whereas for simulation two there is a decrease in the *plant* functional group. For simulation three, as shown in Figure 2, the functional groups did not collapse completely as in Figure 1 but were significantly reduced. This suggests that the inclusion of inhibition and facilitation interactions gives stability at low biomass densities which may be due to a regulation affect reducing the affect of cascades through functional groups via the biomass flux interactions.

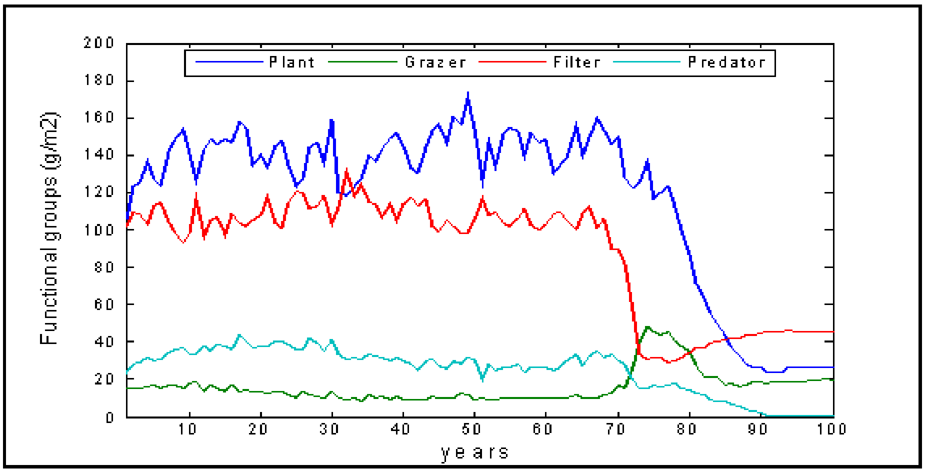

Figure 2. Output of simulation three by Model 2.

For Model 3, the output was not similar to Model 1 and Model 2 for simulation one and two but instead the biomass densities of the functional groups remain relatively constant. As shown in Figure 3, for simulation three the biomass densities of the functional groups remain relatively constant and did not decrease as for Models 1, shown in Figure 1, and Model 2, shown in Figure 2. This suggests that the inclusion of adaptation in the model gives greater stability to all functional groups.

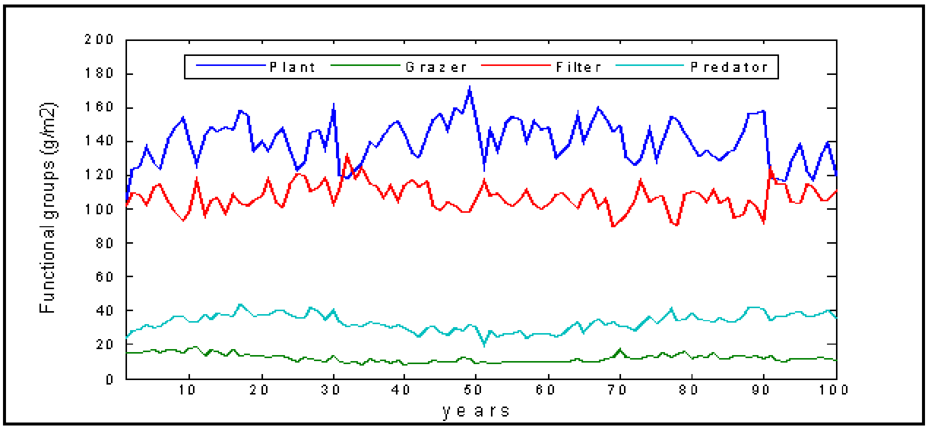

Figure 3. Output of simulation three by Model 3.

4 DISCUSSION

In modeling today there are many modeling approaches and models to choose for any ecosystem modelling task. Jørgensen 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. Model 1 and Model 2 had similar outputs for simulation one and simulation two but differed for simulation three. In simulation three where the combined influence of temperature and storminess was considered, the models gave different outputs. As shown in Figure 1, for Model 1 all functional groups collapse before the end of the 100 year simulation. As shown in Figure 2, for Model 2 all functional groups are significantly reduced but did not collapse. The outputs for Model 3 differed with the other models for all three simulations. The outputs showed no significant change for any simulation. This is shown in Figure 3 for simulation three where the combined influence of temperature and storminess was considered, 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.

The ability of Model 3 to adapt allowed it to be more resistant to changes in the environmental variables. Adaptation gives Model 3 the ability to find a solution to the environmental change. This suggests that adaptation may be a very influential stabilizing system behavior when considering the influence of climate change. With adaptation the outputs from Model 3 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 environmental attribute parameters 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 difference between Model 3 and Model 2 is that the environmental attribute parameters are constant in Model 2 where as these 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 may have a regulatory affect at very low biomass densities as shown in Figure 2 when compared to Figure 1. Inhibition or facilitation interactions may 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.

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 many 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.

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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