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Adaptation of freshwater species to climate change

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Headlines

- Adaptation to environmental changes is not new in nature, but the Earth is now experiencing warming at an unprecedented rate, which is causing major disruption to both biodiversity and ecosystem functioning.
- The consequences of climate change include warming, droughts and floods, all of which can have severe impacts, particularly on freshwater species.
- Freshwater habitats are hotspots for biodiversity, and therefore it is critical to understand the effects of climate change in aquatic ecosystems. This information is fundamental for predicting which species will adapt to this rapid change.
- In some cases, climate change is leading to local species extinctions which can alter the functioning of ecosystems, unless other species can fill its vacant niche.
- Climate change is also affecting the goods and services from freshwater ecosystems which we rely on, such as fish and water, particularly in developing countries that heavily rely on these resources.
- Mitigation and greenhouse gas reduction need to take place in order to reduce climate change. Action can be enhanced by rapidly communicating scientific outcomes to policy makers who can directly tackle this global issue.
- Warming is not occurring with the same intensity around the world – with high latitude regions being especially exposed and vulnerable to change. Understanding the impacts of climate change in these more vulnerable, higher latitude systems will be crucial for predicting future responses in lower latitude regions.

Introduction

Warming is occurring at a pace unprecedented in recorded human history[1] with freshwater ecosystems increasingly under threat[2,3]. According to NASA, February 2017 was the second warmest February in the last 137 years, while in March 2017 sea ice extent has reached the lowest record at both poles[4].

Anthropogenic climate change is now having major effects across the planet, particularly in freshwater ecosystems[5], which are already influenced by a host of other interacting stressors (e.g. water management, biological invasions, land use change). These stressors vary in timescale and spatial coverage, from long-term atmospheric drivers (e.g. climate change) to those that operate at the catchment scale (e.g. diffuse agricultural pollution), or more locally (e.g. water abstraction, point-source urban pollution).

The latest Intergovernmental Panel on Climate Change (IPCC) report[1] forecasts surface temperature to increase by up to 7.5°C at high latitudes by the end of the century, particularly in Arctic and Subarctic regions, while warming is expected to be less pronounced in lower latitudes. Studying the effects of warming in these higher latitude, so-called 'sentinel systems'[3] will allow us to draw predictions for ecosystems at lower latitudes (e.g. United Kingdom) in the near future. As such, they act as an early-warning system to alert us to potential future threats closer to home[6]. The degree of adaptation to warming in most species is still poorly known and difficult to quantify, yet we can make some general predictions by using model systems as a starting point[7].

Warming is not the only effect of climate change. Many ecosystems are affected by raising sea levels, ocean acidification, and extreme events such as floods, droughts, and heavy rain[8,9,10,11], which are becoming more frequent and pronounced with climate change. These environmental changes reshape ecosystem structure, inducing species range shifts[12,13] towards more suitable habitats. Understanding how communities will respond to these changes is important, particularly from a management perspective. Species migration towards more suitable habitats cannot occur if access is blocked by either man-made or biological barriers, such as construction of dams or competing species, respectively[13]. For this reason management plans at a local or catchment scale are fundamental to allow possible migrations.

Why freshwater ecosystems?

Freshwater habitats, such as streams and lakes, can be particularly vulnerable even to seemingly minor environmental changes, and provide very important ecological and economic resources. Freshwater constitutes only 2.5% of the total global water stock and only 0.3% of this water is available in rivers and lakes[14]. Although freshwater habitats are disproportionately smaller than their marine counterparts, they are hotspots for biodiversity and provide home for more than 25% of described vertebrates, and 9.5% of the total number of animal species recognised globally[15]. Moreover, freshwaters provide a wide range of ecosystem services of direct and indirect benefit to human societies, including waste removal, and the production of drinking water, energy, food and fibre. Nowadays, fishing extracts the largest amount of wildlife in the world with 149 million tonnes in 2010 combining both wild capture and aquaculture[16]. Freshwater aquaculture is becoming more popular around the world. In 2010 50% of global aquaculture was in freshwater[17]. Despite their high value, freshwaters are in a precarious position. According to the World Wide Fund for Nature's Living Planet Index, between 1970 and 2012 freshwater species populations have suffered an 81% decline, an average loss much greater than in terrestrial and marine systems[17].

Will species adapt to climate change?

Considering climate change from a biological point of view, it is critical to understand how species will adapt to increasing temperature. Species have always been adapting to environmental changes, but their capacity to cope with the current unprecedented rates of warming could lead to local, or even global, extinctions. Climate change and global warming have been hot research topics over the past decade. Initially, the focus was on monitoring the status of this phenomenon, while more recently, it has turned towards understanding and predicting what the future will look like. Most of the climate change monitoring in freshwaters has focused on the physical aspects of warming (IPCC); there is a lack of understanding of how natural multispecies systems are affected by global warming (i.e. the biological response), and even less on the impacts of associated extreme events, such as floods, droughts and wildfires.

In terms of biological systems, most studies have investigated the impacts of warming either on single species[18,19] or on simple pairwise interactions between species[20,21], with very few that have covered the higher organisational levels, such as the food web[22]. Species richness has been observed to be lower in a warm stream, resulting in a simpler food web (see figure 1).

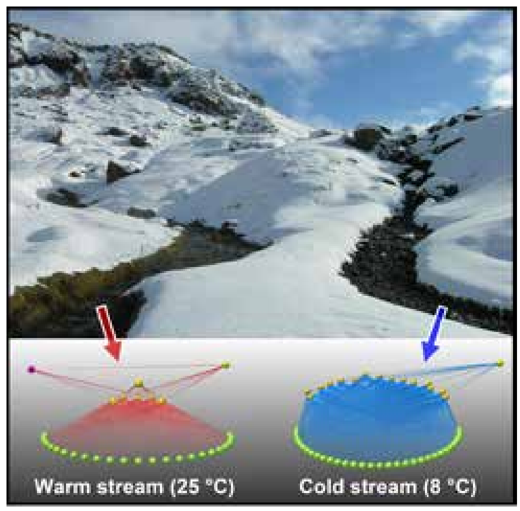

Figure 1: Food webs from a warm and cold stream at Hengill, Iceland[22]. Brown trout (shown as the purple circle) only occur as top predators in the warm stream. The only other consumers are insect larvae and other invertebrates (yellow circles), which predominantly feed on diatoms (green circles), with feeding interactions represented by the red and blue lines.

One of the main responses of individual organisms to warming is increased energy demands and metabolism, which then ripples through the wider ecosystem[23]. In ectotherms[a], which dominate freshwater ecosystems, metabolic rates are dependent on the surrounding environmental temperature, and they are therefore sensitive to warming[24]. Since they cannot regulate their body temperature independently, any change in the environmental temperature will alter their metabolism, and associated physiological and life-history traits; life speeds up under warming, with faster growth rates, shorter generation time and higher demands for resource consumption (see box 1).

a. Ectotherms are organisms that are dependent on external sources of heat to regulate their body temperature.

Box 1: Brown trout responses to warming

Brown trout *Salmo trutta* ia a common and widespread predator, with a thermal optimum for many physiological processes around 11-12°C. However, recent findings have shown that this predator can adapt and thrive at temperatures of up to 25°C in a geothermal catchment in Iceland[7], where streams have a wide range of temperatures (5-25°C). This predator is commonly found across the whole catchment, and performs very well under warmer conditions where it shows high feeding and growth rates. However, fish still migrate to cooler streams to reproduce and spawn. This is an essential step in the life cycle and population growth of this species. We still do not know if this species will manage to adapt under warmer conditions, particularly when access to cooler streams will be prevented due to increasing global temperatures (figure 2).

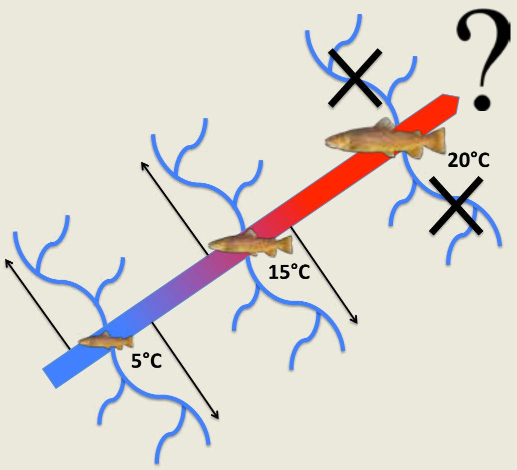

Figure 2: Brown trout responses to warming. Temperature increases feeding and growth rates, but access to cold streams is needed for reproduction and spawning. In the absence of the cold streams that can act as temporary refugia at these key points in the lifecycle, fish responses are unknown; can they survive if the entire system warms or if they are denied access to cooler waters?

In other aquatic ecosystems phytoplankton growth in the water column is also affected by temperature and light availability. Under light-limited conditions, species temperature optimum drops by around 5°C which could be an adaptation to how light and temperature vary with depth[25]. Moreover, different phytoplankton groups adapt in different ways according to their environment. They have similar growth rates in the tropics, while they diverge in high latitude systems. This is probably due to the inability of some groups to adapt to lower temperatures, but also a different nutrient requirement amongst groups[26]. Given the complexities of natural systems, understanding how quickly these species can adapt, and what thermal limit they can tolerate, is challenging and a major focus of ongoing research.

At the same time, research is trying to disentangle and predict species range shifts due to climate change. This phenomenon is occurring on a large scale across the whole planet where species are moving to greater depths, polewards, and towards higher altitudes. Mosquito distribution is shifting towards areas that were previously unsuitable, carrying malaria into new regions where the transmission season is also longer, thus expanding the chances of the spread of disease[27]. The carmine shiner *(Notropis percobromus)*, an ecologically important fish species in North America which has been predicted to shift northwards of its current distribution[13]. Most of the habitats suitable for this species in the future are currently inaccessible due to dispersal limitation, which could lead to severe consequences and eventually species extinction. Global analyses show that, on average, terrestrial species[28] move 17km poleward per decade, while marine species move 72km per decade[29], highlighting stronger effects of climate change in aquatic systems.

Extreme events, such as flooding and droughts, have profound consequences for ecosystems functioning and biodiversity loss[9]. Some species, such as most Amazonian fishes, are more vulnerable to warming than they are to high or low flow regimes[8]. Others, such as the semi-aquatic freshwater turtle *Chelodina longicollis*, are highly sensitive to droughts because they heavily rely on freshwater subsidies[30]. There are also groups of freshwater species, such as apple snails (*Pomacea spp.*), which show high tolerance and rapid restoration to exposed drought conditions[11], strong advantages under climate change. However, these resilient species are often undesirable or invasive. Having a global understanding of how climate change is reshaping species distribution and community structures is very challenging. By using predictive models and studying species behaviour we can understand which species will be most threatened. Nevertheless, further research is needed to test how these responses will vary between species and over different spatial scales.

Arctic regions are especially vulnerable to global warming

Some of the findings outlined here are from Arctic and Subarctic regions, which will be exposed to some of the highest rates of warming on the planet according to the latest IPCC report[1]. A series of ambient and geothermally heated streams in Iceland have been used as a natural laboratory to quantify the impacts of warming on freshwater ecosystems, and this work is currently being expanded to other systems in the Arctic[3]. This additional suite of 'sentinel systems' (figure 3) will be used to test if the impacts observed so far are also manifested in areas with very different species composition and evolutionary history. By working in these 'sentinel systems', where the effects of temperature can be isolated, scientists can disentangle the effects of warming from other drivers. This will allow predictions to be made on how freshwaters will respond to climate change in the future. By measuring gene-to-ecosystem[b] responses, it is possible to test if the mechanisms are truly universal, and to anticipate impacts at lower latitudes. These geothermal systems act as natural laboratories. The Icelandic systems have been intensively studied for over a decade[3,6,7,18,22,31] and we are developing a good understanding of how temperature shapes food web structure and drives ecosystem dynamics as we continue to expand these approaches into other parts of the world.

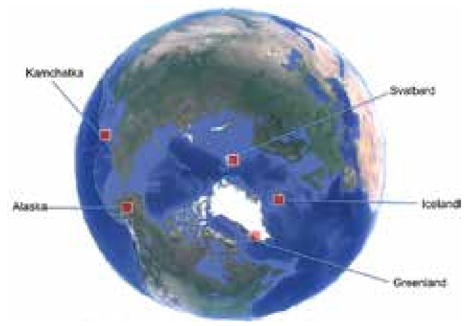

Figure 3. Ecological studies of climate change in the Arctic and Subarctic region. The highlighted red boxes indicate a number of sentinel systems used to study the effects of warming in freshwater ecosystems, as part of a large NERC-funded project called the Ring of Fire.

Climate change threats and implications

The adaptation rate of species to climate change has important implications from both a biological point of view (e.g. species extinction and biodiversity loss) and from a global socio-economic perspective. From a health perspective, species distribution shifts can move disease-carrying insects (e.g. mosquitos) to new areas, or pests closer to new crops[27]. Increased carbon dioxide in the atmosphere can affect crop yields and, overall, climate change could make it more difficult to grow crops and raise animals in the same places as we have done in the past. For example, coffee plantations are affected by climate change in low elevation areas of Mexico, Guatemala and Costa Rica, where cultivation is shifting to higher altitudes[32]. These countries are heavily dependent on the coffee industry and will be greatly affected by future changes. The majority of freshwater fisheries are in developing countries (e.g. Asia)[34], which are mostly located at low latitudes in tropical and sub-tropical regions. Although warming is slower here than in the Arctic, even a modest change can have strong effects on these ecosystems, as seen in the widespread loss of reef ecosystems due to 'coral bleaching'[26]. Freshwater fish make up more than 6% of the total animal supply for humans each year[33], and in areas such as Bangladesh, Indonesia, and Thailand, freshwater fish is the main source of protein[35]. Fisheries provide food and employment for millions of people in developing countries. They also contribute to a country's overall growth by means of export trade, tourism, and recreation[34]. Notably, aquaculture is now the fastest growing food-producing sector in the world. In particular, it contributes to the majority of the overall food supply of most developing countries[36]. Therefore it will be critical to understand if animals grown in aquaculture systems can withstand higher temperatures in the future. This adaptation will depend not only on the direct physiological responses of fish species, but also the indirect food-web effects[36,37] in the wider network of interconnected species.

Where to next?

It is fundamental to take a holistic approach to understand whole ecosystem responses[38,22] to global warming, rather than the single species studies that have dominated the field to date.

Global warming will be faster in the high latitude regions, where the scope for adaptive or compensatory responses are likely to be lower due to the lower biodiversity and slower pace of life of organisms that live there. In contrast, the majority of the resources and ecosystem services in the form of fisheries are drawn from the lower latitudes where warming is less pronounced, but its effects are increasingly evident. Understanding the underlying mechanisms in high latitude systems provides a means of developing a more universal and predictive framework for anticipating future global impacts and responses. In the coming years climate change will continue to happen, but there is an urgent need to reduce the rate of this phenomenon.

Mitigation can be a solution, either by reducing the emission of greenhouse gases (e.g. by burning less fossil fuels or adopting a more plant based diet), or by improving sinks (oceans, forests and soil) that can store and accumulate these gases[1]. Reducing greenhouse gas emissions has been one of the main global objectives of the last 25 years through the United Nations Framework Convention on Climate Change (UNFCCC) in 1992, the Kyoto Protocol in 1997, and lately in 2015 with the Paris Agreement[39]. Nevertheless emissions are still increasing and there is an urgency to find other solutions. Adaptation measures can anticipate and reduce damages caused by climate change and sometimes take advantage of new situations. Adaptation plans consist of: efficient use of water resources, new flood defences, plantation/forestry practices that are less vulnerable to storms and fires, and creation of land corridors to aid migration.

It is also vital that scientists and policy makers work together to speed up the process of moving from the identification of problems to finding solutions. Researchers need to gather and analyse high-quality data sets and integrate this information into decision-support frameworks, enabling policy makers to make informed decisions more rapidly. Therefore there is a need to find new platforms on which science and policy can rapidly communicate and interact to tackle climate change together.

b. The genes-to-ecosystem approach: Genes are the building blocks of organisms, which form populations, which interact in ecological communities, which carry out the important processes and functions of ecosystems. To understand how ecosystems function we need to study the connections between these lower levels of organisation and how they respond to stress, such as increasing temperature.

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