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Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems.

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SUMMARY

Most studies that forecast the ecological consequences of climate change target a single species and a single life stage. Depending on climatic impacts on other life stages and on interacting species, however, the results from simple experiments may not translate into accurate predictions of future ecological change. Research needs to move beyond simple experimental studies and environmental envelope projections for single species towards identifying where ecosystem change is likely to occur and the drivers for this change. For this to happen, we advocate research directions that (1) identify the critical species within the target ecosystem, and the life stage(s) most susceptible to changing conditions, and (2) the key interactions between these species and components of their broader ecosystem. A combined approach utilising macroecology, experimentally derived data and modelling that incorporates energy budgets in life-cycle models may identify critical abiotic conditions that disproportionately alter important ecological processes under forecasted climates.

Keywords: climate change; ocean acidification; global warming; species interactions; ecosystem shift; productivity and consumption.

1. INTRODUCTION

The role of global environmental change in altering marine ecosystems has received increasing attention over the past decade. Global sea surface temperatures have been warming at ~0.13°C per decade since the current period of climate warming began in the mid-1980s [1]. Further, marine waters have absorbed ~30% of CO_2 emissions and many marine species are already being forced to cope with increasing ocean acidification in combination with rising temperatures and other anthropogenic stressors (e.g. eutrophication and over fishing) [1, 2]. While there is now a substantive body of literature demonstrating some of the potential negative and positive effects of these combined stressors, the vast majority of studies currently focus on a single species and life-stage and very few examine effects on species which play dominant structuring roles in ecosystems (e.g. herbivores, [3]; habitat forming species [4, 5]). Knowledge of the physiological responses of individual species to environmental change and their limits to performance is an informative first step in understanding the possible effects of climate change [6]. Extrapolating these physiological effects on single life history stages of individual species to generalise about changes in populations or ecosystems is, however, fraught with potentially large forecasting errors because it fails to take into account two important aspects: (1) the effect of altered environmental conditions across entire life cycles of the organism; and (2) the interactions of these species with other components of their ecosystem (e.g. trophic interactions). Yet experimental manipulations of complete life histories and whole-ecosystems are often impractical, so an approach which combines experiments and modelling may be necessary.

To reconcile these issues, a workshop was convened at the University of Plymouth, UK, 28th June – 1st July, 2011, to identify gaps in the current research into the role of climate change in causing ecosystem shifts, how these shifts may be countered by adaptation of plants and animals, and to set future directions for linking seemingly disparate fields of research (e.g. physiology and macroecology). The workshop included a selection of international specialists spanning plant and animal physiology, experimental and broad-scale ecology, and ecosystem modelling.

2. INTEGRATING INFORMATION ACROSS LIFE STAGES

(a) ***Empirical experiments***

Understandably, most experimental studies to date have focused on the most easily manipulated life stage of species, usually mature adults, to quantify physiological changes and early life stages (e.g. larvae and spores) for growth and development. However, adult stages often respond differently to earlier life stages and either or both, may be responsible for regulating population growth and equilibrium population size. For example, it may be of limited predictive value to detect minor effects of increasing temperature on the adult stage of a species if it has higher thermal tolerances and/or lower body temperatures than the juvenile stage [e.g. 7]. Conversely, altered mortality of the early life-stages may be trivial if recruitment rates are more than sufficient to saturate adult habitat [e.g. 8].

In addition to this current narrow focus, the perceived necessity of having significant biological differences among treatments in order to publish has meant that experimental conditions are often manipulated to unrealistic levels (e.g. CO_2 of >1500 ppm, acute temperature gradients >20°C) to detect an effect on the more robust adult life stages. While such extremes are informative about the tolerance limits of the species in question, their use neglects to identify smaller biological effects that may have multigenerational effects in populations. Further, these extreme manipulations may not reflect real changes to conditions over the next century. For example, mature marine molluscs may survive temperature increases within what is predicted in the next 100 years [9, 10], yet if increased temperatures within this range cause altered reproductive capacity which is not identified in short-term experiments, then potentially important population and ecosystem effects may not be predicted. One way to potentially overcome this issue would be to identify the energy budget of animals and how they allocate resources to different biological processes. This should then identify if individuals are changing their allocation of energy to ensure maximum survival in altered environmental conditions at the expense of, or benefit to, other processes important to population dynamics, such as gonad development [11].

(b) *Multi-life stage models*

Identifying the stage in the life cycle which is most susceptible to changing environmental conditions can be challenging, yet necessary to discover where population effects may occur and any appropriate management or conservation actions to counter them. Detection of an effect of predicted future conditions (e.g. increased CO_2 and temperatures) with empirical experiments does not necessarily demonstrate that a particular life stage is the most susceptible to these conditions *or* that impacts on this life stage will alter population size unless experiments are conducted across all of the life stages *and* these life stages are integrated into a complete life cycle. Demographic population models incorporating all life-cycle stages, which force different scenarios of environmental conditions, can be useful tools to identify which life-stages are most susceptible, and how this susceptibility may respond to different combinations of stressors. For example, time-series data for co-occurring species of warmwater, coldwater and non-native barnacles in the UK have been used to build population models which show alternate responses of the species to changing conditions; the coldwater *Semibalanus balanoides* is directly affected by temperature, with pre-recruitment larvae being the most susceptible stage, whereas the warmwater *Chthamalus montagui* and *C.*

stellatus are predominantly controlled by competition for settlement space. Importantly, the invasive *Austrominius (Elminius) modestus* is least likely to be affected by temperature or acidification, due to its wide thermal and pH tolerance ranges [12, 13], suggesting that a community shift is likely under future conditions. We suggest that this comparative approach between interacting species is one of the next key steps in identifying potential ecosystem shifts driven by changing environmental conditions.

3. CASE STUDY

Variation in abundance of ecosystem dominants (e.g. kelp forests, coral reefs) reflects a balance between rates of primary production and its consumption, and ecosystem shifts may occur when environmental conditions cause large changes in consumption [e.g. 14, 15, 16] or production [e.g. 17]. We chose to use temperate rocky reefs naturally dominated by kelp forests as a case study. For simplicity, we assumed that no new species were introduced to the system because of changing conditions (c.f. range expansion of herbivores due to warming and the associated ecosystem shift; [18]). In this system, predictions of phase-shifts from kelp forests to small filamentous turf-forming algae centre on increased productivity of turfs with increased CO_2 and temperature [17, 19]. However, metabolic theory predicts that herbivores should be able to consume this additional primary productivity and biomass [15], thus enabling the system to resist the phase-shift. On the level of an individual adult herbivore this may be true [20]. When a stressor is integrated across all stages of the life-cycle, however, a population-level response may become apparent. For example, adult herbivores, in this case predominantly molluscs, but also including urchins, may be able to function at their normal levels under temperatures predicted in the next century. Indeed, they may increase their consumption to compensate for their responses to increasing stress [21]. In short-term experiments at this single level of ecosystem organisation, it would appear that herbivores increase ecosystem resistance to elevated temperature and CO_2 by consuming the extra algal biomass resulting from greater rates of primary productivity. Yet natural long-term experiments at CO_2 vents show that this is unlikely, as herbivore populations tend to decline under predicted conditions [21]. Therefore, while initial experiments suggested increased ecosystem resilience as a result of increasing herbivory, population responses to stressors can be diminished [21], leading to a reduction in ecosystem resilience and potential phase-shifts as kelp competitors increase in abundance [17, 22].

4. OUTCOMES AND CONCLUSIONS

There is clearly a need for research into the potential effects of climate change to move beyond studies of single species and towards identifying where ecosystem change is likely to occur and the drivers for this change. The derivation of conceptual models that can be tested across multiple coastal systems globally will also help to address the current problem faced by studies of regime shifts; namely that although detection of past shifts is improving with the benefit of time-series spanning multiple trophic levels, it is still not possible to predict when and where future events may occur [23]. For this to happen, we advocate two directions of research: (1) identifying the critical species within the ecosystem in question, and the life stage(s) which is most susceptible to changing conditions and (2) the interactions of these species with other components of their ecosystem (e.g. increased or decreased consumption, whether individual or population based). A combined approach using macroecology, manipulative experiments and modelling, incorporating energy budgets in life-cycle models, may identify points where critical biological processes are strongly altered at predicted future conditions. Importantly, bringing this group of researchers together from seemingly disparate fields revealed consensus on the need for the field to progress beyond single species studies. We advocate that with a combined approach it may be possible to predict likely ecosystem changes before reaching what is currently thought of as critical thresholds that are notoriously difficult to predict.

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