Impacts of climate change on wildlife

Edited by

Rhys E Green
Mike Harley
Mark Spalding
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RSPB UNEP WCMC ENGLISH NATURE WWF

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Introduction

Mike Harley

Climate change is the most significant and far-reaching environmental threat facing humanity today. Scientists, policy makers and governments from around the world are seeking to understand the nature of the changes that are likely to occur in the 21st Century and beyond, and the effects these could have on human populations and the socio-economic systems that underpin them. Mitigation measures are being developed to reduce the long-term impacts of human-produced greenhouse gases on the Earth's climate, whilst a wide range of 'sectors' are considering how they might adapt to the inevitable effects of climate change in the shorter term.

There is already clear evidence to show that wildlife from the poles to the tropics is being affected by climate change. Species migrations, extinctions and changes in populations, range and seasonal and reproductive behaviour are among a plethora of responses that have been recorded, and these are likely to continue apace as climate continues to change in decades to come.

In recent years, natural scientists and nature conservationists have been acquiring knowledge of the current and future impacts of climate change on global wildlife. In an attempt to share this information and identify future research priorities, four UK-based nature conservation organisations convened 'The Norwich Conference' at the University of East Anglia, England, in September 1999. The conference brought together many of the world's leading research scientists in the field; this book synthesises the main messages from their presentations in a way that is accessible to the non-specialist reader. Contact details for each contributor are given on pages 4–5 to enable readers to obtain further information on subjects of particular interest to them.

Defining future climates – from scenarios to risk assessments

Mike Hulme

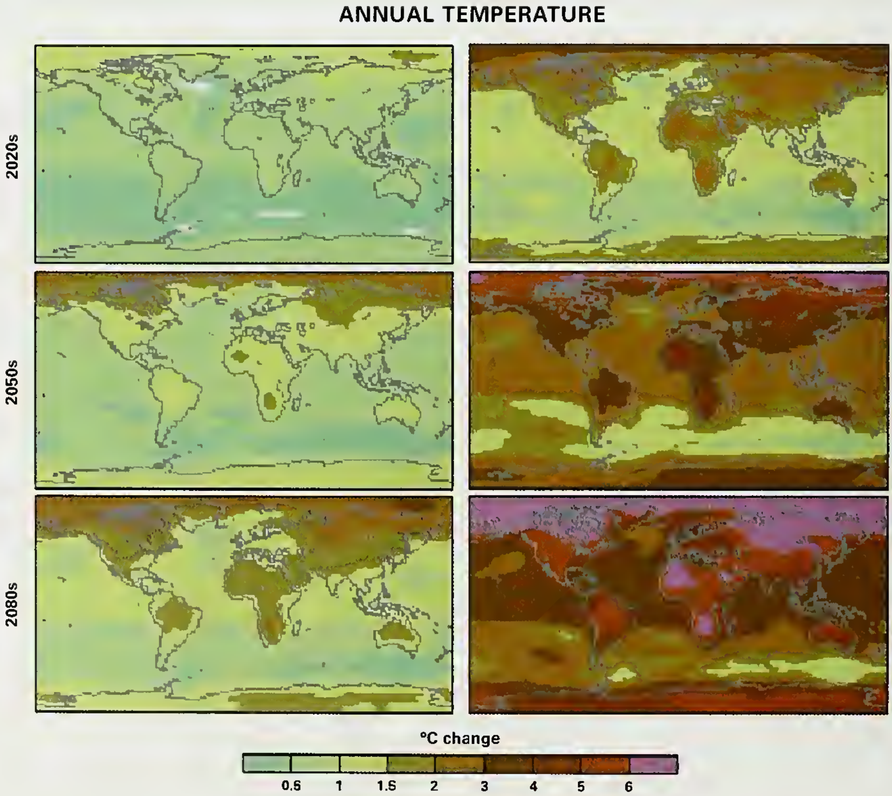
Climate is changing. Global average temperature is now about 14.3°C compared to about 13.7°C a century ago. The 1990s were, by some margin, the warmest decade ever recorded by instrumental data and very likely the warmest of the last millennium. Global average sea level has increased by between 10 and 20 cm over the same period. There are suggestions that Arctic sea ice has declined in extent by up to 40% over recent decades. Alpine continental glaciers are also retreating. In regions where data have been analysed, there is evidence for increases in the frequency of the heaviest precipitation events. Human society, through its emission of greenhouse gases into the atmosphere, is deeply implicated in the causes of these changes. The 1996 assessment of the Intergovernmental Panel on Climate Change (IPCC) concluded that, '...the balance of evidence suggests a discernible human influence on global climate'. Work undertaken since then has only supported this judgement.

That humans are changing the climate *now* means that we will be changing the climate over the 21st Century, given the inertia in our energy systems and the momentum for accelerated energy use world-wide. This situation has major implications for the way in which society views its relationship with climate. No longer can we use historical weather statistics as a sure guide for future anticipated weather, as has been done conventionally for many decades in engineering design, environmental management and social planning. Future climate will look and feel different from the climate of the present and the past. But how different? At what rate will these changes in our climate regimes materialise? How will they be distributed across the planet? With what confidence can we provide quantitative descriptions of these new emerging climate regimes? Before we can determine robust responses to climate change – whether identifying how best to accommodate and adapt to future climates, or defining what might be sustainable greenhouse gas emission levels to strive for – we need some sense of just what these changes might be.

Predicting future climate is an activity fraught with difficulties. Some of these difficulties are purely scientific; for example, quantifying the processes that affect climate, whether feedbacks between rising temperature and cloud cover, or the importance for climate of changing solar activity. Some of the difficulties are methodological and computational; for example, constructing adequate models of the coupled climate system that capture our scientific knowledge, and having sufficient computational capacity to use these models to generate the required level of detail about future climate. And some of the difficulties take us into the fuzzy area between science and visioning; for example, how do we know what sort of future society will be generating what sort of mix and magnitude of greenhouse gases in 50 or 100 years time?

Figure 1. (Left panels) Change in mean annual temperature for the 2020s, 2050s and 2080s (with respect to 1961–90) for the B1-low scenario; median of 10 model simulations. (Right panels) As left, but for the A2-high scenario.

NB: The light grey areas are those where changes in temperature are small relative to natural decadal variability.



These difficulties, particularly the last of the three, have led climate scientists to prefer the generic term 'climate scenarios' (although IPCC has unfortunately adopted the misnomer 'climate projections') over 'climate predictions' to label the descriptions of future climate(s) that ensue.

Current scenarios assume that carbon dioxide concentrations will rise from their present level of about 370 parts per million volume (ppmv) to between about 500 and 900 ppmv over the 21st Century, leading to additional global warming of between about 1.4° and 5.8°C and an additional increase in sea level of between about 9 and 88 cm. The regional patterns of climate change associated with this warming are not robustly defined by current climate models, but Figures 1 and 2 show examples of changes in mean annual temperature and precipitation for two possible scenarios – a scenario of rather slow warming (B1-low) and a scenario of more rapid warming (A2-high).

The term 'climate scenarios' makes it clear that the descriptions are based on a variety of assumptions and that alternatives are possible. But for planners, engineers and policy advisors, it is this very fact – a scenario is only one of many – that has made the problem of determining future climate change impacts, and hence identifying robust adaptation and mitigation strategies, so troublesome. Is one scenario as valid as another? Is yours better than mine? How uncertain is a given scenario? Is there such a thing as a 'best-guess' scenario? Should we use one scenario, five scenarios or as many as we can lay our hands on? And what about the worst-case scenario? What is this anyway, and should we plan for it?

Recently, a number of climate scientists have made efforts to move beyond climate scenarios of the future, towards more comprehensive probability-based statements about how future climate may change. Although not yet climate predictions (key prior assumptions are still required and all uncertainties are not fully assimilated), these types of future climate descriptions fit more easily into risk assessment frameworks and integrated assessment models, the tools that decision makers and policy advisors will increasingly need to use. There is the potential for developing more sophisticated descriptions of future climate using these sorts of approaches – incorporating quantifiable uncertainties about the climate system, about future forcing and feedbacks, and about the possibility of large, abrupt non-linear changes in our climate. This work will need to be done in conjunction with engineers and environmental managers to provide the right sort of information that will lead to the right sort of decisions about transforming the relationship between climate and society into a sustainable one.

Mike Hulme is Executive Director of the newly established Tyndall Centre for Climate Change Research, a distributed UK Centre, but based at the University of East Anglia in Norwich, UK. The challenges outlined above represent one area in which the Tyndall Centre will be working alongside UK and international stakeholders in the years to come.

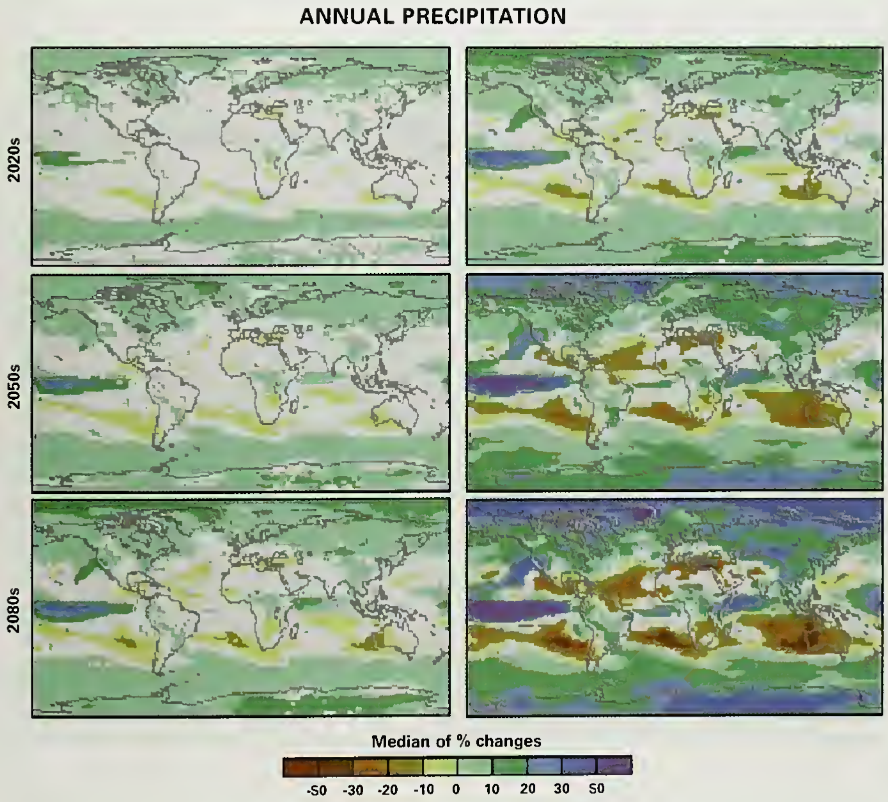


Figure 2. (Left panels) Change in mean annual precipitation for the 2020s, 2050s and 2080s (with respect to 1961–90) for the B1-low scenario; median of 10 model simulations. (Right panels) As left, but for the A2-high scenario.

NB: The light grey areas are those where changes in precipitation are small relative to natural decadal variability.

Climate change and butterflies

Introduction by Camille Parmesan

Many attributes of individual animal species, their size, shape and colour, and their feeding and sexual behaviours, are adapted to the climatic conditions in which they live. Changes in climate influence the size of populations, which in turn affects the distribution and abundance of species, and ultimately ecosystem structure and function. Consequently, long-term climatic trends have enormous impacts on shaping the tapestry of life in the wild.

For many organisms, we can infer the impacts of changes in climate from basic physiological and biogeographic research. A recurring theme is that many biological processes undergo sudden shifts at particular thresholds for temperature or precipitation. In particular, plant and animal range boundaries are often determined by freeze tolerance, or by minimum levels of yearly precipitation. Extreme weather events often bring about sudden changes in population status. Single drought years have caused drastic crashes in some insect species on a continental scale, while leading to population booms in other species. It is likely, then, that changes in proportions of days exceeding species-specific temperature thresholds, or changes in frequency of droughts or extreme seasonal precipitation, will lead to physical and behavioural changes in a few species, and dramatic changes in the distributions of many species.

A major difficulty with research in this field is that climate change is only one of the forces which fall under the umbrella of 'global change'. Land use change, pollution and invasive species also affect where wild animals can live. Loss of habitat, either through destruction or by more subtle management changes, not only results in local extinctions, but endangers surrounding areas of good habitat by increasing the isolation of each population. As areas of good habitat get smaller and more isolated from other good areas, the populations on those areas are more likely to become permanently extinct.

In the past, the natural ranges of species have shifted in response to changing climates. However, fragmentation of habitats is likely to impede the ability of species to move with the rapidly changing climates that we are likely to experience in the future.

The Sooty Copper *Heodes tityrus* is one of the European butterfly species found to be extending the northern limit of its range, while retracting the southern limit.

Photo: Richard Revels.

Effects of climate change on butterfly distributions

Camille Parmesan

There has been a flurry of recent research which has shown changes in the regional distribution and local abundance of wild species that appear attributable to general climatic warming trends during the 20th Century. My own research has focused on butterfly species and here I outline two studies – one in Europe and one in the western USA – which contribute to this debate.

A multi-species approach

In an attempt to tease apart the climatic and non-climatic influences on animal distributional change, I, and 12 European colleagues, studied 57 European butterfly species. Our general approach was to isolate climatic impacts, as far as possible, by eliminating from consideration species which were likely to have been severely impacted by other, non-climatic, forces. Because we were interested in isolating the effects of climate from the effects of habitat change, we instituted criteria designed to restrict our study species to those thought not to have been much affected by land use change at the boundaries of their ranges. We used only non-migratory species, because migratory species, by responding rapidly to yearly temperature fluctuations, will show rapid shifts in their range limits, requiring yearly records over a very long time in order to pick out an overall trend from the yearly variation.

Systematic northward shifts in distributions have occurred in the majority of the non-migratory species during the 20th Century. For 35 species for which we had data from both the northern and southern range limits, nearly two-thirds have shifted their entire range to the north by 35–240 km and only 6% have shifted to the south (Figure 1). By studying distributional changes at both latitudinal range boundaries, we were able to distinguish general range expansions or contractions from actual range shifts.

The study is the first continental-scale evidence of poleward shifts in species' ranges for any taxon. The results have been repeated in more localised studies of many other kinds of organism. For example, upward shifts have been recorded for plants in the Swiss Alps and birds in Costa Rica. Similarly, the Red Fox has moved northward into Arctic Fox territory, as the Arctic Fox retreats to the poles. When the results of all these studies are put together, they indicate that systematic changes in where species live have occurred world-wide during the 20th Century. These changes were predicted by global warming scenarios more than a decade ago. Thus, even though scientists cannot perform controlled experiments on the effects of global warming on species' distributions, the replication of the same pattern of movements in all studies provides strong evidence that current levels of climate change are, indeed, affecting natural populations.

How does climate shift species' ranges?

Usually, our knowledge of the basic biology of a species is insufficient for us to identify the precise mechanisms by which climate change influences populations. Occasionally, direct observations through time reveal the mechanism of the response to long-term climatic trends. Edith's Checkerspot butterfly *Euphydryas editha* has been intensively studied for 40 years by dozens of scientists. For this species, extreme weather events appear to drive local population dynamics, which in turn drive range limits. Such events are likely to become more frequent as climate changes.

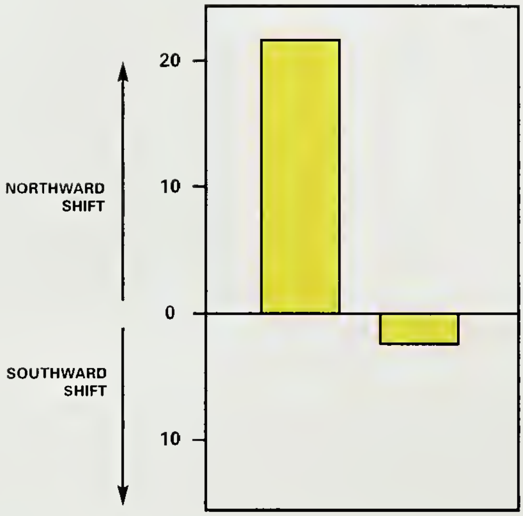


Figure 1. Numbers of butterfly species whose ranges have shifted north or south in Europe during the 20th Century.

Using historical records combined with current field censuses, I found that the range of Edith's Checkerspot butterfly in the western USA had shifted northward by 92 km and upward in altitude by 124 m over the 20th Century. The magnitude of this change matched the observed warming trend over the same region, in which the mean yearly temperature isotherms (temperature contours) shifted 105 km northward and 105 m upward. Population extinction increased dramatically below 2,400 m. This breakpoint matched that for changes in snowpack depth and timing of snowmelt; increased depth and later melt date was observed above 2,400 m, and decreased depth and earlier melt below 2,400 m (Figure 2).

At the population level, many extinctions of Edith's Checkerspot have been associated with particular climatic events. The 1975–1977 severe drought over California caused the extinction of five out of 21 surveyed populations. In the Sierra Nevada mountains of California, 20 years of observation have implicated three extreme weather events in carving a pathway to extinction of a whole set of these montane populations. The first catastrophe occurred in 1989, when very low winter snowpack led to an early and unusually synchronous adult emergence in April (as compared to the usual June flight); so early, in fact, that flowers were not yet in bloom and most adults died from starvation. Just one year later, another relatively light snowpack again caused adults to emerge early. Adult butterflies, adapted to summertime conditions of warmth and sun, suffered many deaths during a 'normal' May snowstorm. Each of these events decreased the population size by an order of magnitude. The finale came but two years later in 1992, when unusually low temperatures of -5°C on 16 June, without insulating snowfall, killed an estimated 97% of the host plants. The butterflies had already finished flying and left behind young caterpillars that were not killed directly, but starved in the absence of hosts. Up to the latest census (1999), the butterflies remained extinct at these sites.

In response to long-term climatic changes in the western USA, Edith's Checkerspot butterfly populations in the south of its geographical range and at low elevations have shown a greater tendency to go extinct.

Photo: Camille Parmesan.

Figure 2. The links between changes in climate and changes in distribution of Edith's Checkerspot butterfly during the 20th Century.

Climatic connections of Edith's Checkerspot in the USA

0.7°C warming over Western USA leads to a shift in the equivalent climate –	105 km North and 105 m up the mountain
The mean location of the butterfly's range shifted –	92 km North and 124 m up the mountain

Both snowpack and Edith's Checkerspot extinction trends alter at 2,400 m:

	% change snow/50 years	% extinctions of butterfly populations
Below 2,400 m	14% less snowpack; melt 7d earlier	46%
Above 2,400 m	8% more snowpack; no change in melt date	14%

The observed northward and upward range shift of Edith's Checkerspot during the 20th Century has occurred as a result of increased numbers of population extinctions at the southern range boundary and at lower elevations, with symmetrical tendency towards population stability along the northern range boundary and at the highest elevations. Thus, infrequent and severe climatic events appear to be driving a gradual range shift in this butterfly species, via short-term responses at the population level.

Predicting the future

Unfortunately, because of modern human domination of landscapes, natural ecosystems are increasingly confined to smaller and more isolated fragments, and population sizes of wild species have generally declined. This has limited the options by which natural systems may contend with the predicted rapid changes in climatic extremes, or in frequency and intensity of disturbances. Reduced population sizes often result in diminished genetic variation, which could limit potential for local adaptation. The increase in mean distance between natural habitats decreases successful dispersal, thereby hindering simple shifts of species' distributions. Increased fragmentation also lowers the probability of successful colonization of devastated areas after catastrophic disturbances, because colonists not only have farther to travel, but are coming from small source populations within impoverished communities. Wildlife in the distant past could cope with major climatic shifts (as during the Pleistocene ice ages) by moving across the planet to track their hospitable climate. Much modern wildlife, hemmed in by barren wastelands of concrete, cropland and sterile pine plantations, does not have this option, making species' extinctions the more likely scenario.

Further reading

Parmesan, C (1996) Climate and species' range. *Nature* 382: 765–766.

Parmesan, C, Ryrholm, N, Stefanescu, C, Hill, J K, Thomas, C D, Descimon, H, Huntley, B, Kaila, L, Kullberg, J, Tammaru, T, Tennent, J, Thomas, J A and Warren, M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579–583.

Hughes, L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56–61.

Impacts of climate and habitat availability on range changes in the Speckled Wood butterfly

Jane K Hill, Chris D Thomas and Brian Huntley

Butterflies are a charismatic and highly visible group of animals; their natural history has been a focus of interest for hundreds of years. As a result, there now exists an excellent historical record of changes in butterfly distributions in the UK over the past 150 years. During this period, many UK butterflies, including the Speckled Wood *Pararge aegeria*, have undergone marked changes in their distributions, probably in response to changing climates.

Historical changes in distribution

Along with other insects, butterflies are particularly responsive to climate change because of their cold-blooded nature and high dispersal ability. During the 19th Century, the Speckled Wood was widespread throughout the UK, occurring as far north as central Scotland. However, along with several other species, it started to decline towards the end of the 19th Century and from 1900–1939 was essentially restricted to south west England and Wales, with a single refuge population around Oban in Scotland. However in the 1940s, the Speckled Wood started to expand and this has continued to the present day. The northern range margin in England now lies in North Yorkshire and Cumbria, and individuals from Scottish populations have recently been recorded along the north coast of Scotland. Over the past 60 years, the northern range margin in England has shifted northwards by approximately 110 km, corresponding with shifts in climate isotherms of 120 km over the same period. Over the past 30 years, the Speckled Wood has been expanding at approximately 1.5 km per year and range expansions have been greatest during decades with the greatest amelioration of climates. Figure 1 shows the current distribution of the Speckled Wood in the UK, and its range expansion during the 1990s.

The Speckled Wood has not yet re-colonised all areas that it occupied historically, and the availability of suitable breeding habitat is likely to impact greatly on its ability to expand into new areas. The Speckled Wood is essentially a woodland species, particularly towards the margins of its distribution, and recent destruction of woodland habitats may affect its range expansion, both now and in the future. We have addressed these issues by studying the importance of climate in limiting distributions at a European scale. We have also focused on the UK in order to study the importance of climate, in addition to the distribution of woodland, in determining UK range limits.

European distribution

The Speckled Wood occurs throughout continental Europe, as far east as the Ural Mountains. It reaches its southern limit in

Speckled Wood butterfly *Pararge aegeria*. Photo: Hans Christoph Kappel, BBC.

Figure 1. UK distribution of the Speckled Wood butterfly from 1940–1989 (black squares) and 1990s expansion (red squares). Blue crosses show 19th Century distribution in areas which it has not yet re-colonised.

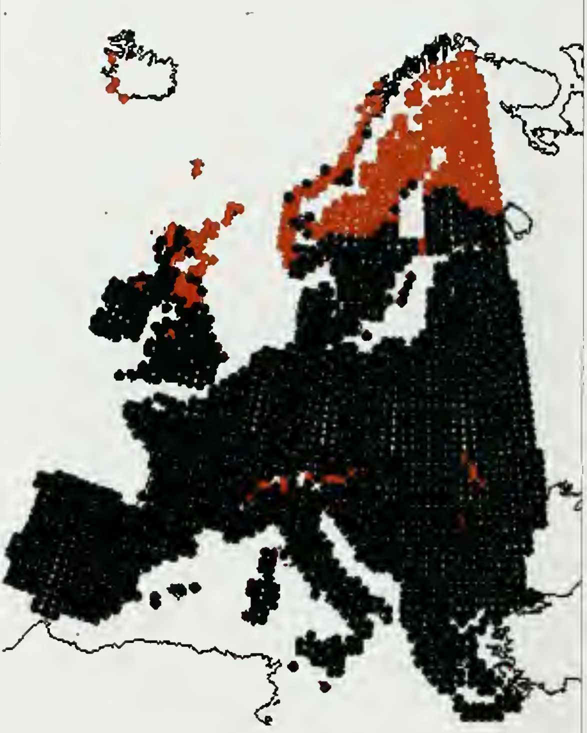


Figure 2. Predicted current distribution of the Speckled Wood butterfly in Europe (black circles) and future (2070–99) extension of the distribution (red circles)

the Atlas Mountains of Morocco and its northern limit in central Scandinavia. We related its distribution throughout Europe to a combination of three climate variables. We chose variables that are important in its development and survival; temperature of the coldest month, length of the growing season, and availability of moisture. This combination of climate variables accurately describes the current distribution of the Speckled Wood, showing that climate is important in limiting butterfly distributions at a European scale. We also used this information to predict where the Speckled Wood ought to occur in current climates (Figure 2). There is a good fit between recorded and predicted distributions, although the butterfly was not predicted to occur in very mountainous areas, where it is restricted to very specific habitats (for example, southerly-facing valley bottoms, where microclimates are more favourable than the mean climate of the local area). We also predicted that it should occur further north than it currently does. This suggests that the Speckled Wood is lagging behind current climates.

UK distribution

We predicted the distribution of the Speckled Wood in the UK at a finer-scale resolution and, in addition to suitable climate, included the availability of woodland breeding habitat into the study. There is a good fit between recorded and predicted distributions (light and dark blue circles in Figure 3). However, even after accounting for availability of habitat, the butterfly was predicted to occur in several areas beyond its current range margin (red circles in Figure 3); these include northern England and southern Scotland, areas which the Speckled Wood occupied historically. This shows that, as at the European scale, it is lagging behind current climates. Also as at the European scale, the Speckled Wood was not predicted to have such an extensive distribution as is currently observed in mountainous regions (the west coast of Scotland and Cairngorms; pink circles in Figure 3); again, this is probably because it is occurring in very specific, microclimatically favourable habitats in these areas.

Future distribution

We also predicted the potential future distribution of the Speckled Wood for the period 2070–99. Climates in Europe are likely to get generally warmer and drier, with the temperature of the coldest month increasing by over 4°C by the end of the 21st Century. In line with this climate warming, the Speckled Wood will have the potential to shift its distribution northwards. Figure 2 shows how it could potentially extend its range in Europe. In Fennoscandia, the species' potential range extends almost to the Arctic coast, reaching southern Finnmark, and extends along the west coast of Norway as far as the Lofoten Islands. Figure 4 confirms that, even after taking account of current availability of

Figure 3. **Comparison between recorded and predicted UK distribution of the Speckled Wood. Light and dark blue circles are areas where the predicted distribution is in agreement with recorded distribution (dark blue – present, light blue – absent). Red circles show regions where the butterfly is predicted to occur, but does not occur. Pink circles are mountainous regions where the butterfly occurs, but is not predicted to occur.**

Figure 4. **Predicted UK distribution of the Speckled Wood in 2070–99.**

woodland, the Speckled Wood will have the potential to extend its range throughout most of the UK, with only the highest mountains in Scotland being excluded.

Implications for conservation

Our studies indicate that, in the UK and Europe, the Speckled Wood is lagging behind current climates. The species is fairly mobile and does not have particularly specific habitat requirements. It is likely that many more UK butterfly species will be lagging behind current climates, as most are more sedentary and more habitat specific than the Speckled Wood. Recent fragmentation and destruction of natural habitats may mean that many species will be unable to shift their distributions northwards in the UK to more climatically suitable areas. There are also a few butterfly species which reach their southern range margins in the UK. Our studies indicate that these species are likely to disappear from all but the most mountainous regions of Scotland. Thus, conservationists will be faced with the twin problems of butterfly species disappearing in the north, and southerly species being unable to expand northwards and keep track of suitable climates because they cannot reach new breeding habitat.

Further reading

Hill, J K, Thomas, C D and Huntley, B (1999) Climate and habitat availability determine 20th Century changes in a butterfly's range margin. *Proceedings of the Royal Society B* 266: 1197–1206.

Hill, J K, Thomas, C D and Blakeley, D S (1999) Evolution of flight morphology in a butterfly (*Pararge aegeria*) that has recently expanded its geographic range. *Oecologia* 121:165–170.

Climate change in polar regions

Introduction by Christoph Zöckler

According to the models developed by climate scientists, the polar regions will be the most significantly affected by climate change. Arctic and Antarctic biomes are thus highly vulnerable, with the Arctic region being likely to experience the strongest warming. Regional differences are also likely, with the greatest warming predicted over the land areas of the Mackenzie Mountains and north-west Canada, Alaska and central northern Russia. By contrast, one region, extending from eastern Canada through to eastern and southern Greenland and Iceland, will actually experience a cooling through all seasons.

The Arctic is a very suitable region for research into the impacts of climate change on wildlife; other influences, such as direct human impact, are very low, and changes related to climate change can be more easily distinguished than in temperate or tropical regions. The region is also ideal for making comparisons between biomes and with records from the recent geological past.

Arctic biodiversity will undergo great changes under a changing climate and the effects are likely to be very diverse. The Arctic is not very rich in biodiversity, but many species spend crucial periods of their life history here. Marine species are considered to be vulnerable to changes in sea ice distribution, and special attention has been paid to Polar Bears and their behaviour in a warming climate. Comparable evidence of changes in the extent of sea ice has also been gathered for the Antarctic in relation to the distribution of Adélie Penguins.

The Arctic is also a major food resource for many subsistence societies which rely on fish stocks, and Reindeer or Caribou. The latter has been investigated in relation to the recently observed 'greening of the tundra' and its impacts on food availability. The impact of global warming is not always harmful for species, and can even be beneficial. The regulation of animal populations is a very complex issue, involving a wide range of inter-related factors, which further complicate the production of reliable scenarios for the future. This is well illustrated with geese and sandpipers which breed in the Arctic. Changes in climate will directly impact on the breeding success of these birds, while vegetation and habitat structure will also alter in response to climate change, and will become less suitable for these species.

Effects of recent climate warming on Caribou habitat and calf survival

Brad Griffith, David C Douglas, Donald E Russell, Robert G White, Thomas R McCabe and Kenneth R Whitten

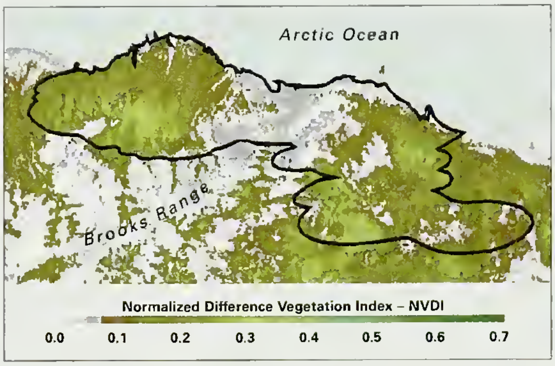
Migratory Barren-Ground Caribou *Rangifer tarandus granti* are the most important subsistence resource for northern indigenous peoples. They are likely to respond to global climatic changes that affect the distribution of their forage resources and the availability of forage through the year. The Porcupine Caribou herd is a large, internationally migratory herd of about 128,000 individuals that occupies the Alaska–Canada borderlands and uses a 300,000 km^2 annual range. The calving ground is a traditionally-used portion of the annual range that comprises 23,000 km^2 at approximately 70° north. Caribou migrate several hundred kilometres from winter ranges to the calving ground, arriving in mid- to late-May each year. Calves are born during the first week of June, and cows and calves remain on the calving ground for 4–6 weeks before dispersing to late-summer, fall, and winter ranges.

We measured the relative amount of green vegetation using data from polar orbiting satellites (Figure 1) to assess decade-long temporal trends in large scale habitat conditions on the calving ground and to investigate Caribou response to this habitat change. The vegetation index has shown a tendency toward earlier greening in spring and later plant senescence (dying off) in much of the northern hemisphere the 1980s, concurrent with independent estimates of climate change. High density calving was consistently located where the daily rate of increase in the amount of green plant biomass during lactation was greatest, in the period 1985–1996. This was probably because of the lactating cows' need for highly digestible new plant growth. Nutritional requirements of lactating cows are about double those during the remainder of the year.

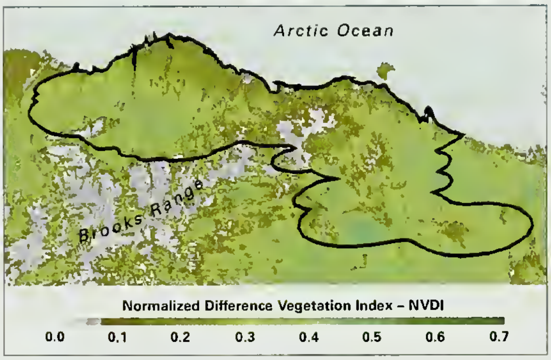
There has been a temperature increase on the calving ground of about 2°C from the mid-1960s to date. We used a sequence of satellite images to calculate the seasonal changes in the amount of available forage in this area (Figure 2) and observed a linear increase in the amount available to lactating Caribou during late-June, from 1985–1996 (Figure 3). As summers have warmed, vegetation growth has begun earlier, so greater amounts of plant biomass have accumulated by late-June. A dramatic exception to this general trend occurred in 1992 (Figure 3) when aerosols (tiny particles of liquids or solids) from the 1991 eruption of Mount Pinatubo in the Philippines finally reached the Arctic and resulted in cooler conditions and delayed plant growth.

Most of the differences in survival of Caribou calves while on

Migrating group of Caribou. *Photo: Mark Newman, FLPA.*



1996: 28 May – 02 June



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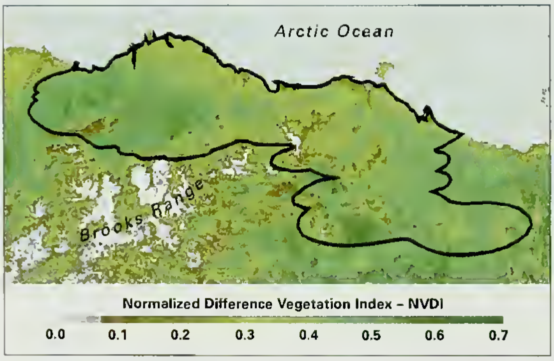


1996: 03 July – 06 July

Figure 1. Seasonal pattern in the amount of green plant biomass (Normalized Difference Vegetation Index (NDVI)) for the calving ground (black outline) of the Porcupine Caribou herd in Alaska, USA, and Yukon Territory, Canada, 1996. Larger (greener) values indicate relatively greater quantities of plant biomass.

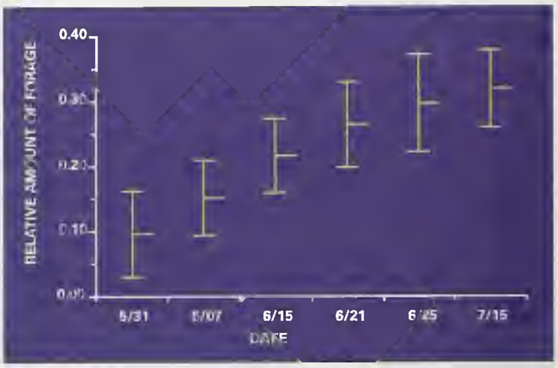


Figure 2. Seasonal profile of the relative amount of green plant biomass on the calving grounds of the Porcupine Caribou herd, Alaska and Canada. Averages from late May to early July, 1985–1996.

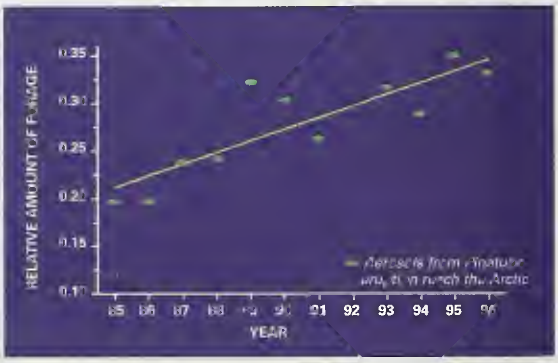


Figure 3. Annual trend in the relative amount of green plant biomass available to lactating cows of the Porcupine Caribou herd in late-June, 1985–1996.

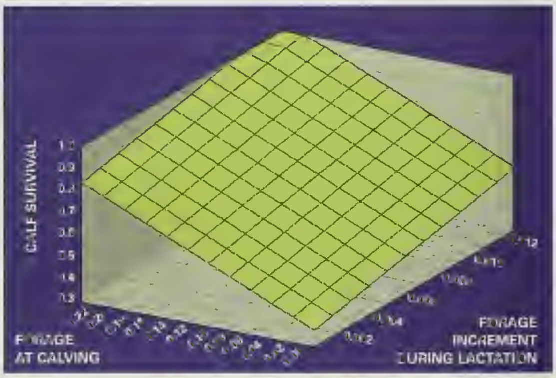


Figure 4. Relationship of Caribou calf survival to the amount of forage available to cows at calving and to the rate of increase in available forage during lactation, Porcupine Caribou herd, Alaska and Canada, 1985–1996.

Tundra in early summer.

the calving ground from 1985–1996 can be explained by the relative amount of green forage available to cows at calving and the daily rate of accumulation of green forage after calving and during lactation (Figure 4). When greater amounts of forage are available during late-June, cows are better able to cope with the nutritional demands of lactation. They then have a higher probability of early conception in the fall. Thus, in years following warmer summers, calves are born earlier. This phenomenon suggests that Caribou are adaptable and able to track climate warming effects on their habitats. Analysis indicated no additional effect of the severity of the previous winter or predation risk from Grizzly Bears *Ursus arctos.*

Our preliminary conclusions are that climate change effects are evident in summer temperatures, forage available for lactating cows, June calf survival, and in calving date for the Porcupine Caribou herd. However, in spite of increasingly favourable spring and summer habitat conditions, the herd has not shown a consistent increase. The population increased at about 5% per year until 1989, but has decreased by about 5% per year since. Deeper or more persistent snow on winter ranges might theoretically reduce access to forage or increase energetic demands by Caribou and reduce their survival, however, our limited data on snow depth and duration during winter months do not suggest this is occurring. Furthermore, estimates of spring body condition of Caribou in the herd do not suggest declining health, which might be expected if icing events were reducing access to winter forage. Increased summer insect harassment might similarly be expected to reduce body condition and thus conception rates in the fall. However, our observation that calving date has advanced with warming summers is inconsistent with this hypothesis.

Much remains to be learned of the mechanisms governing long-term population behaviour. The effects of climate change on wildlife populations may be quite complex, variable, and counteracting among seasons. Assessment across many years and throughout the entire annual cycle of an organism is essential to any understanding of the population implications of climate change.

Further reading

Cameron, R D, Smith, W T, Fancy, S G, Gerhart K L, and White, R G (1993) Calving success of female caribou in relation to body weight. *Canadian Journal of Zoology* 71: 480–486.

Myneni, R B, Keeling, C D, Tucker, C J, Asrar, A and Nemani, R R (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.

White, R G (1983) Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40: 377–384.

Waterbirds on the edge: climate change impact on Arctic breeding waterbirds

Christoph Zöckler and Igor Lysenko

More than two-thirds of all species of geese and almost all sandpipers breed in the Arctic; hence the region is of crucial importance for waterbirds. Weather conditions directly impact on the breeding success of these birds. Indirectly, longer-term changes will also alter breeding success through changes in vegetation and habitat structure. It is expected that climate changes will lead to major habitat shifts in the Arctic and result in an environment less suitable for breeding water birds.

Arctic birds are migratory and spend most of their annual life cycle outside of the Arctic. Their well-being depends on many different factors, as illustrated in Figure 1. Weather and climate are important matrix factors during the three to four months when these birds breed and rear their young. Geese and ducks also moult in the Arctic.

The majority of Arctic water birds spend their breeding season in areas of tundra vegetation. In this study, current species distributions were correlated with current vegetation, and then the likely changes in the vegetation were modelled to look at the impacts that this would have on species distributions. To understand how vegetation patterns might change, maps of current vegetation were linked with climate models to predict future scenarios. All available models use a rather broad classification of vegetation types, with only three major types distinguished in the Arctic: tundra, taiga/tundra and boreal forest (mainly coniferous). Although broad, these are sufficient for a first approximation of the impacts.

For mapping vegetation changes, the MAPSS (Mapped Plant Soil System) equilibrium biogeography model was used, which links vegetation patterns to climate. The HadCM2GSa1 model was then used to project the climate conditions at the time of CO_2 doubling (2070–2099). This model is derived from the Hadley Centre simulations, with combined greenhouse gas and sulphate aerosol forcing, and predicts a moderate warming of 1.7°C globally and 4°C for high (Arctic) latitudes. Other models predict temperature increases of up to 5.2°C globally and 7°C for Arctic latitudes. In order to provide a more extreme scenario, the UK Meteorological Office (UKMO) model (low resolution), although now relatively old, was applied.

Changes in vegetation patterns will be most extreme for tundra areas. Overall losses of current tundra distribution are estimated between 40 and 57%, with most being replaced by forest. Movement of tundra into new areas is highly restricted due to the northern barrier of the Arctic Ocean; new tundra areas amount to only 5%. These changes will have major implications for population size and development of Arctic birds. Geese and sandpipers will be particularly affected as they breed almost entirely in the tundra areas.

An estimated 8.4 to 10.4 million geese breed in the Arctic tundra. Assuming that habitat area is a limiting factor, and that birds are evenly distributed within their ranges, the predicted change in vegetation could mean a loss of almost half of the goose population as taiga and boreal forest encroach on their habitat. Under such simplified assumptions, only 4 to 5 million geese and about 7.5 million Calidrid sandpipers will remain in the tundra by 2070–2099. These changes will not be evenly distributed between species. Table 1 and Figure 2 show how the impacts will vary for selected species. The few areas where tundra appears to increase will be of minor importance. For a few species, more detailed data is available which shows the

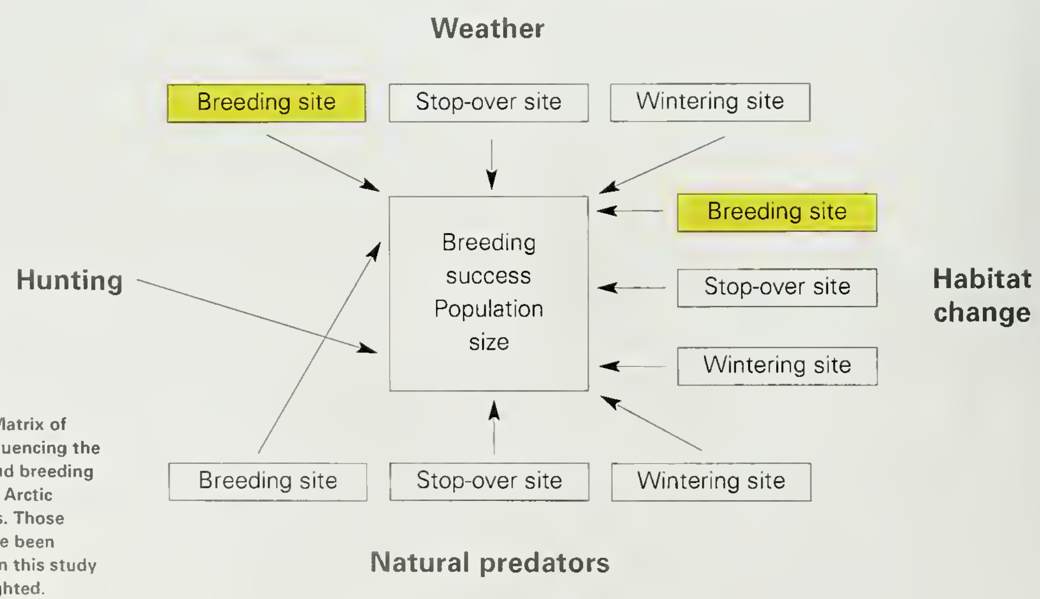
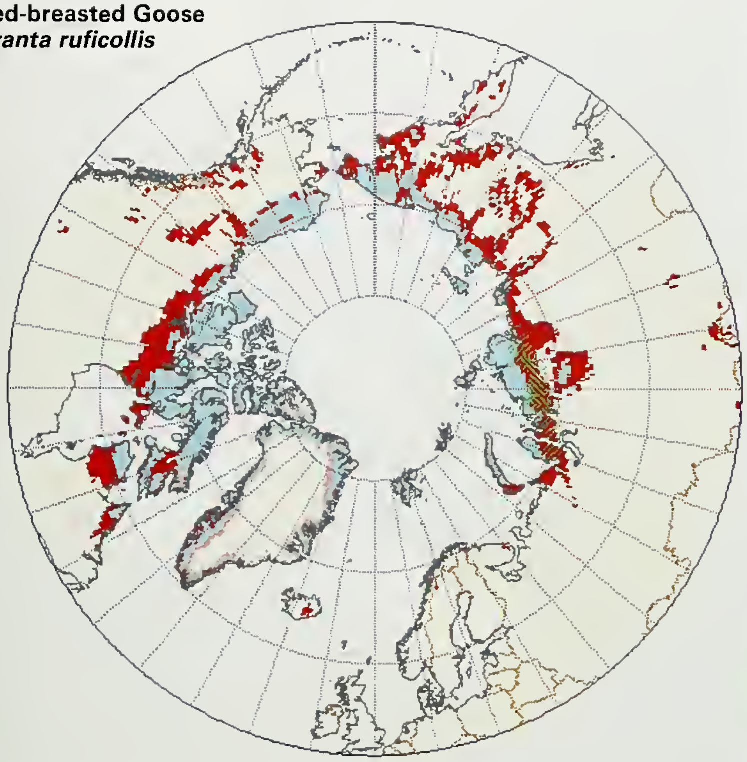


Figure 1. Matrix of factors influencing the survival and breeding success of Arctic waterbirds. Those which have been analysed in this study are highlighted.

Red-breasted Goose
Branta ruficollis



Knot
Calidris canutus

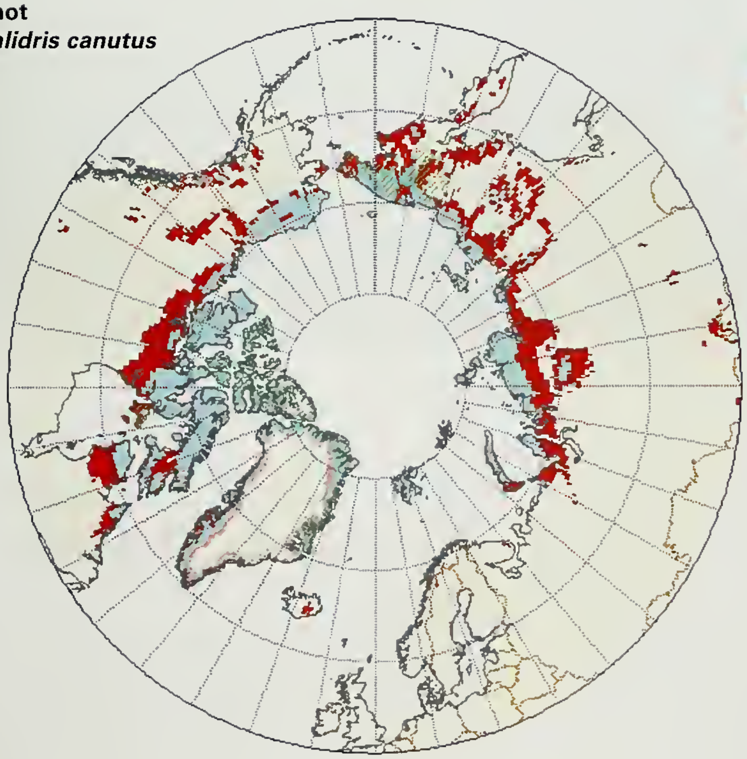


Figure 2. Current breeding distribution and predicted changes in breeding habitat (2070-2099) of the Red-breasted Goose *Branta ruficollis* (top map) and the Knot *Calidris canutus* (bottom map).

Key

▨ Breeding areas

▩ Breeding areas, high density

Change in tundra zone over the period of doubling of CO_2 (80–100 years) predicted as moderate warming by HadCM2GSa1 Climate Change Model.

🟦 Tundra, no change

🟥 Tundra loss

▭ Expansion of tundra

☐ Unclassified land

Red-breasted Goose. *Photo: Tom Ulrich, OSF*

distribution of areas of particularly high breeding density; the impacts of changing scenarios on five of these species are illustrated in Table 2.

Overall, the study predicts that there will be considerable changes in the distribution and a reduction in the total area of Arctic tundra. This suggests that such changes will have highly significant impacts on Arctic water birds. These impacts will vary considerably between species, but in patterns that are similar irrespective of the climate model used. For the Tundra Bean Goose *Anser fabalis rossicus/ serrirostris*, 76%* of its tundra habitat is expected to change, whereas only 5%* of tundra habitat currently occupied by the Sanderling *Calidris alba* is likely to change.

Three species of globally threatened water birds may be severely affected: the Red-breasted Goose *Branta ruficollis* is projected to suffer a loss of 67%* of its current habitat to forest; 57%* of the habitat of the Spoon-billed Sandpiper *Eurynorhynchus pygmaeus;* and 54%* of that of the Emperor Goose *Anser canagicus* are also likely to disappear (see Table 1). The latter is already in decline and is highlighted as needing further conservation attention. Its status is already under consideration for listing in the IUCN (World Conservation Union) Red List and this additional threat might well justify its inclusion. However, the Curlew Sandpiper *Calidris ferruginea* appears to fare better, with only 14%* of its core breeding area

* *According to the moderate Had CM2GSa1 model.*

Table 1. Loss of breeding area (as a %) for 23 Arctic waterbird species applying two different circulation models (HadCM2GSa1 = moderate warming; UKMO = extreme warming).

SPECIES		HadCM2GSa1*	UKMO*
Tundra Bean Goose	*Anser fabalis rossicus/serrirostris*	76	93
Red-breasted Goose	*Branta ruficollis*	67	85
Spoon-billed Sandpiper	*Eurynorhynchus pygmaeus*	57	57
Emperor Goose	*Anser canagicus*	54	54
Ross's Gull	*Rhodosthetia rosea*	51	73
Red-necked Stint	*Calidris ruficollis*	48	68
Sharp-tailed Sandpiper	*Calidris acuminata*	46	74
Little Stint	*Calidris minuta*	45	65
Curlew Sandpiper	*Calidris ferruginea*	41	70
Pectoral Sandpiper	*Calidris melanotos*	38	60
Dunlin	*Calidris alpina*	36	58
White-fronted Goose	*Anser albifrons*	36	57
Long-billed Dowitcher	*Limnodromus scolopaceus*	31	54
Great Knot	*Calidris tenuirostris*	31	42
Lesser White-fronted Goose	*Anser erythropus*	28	29
Barnacle Goose	*Branta leucopsis*	21	27
Western Sandpiper	*Calidris mauri*	19	21
Brent Goose	*Branta bernicla*	16	44
Knot	*Calidris canutus*	16	33
Snow Goose	*Anser caerulescens*	14	46
Canada Goose	*Branta canadensis*	13	22
Pink-footed Goose	*Anser brachyrhynchus*	10	10
Sanderling	*Calidris alba*	5	25

*Value could be substantially higher as unclassified areas in this GIS analysis may contain different tundra types eg mountain tundra.

changing to unsuitable habitats. The situation is reversed for the Dunlin *Calidris alpina* and the Pectoral Sandpiper *Calidris melanotos*, where there is a greater proportional loss of habitat from their core breeding areas compared to the total area of tundra loss in their entire breeding area (see Table 2).

Numerous variables will affect the interplay between climate change and population sizes. These are compounded by the limitations of the models. Of critical importance is that mobile species, rather than static ones are being considered. Geese, in particular, have demonstrated flexibility and will respond to changing habitats. Barnacle Geese *Branta leucopsis*, for example, have established large colonies outside the Arctic in the Baltic Sea. Most of the sandpipers are unable to move so easily, although some, like the Temminck's Stint *Calidris temminckii* (not included in this study), are likely to adapt, as has been observed recently in the colonisation of semi-natural horse pastures. Some populations might even benefit from the change in vegetation as well as from warmer conditions. Many species will be able to extend their ranges concurrently with the northward shifting distribution of their favoured habitat. But those species breeding on the margin of high Arctic habitats will be unable to find any space to move to, as southern vegetation types shift further north under a warming climate. There is still little known about the natural capacity of species in Arctic habitats. Densities are also determined by factors outside of breeding ranges, including stop-over sites and wintering areas. If population sizes are to remain at current levels, there would have to be considerable increases in the density of individuals in the remaining tundra, which may increase interspecific and intraspecific competition.

Records show that forest shifts of up to 2,000 km have been recorded in recent geological times. However, there are a number of factors which may prevent, or slow, the northward migration of forest today. These factors may include: poor or cold soils with underlying permafrost, wetlands, mountain ridges, lack of birds or mammals to carry seeds, increasing storm activity and improving conditions for pest insects. Grazing mammals, such as Reindeer or Caribou, often neglected in consideration of vegetation development, might limit the rate of tree growth considerably and keep tundra habitats actively open. Fires have both negative and positive influences on forest growth.

There is evidence of a recent northward migration of forest in Alaska. However, the rate of movement observed is still far slower than that of prehistoric times, which supports the theory of a lagged response to an accelerating change in climate. Estimates of the rate of forest migration range between 200 and 2,000 m/year.

The shifts in the forests themselves may have implications for both global carbon budgets and for other aspects of biodiversity. Forests are important habitats with their own suite of species, and it seems likely that increases in the total area of boreal forest will benefit many other species. Increases in forest area will act as an important additional CO_2 sink and a compensation for lost

Table 2. Possible scenario for changes in the area of tundra habitat and arctic bird populations with CO_2 at twice its preindustrial level, obtained by applying the HadCM2GSa1 model. The proportion of tundra lost from each bird species' range is taken to be the absolute area lost as a percentage of the current range. A simple estimate of the bird population after habitat loss assumes that the population changes from its current level in direct proportion to this change in tundra area within the range. A more refined estimate takes into account the existence of core areas holding high bird densities and calculates bird losses from losses of tundra from the core area and other areas separately. The following information was used on bird breeding densities: Curlew Sandpiper (4.0 pairs/ km^2 in core areas and 1.4 pairs/ km^2 in other areas); Dunlin (up to 33 pairs/ km^2 in core areas and a maximum of 5 pairs / km2 in low density areas); 83% of Red-breasted Geese were assumed to breed in their core areas. Density data do not exist for Sharp-tailed Sandpipers or Pectoral Sandpipers, so the relative densities in core and low density areas were based on data for Curlew Sandpipers, which need to be verified.

Species		Total area of current breeding distribution. $km^2 x10^6$	Tundra within the current distribution. $km^2 x10^6$	Current Arctic pop. size (pairs)	Tundra lost from range by 2070/99*. $km^2 x10^6$	Prop. of tundra lost (%)*	Area of high density (core breeding areas). $km^2 x10^6$	Core area lost by 2070/99*. $km^2 x10^6$	Prop. of core area lost (%)*	Scenario for pop. size 2070/99(exc. core area high density data)	Scenario for pop. size 2070/99 (inc. core area high density data)
Dunlin	*Calidris alpina*	2.350	1.579	2,300,000	0.846	36	0.234	0.115	49	1,472,000	1,094,000
Curlew Sandpiper	*Calidris ferruginea*	0.814	0.786	1,096,000	0.332	41	0.271	0.039	14	646,640	888,000
Sharp-tailed Sandpiper	*Calidris acuminata*	0.129	0.122	166,000	0.059	46	0.021	0.009	43	89,640	103,000
Pectoral Sandpiper	*Calidris melanotos*	2.567	2.068	150,000	0.968	38	0.064	0.039	61	93,000	64,500
Red-breasted Goose	*Branta ruficollis*	0.408	0.348	88,000	0.274	67	0.097	0.086	89	29,040	10,600

*Value could be substantially higher as unclassified areas in this GIS analysis may contain different tundra types eg mountain tundra.

Emperor Geese, Aleutian Islands. *Photo: Authors*

Spoon-billed Sandpiper, Siberian Arctic. *Photo: Roger Tidman.*

forest area at other latitudes. On the other hand an extending forest area reduces albedo (the natural reflectance of light and heat from the earth's surface), which will contribute further to global warming. From the perspective of the Arctic tundra, there is considerable concern that this habitat will be 'squeezed' as there is no room for its extension beyond the northern shores of the Arctic Ocean. This may be further exacerbated by the impacts of permafrost thawing and sea level rise.

The complexity of the impacts of changing climates on biodiversity is well illustrated in the Arctic, where dramatic changes are likely to occur over relatively short time-scales. Climate models can be used to predict changes in vegetation, although further factors will also come into play. These changes in habitat are likely to further influence the distribution patterns and total numbers of animal species which depend on these habitats. The levels of impact may be dramatic for some Arctic water birds breeding in tundra habitats. Many are likely to see losses of over 50% of their current breeding areas, with little or no expansion of tundra into new areas. The impacts, in terms of total bird numbers, are difficult to predict given the many complex factors affecting breeding success and survival throughout their life-histories.

Further reading

Huntley, B (1996) The responses of vegetation to past and future climate changes. In: Oechel, W C, Callaghan, T, Gilmanov, T, Holten, J I, Maxwell, B, Molau, U and Sveinbjörnsson, B (eds). *Global Change and Arctic Terrestrial Ecosystems*. Ecological Studies 124: 290–311.

Huntley, B and Cramer, W (1997) Arctic ecosystems and environmental change. *In: Disturbance and Recovery in Arctic Lands*. NATO ASI Series: 1–24.

Neilson, P R and Drapek, R J (1998) Potentially complex biosphere responses to transient global warming. *Global Change Biology* 4: 505–521.

Zöckler, C and Lysenko, I (2000). *Water birds on the edge: first circumpolar assessment of climate change impact on Arctic breeding water birds*. World Conservation Press, Cambridge, UK.

Zöckler, C (1998) *Patterns in Biodiversity in Arctic Birds*. WCMC Bulletin No. 3. World Conservation Monitoring Centre, Cambridge.

Effects of climate change on Antarctic sea ice and penguins

David Ainley, Peter Wilson and William R Fraser

The first fossil remains of pygoscelid penguins (a small group of species which belong to the genus *Pygoscelis*) date from the beginning of the Pleistocene, about three million years ago. This is thus a group of modern species which has persisted through several major fluctuations in global climate. Throughout their evolution, these penguins have been found only in cold Antarctic and sub-Antarctic seas, so the extent of the area suitable for them is presumed to have varied considerably as regional climates have altered between glacial and interglacial periods. Recent studies of penguins, however, have also highlighted the fact that marked variation in response to climate change can occur, even among similar species.

The Adélie Penguin *Pygoscelis adeliae* inhabits the sea ice zone that rings Antarctica. Unlike all other penguin species, except the Emperor Penguin *Aptenodytes forsteri*, it is found only where sea ice persists well into spring. Most of its breeding colonies are within the Antarctic Circle. By contrast the Chinstrap Penguin *Pygoscelis antarctica* occurs further north and its breeding grounds do not extend into the Antarctic Circle. The two species are so similar in structure that they are thought by some to form a superspecies. They are also similar in diet and foraging methods, feeding mainly on Antarctic krill during summer in the region where their distributions overlap (northwestern coast of the Antarctic Peninsula and southern Scotia Sea). Together these penguins comprise about 80% of the total biomass of birds in the Southern Ocean. The climate of the Antarctic coast has been warming. What have been the consequences for these penguins?

Suitable nesting terrain for both species consists of gravel, free of snow and meltwater, that can be reached after a short walk (<2 km during the chick-feeding period) from the sea. However, to be suitable for Adélie Penguins, such areas have to be adjacent to sea covered by loose pack ice during the southern hemisphere summer breeding season. On the other hand, Adélie Penguin colonies are absent where, in the vicinity of suitable coastal, ice-free land, the adjacent sea ice is usually compacted and extensive. In such cases travelling over this near-shore sea ice between the breeding site and more open sea covered by loose pack requires too much time and energy. During glacial maxima, the last of which was 19,000 years ago, most of the Antarctic coast was covered by glacial ice and with the colder temperatures sea ice extended farther north. Adélie Penguins must have nested mainly on islands further north (where today, in most cases, loose pack ice does not persist and they no longer nest). For most of the period since the last glacial maximum, Adélie Penguin populations have been increasing and colonising new areas to the south, as suitable nesting habitat has been exposed by retreating ice sheets.

More recently, during the last 50 years, colonies of the Adélie penguin have been declining and disappearing from the west coast of the northern Antarctic Peninsula, and offshore islands such as the South Shetlands. This is the northern part of the species' range. The process has accelerated in recent decades and is correlated with the rapid disappearance of sea ice in this region. Air temperature records for the last 50 years reveal a marked warming which has been particularly evident in winter. By contrast, warming in the southern-most part of the Adélie Penguin's range (notably in the Ross Sea) has loosened rather than banished the sea ice. This has coincided with increases in breeding colonies there, though the rates of change have slowed recently. Analysis of annual changes in breeding populations in the Ross Sea, from 1960 onwards, show that the extent of sea ice in late winter/early spring, when sea ice annually reaches its maximal extent, had a negative effect on population growth, with a five-year lag. In other words, in that part of the Southern Ocean where ice is a persistent feature (elsewhere than the Antarctic Peninsula, west coast), a lot of ice

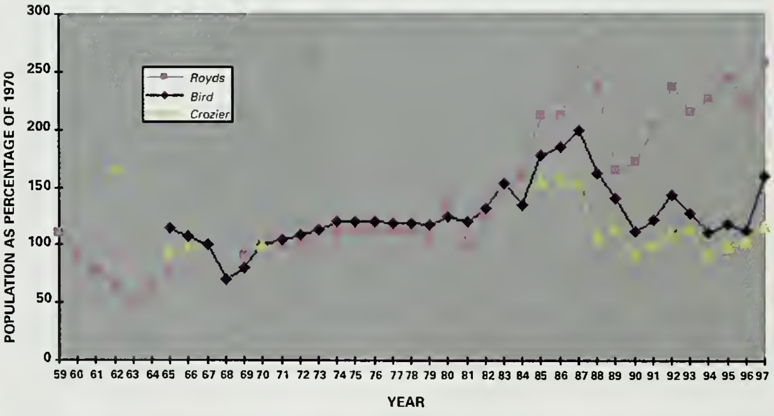


Figure 1. Changes in the numbers of pairs of Adélie Penguin breeding at three colonies (Capes Royds, Bird and Crozier) on Ross Island, Antarctica, 1959–1997. Current numbers at these colonies are: Royds – 4,000 pairs, Bird – 45,000 pairs, Crozier – 170,000 pairs (data from Wilson *et al.* 2000, in press). Numbers are expressed as percentages of those in 1970.

Adélie Penguins. *Photo: Michael Gore, FLPA*

Splitting sheets of sea ice, McMurdo Sound, Antarctica. *Photo: Norbert Wu, OSF*

leads to population decline and less extensive ice leads to population increase. The lag time is consistent with the species' demography, because Adélie Penguins typically join the colonies at about five years old and so population growth is highly sensitive to juvenile survival. An illustration of these effects is provided in Figure 1 for three penguin colonies on Ross Island, located in the Ross Sea at the southernmost edge of the Adélie Penguin's range.

A rather different relationship between population trend and incidence of extensive sea ice is found in the northern part of the range, because there is an optimal extent and concentration of sea ice for this species. The penguins must have access to pack ice in winter in order to feed. In the northern part of the species' range, the frequency of winters with pack ice appears to have fallen below the level required for the population to sustain itself. At the southern edge of the range, pack ice is consistently present in winter and the effect of warming is to loosen the pack and make it a more suitable habitat. Further losses of sea ice are likely to cause the Adélie Penguin population declines observed in the Antarctic peninsula to be repeated further south. By contrast, the Chinstrap Penguin, which avoids pack ice as much as possible and is often found in ice-free waters, is increasing and extending its range southwards along the western coast of the Antarctic Peninsula, apparently in response to warming and disappearance of sea ice cover there. Hence, the distributions of these two closely related species appear to be undergoing rapid but opposite changes in response to recent climate change.

Further reading

Ainley, D G and Divoky, G J (2000) Birds: seabird responses to global/climate change. In Steele, J, Thorpe, S, Turekian, K (eds) *Encyclopedia of Ocean Sciences* Academic Press, London.

Fraser, W R, Trivelpiece, W Z, Ainley, D G and Trivelpiece, S G (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biology* 11: 525–531.

Smith, R C, Ainley, D, Baker, K, Domack, E, Emslie, S, Fraser, B, Kennett, J, Leventer, A, Mosley-Thompson, E, Stammerjohn, S and Vernet, M (1999) Marine Ecosystem Sensitivity to Climate Change. *BioScience* 49: 393–404.

Wilson, P R, Ainley, D G, Nur, N, Jacobs, S S, Barton, K J, Ballard, G and Comiso, J C (2000) Adélie penguin population growth in the Pacific sector of Antarctica: relation to sea-ice extent and the Southern Oscillation. *Marine Ecology-Progress Series*.

Changes in tropical regions

Introduction by Mark Spalding, Stephen Grady and Christoph Zöckler

There is much greater uncertainty in the predictions of climate change in the tropics, compared with high arctic and temperate regions. Under most models, the tropics and near-tropics are predicted to encounter more gradual temperature increases than at higher latitudes, and these regions have certainly shown less extreme changes up to the present time. Predicted patterns of precipitation are more complex. Overall, precipitation levels are expected to increase worldwide, although some areas will receive reduced precipitation.

Major storms and cyclones are an important feature of many tropical regions. Existing research suggests that there may be changes in the frequency and intensity of storms (and other extreme weather events) in many areas, although these will not always be increases, and regional patterns remain almost impossible to predict. Because tropical storms are generated over oceans with a surface water temperature of 26°C or greater, it is probable that as sea surface temperatures increase, the overall distribution of storms will increase north and south of the equator.

The high temperatures which characterise the tropics and near tropics produce highly dynamic patterns of water use and circulation. Water is rapidly lost through evaporation, however complex systems have evolved to hold and maintain water in ecological systems. In some tropical rainforests it has been estimated that water is recycled five times before even touching the ground. Even small changes in precipitation may cause dramatic changes in the water cycle and to the levels of humidity, which could have significant consequences for natural ecosystems. While many areas of the wet tropics are predicted to remain wet or even get wetter, some models predict drying in certain areas, notably in parts of the Amazon basin and West Africa. Such drying has, in fact, been ongoing in the eastern part of the Amazon basin for a number of years and the trend is continuing. Such drying also brings a greater risk of forest fires. The consequences in terms of biodiversity are important, and significant losses of forest area will also act as a positive feedback, as more carbon dioxide from the disappearing forest enters the atmosphere.

Moving towards the edges of the tropics and beyond, there are wide areas of drylands. Over the past century massive changes have been observed in these areas as the result of droughts and the conversion of natural ecosystems to grazing land. Processes of desertification have been widely linked to increasing population pressure, the clearance of vegetation and over-grazing in these areas. The direct role of human-induced climate change on this is less clear, however it is likely to be significant in at least some areas. In the future, patterns of drying may become more widespread. Some models predict considerable levels of drying in some already-dry areas, including much of Australia, East Africa and Central America. In entirely natural systems such changes would probably mean gradual changes in vegetation type, with a loss of tree cover in many areas and a lower carrying capacity for many species. Human presence greatly exacerbates these impacts.

Even our basic understanding of changing biodiversity patterns in tropical regions remains poor, and most existing knowledge is very recent, with base-line data going back only a few years or decades at most. Tropical ecosystems have very high levels of species richness, and these systems have evolved under a relatively long-term stable climate. These species and ecosystems may thus be more sensitive to even small changes in the occurrence of extreme climatic events. Wide areas have been subjected to recent changes in land-use on a massive scale, including deforestation, the intensification of agriculture and livestock grazing, together with considerable urban growth. The extent of these changes also means it is thus currently difficult to distinguish between the impacts of changing climates from the massive changes being wrought by other factors. These problems greatly restrict the study of changes in species distributions or of subtle changes in phenology at regional scales. It is still possible, however, to look at short-term changes in some areas, and to utilise models to predict longer term changes.

Localised changes are more difficult to predict in global models, but it is clear that local changes may significantly effect geographically restricted ecosystems. Mountains are a particularly clear case. One ecosystem of particular concern is that of tropical montane cloud forests. There is already evidence that these ecosystems are being severely impacted by drying out, mainly through the raising of the cloud base, and subsequent changes to the species composition are already being reported from a number of locations. One such example is the decline in the numbers of the Harlequin Frog and disappearance of the Golden Toad in Costa Rica's Monteverde cloud forest following the abnormal weather conditions of the 1986–87 El Niño event, with exceptionally high temperatures and low rainfall.

Wetland areas are likely to be impacted by higher temperatures and changes in precipitation. There is concern that two extremely important wetland regions in Brazil, the flooded forest of Várzea in the Amazon and the Pantanal in Southern Brazil, may well become highly reduced in area, with subsequent losses of biodiversity. Sea level rise will also impact a number of coastal ecosystems. Mangroves are highly adapted trees that thrive in intertidal waters, and are a critical resource for biodiversity, as well as for their role in fisheries and forestry. Although mangrove species are highly opportunistic, in those areas where these forests are backed by agricultural land, there may be nowhere for them to retreat as waters begin to encroach on coastal lowlands.

More research has been undertaken in assessing the impacts of climate change on agricultural biodiversity. Changes have been observed in the phenology of annual crop species, which are found to reach maturity more quickly under increasing temperatures. Also, under enriched CO_2 environmental conditions, temperate crops have been observed to have a stronger growth response than tropical varieties. Hence some tropical crops may show a negative response under an increasingly CO_2-rich environment, with subsequent warming. For example, recent models predict that rice yields could decrease by 7.4% per 1°C increase. These factors illustrate the potential changes that could also occur to the growing patterns of species in natural tropical ecosystems.

The tropics and near-tropics also have a very large number of islands and some entire nations live at, or very close to sea level. Biodiversity in these areas is extremely important, often with high numbers of endemic species, major seabird nesting colonies and nesting beaches for marine turtles. Sea level rise represents a particular threat to human populations as well as to the biodiversity on these islands. Even before islands become inundated, it is likely that the rising water levels will contaminate the thin layers of freshwater which make up the water table, rapidly impacting the vegetation. Offshore from many islands and tropical coastlines, the coral reefs, which play an important role in the protection of coastlines from erosion, are also under considerable threat and may in fact be one of the natural habitats most threatened by climate change.

Many tropical ecosystems have evolved over millions of years, and some refugia have survived through the ice ages, evolving into complex and highly diverse communities. Many are finely balanced ecosystems with high species diversity, and some species have very tightly defined ecological requirements. Such species, and the ecosystems in which they live, could thus be highly sensitive, even to the lower rates of change predicted for the tropics. The examples of cloud forests and coral reefs provide the first warnings of such sensitivity.

Impacts of climate change on birds, amphibians and reptiles in a tropical montane cloud forest reserve

J Alan Pounds

Tropical montane cloud forests occur where moisture-laden tradewinds blow onto a mountain range, leading to the formation of cloud and mist at high elevations. The deposition of this moisture onto the vegetation and soil plays a key role in the hydrological cycle. Montane cloud forests, characterised by persistent high humidity, hold the highest levels of animal endemism to be found on the continents and consequently they rank high when areas are prioritised for the conservation of biodiversity. Their richness in species has come about partly because they often form archipelagos of habitat islands, isolated from each other by lowland habitats that are unsuitable for the specialised inhabitants of the cloud forest. This has frequently led to the evolution of species unique to each cloud forest patch. However, another important factor is the extremely long periods for which the distinctive physical and climatic conditions of cloud forests have persisted in the same region and the influence of the glacial cycles on the extent and interconnectedness of cloud forest fragments. It is to be hoped that the biodiversity of these areas can be protected in perpetuity by establishing protected areas to prevent damage from forestry or other human land use. However, recent studies, including global climate modelling and long-term monitoring of the fauna and physical conditions in cloud forests, indicate that setting aside tracts of cloud forest does not ensure the survival of this unique ecosystem in the face of global warming.

Evidence from Costa Rica's Monteverde Cloud Forest Preserve indicates that animal populations representing a wide taxonomic range have undergone changes in distribution and abundance in response to changes in hydrology. The altered hydrology is related to increases in tropical air and sea surface temperatures since the mid-1970s. Monteverde is a 25,000 ha preserve in the Cordillera de Tilarán, straddling the continental divide in Costa Rica. Climate trends measured at an elevation of 1,540 m suggest that isopleths of relative humidity, and hence zones of cloud and mist formation, have shifted to higher elevations, reducing the frequency of mist during the dry season. Mist frequency is negatively correlated with sea-surface temperature in the equatorial Pacific 850 km away and has declined markedly in recent decades. Runs of days with no mist have increased and annual minimum streamflow has declined even though average rainfall shows no clear trend (Figure 1). The incidence of dry days is correlated with El Niño oscillations in sea-surface temperature but, after this effect is allowed for, there remains an increase in their frequency. Associated with the declines in mist frequency is a constellation of changes in populations of birds, lizards, and amphibians.

Among breeding birds, cloud-forest intolerant foothill species, scattered widely across taxonomic groups, have increased in abundance and diversity at 1,540 m as they have extended their distributions up the mountain slope. Year-to-year fluctuations in net colonisation rates of foothill bird species were strongly related to annual variation in mist frequency. Bird species associated with cloud forest have not yet shown much evidence of population decline at 1,540 m or retraction of range to higher elevations. This may be because the measure of bird abundance (proportion of six-day periods with the species present) may not detect subtle population declines, but it is also possible that long-lived cloud forest birds are staying on their territories as long as they can, despite climate change. Colonists of the foothill species are probably young birds seeking territories for the first time. As a result of these changes unusual bird communities have developed – for example it is very infrequent elsewhere to find the current coexistence of Resplendant Quetzal (characteristic of cloud forest) and Keel-billed Toucan (typical of the foothills) in the same community.

Anoline lizard populations have also declined in association with reduced mist frequency, but the most dramatic change has been the disappearance of 20 of the original 50 frog and toad species from a 30-km^2 study area following a warm, dry period in 1987. The most spectacular example was the rapid, complete disappearance of the Golden Toad from the study area. In 1987 1,500 individuals were recorded at the principal known breeding site, but only one male was observed there in 1988 and 1989. None have been found anywhere from 1990 onwards. It now seems probable that this species, which was endemic to Monteverde, is now globally extinct and is perhaps the first documented casualty of the current global climate change. The

Golden Toad. *Photo. Mike Linley, RSPB Images.*

Monteverde forest, Costa Rica. *Photo: Michael Fogden, OSF.*

synchronous crash of many of the frog and toad species and two subsequent downturns of surviving populations form a pattern that is significantly associated with the timing of changes in mist frequency. Many population crashes of highland amphibian populations have been reported worldwide. Factors such as epidemic disease (including fungal outbreaks) and damage to embryos by ultra-violet radiation are among the proximate causes suggested. A single disease that attacks the moist skin of amphibians is unlikely to account for the population extinctions at Monteverde, because many unrelated species (including reptiles) have been affected. UV radiation is also unlikely as a general driver because species which live in shade or bury their eggs have also been affected. The patterns at Monteverde suggest that hydrological change is a key factor. Because its effects on natural populations may be indirect and subtle (stimulating pathogen outbreaks, for example), intensive investigation may be needed before the mechanisms of biological change are understood.

Prospects for the future of tropical montane cloud forests and their biota are not good. Global climate models have been used to predict the elevation at which conditions suitable for cloud forests will occur in future climates as carbon dioxide continues to accumulate in the atmosphere. The same models have been used to study past climate change. They indicate that cloud forest conditions at the last glacial maximum occurred at much lower elevations than they do today. This finding is in accord with analyses of the pollen paleorecord, which shows that cloud forest plant species occurred lower on mountain slopes during glacial times. In the climates likely to prevail at the end of the present century, conditions suitable for cloud forests are expected to occur several hundred metres higher in elevation than they do today. Thus, many cloud forests, including Monteverde, may undergo a severe reduction in area and could disappear altogether as the zone of cloud formation shifts to elevations above the highest peaks. These forests are sensitive indicators of climate change and are among the areas where the greatest losses of biodiversity may occur.

Resplendant Quetzal. *Photo: MPL Fogden, Bruce Coleman.*

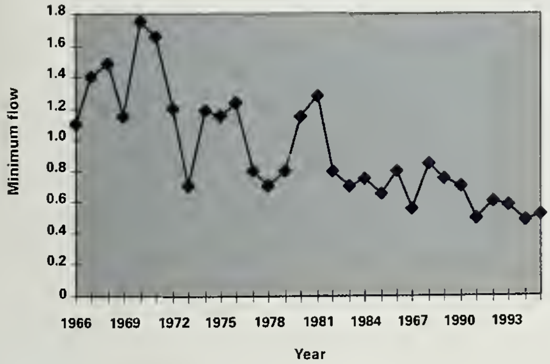


Figure 1. The minimum daily average rate of stream flow (in cubic metres per second) 1966–1995 in the Rio Cañas near Monteverde Cloud Forest Preserve.

Further reading

Long, A J (1995) The importance of tropical montane cloud forests for endemic and threatened birds. In Juvik, J O and Scatena, F (eds) *Tropical montane cloud forest* pp. 79–106. Springer Verlag (Ecological Series 110), New York.

Pounds, J A, Fogden, M P L and Campbell, J H (1999) Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.

Still, C J, Foster, P N and Schneider, S H (1999) Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608–610.

Changes in marine and coastal areas

Introduction by Mark Spalding

Global sea-surface temperatures have already begun to rise significantly, notably over the last 100 years, although these changes have been slightly less marked than the equivalent air temperatures (Figure 1). During this same period, mean global sea levels have risen approximately 18 cm. Most of these changes have occurred during the last 40–50 years. Such changes are already significant, but further provide an important pointer towards the changes which will continue for decades or even centuries to come.

The overall effects of these changes are highly complex and not fully understood. In addition to the direct impacts of rising temperatures and changing sea levels, it seems likely that there will be changes in ocean currents, changes in the distribution and intensity of extreme events, and more complex chemical and physical changes to the ocean environment.

Perhaps the most dramatic example of the impacts of ocean warming to date has been the global phenomenon of coral bleaching. More gradual changes may be largely unnoticed over wide areas, however, studies along the Californian coast clearly show that subtle changes may have already begun. Changes are also occurring in the open oceans. Alterations in the distribution patterns of some commercially important fish populations may be directly linked to changing temperatures. These changing temperatures are also likely to alter the patterns of water circulation and mixing.

Ocean surfaces are made up of a complex, but predictable, pattern of currents, upon which many species depend for the provision of food or the transport of larvae. Below the surface, there runs an equally important network of currents which play a critical role, for example, in bringing oxygenated water to the deep oceans and in transporting nutrient rich waters to areas of upwellings. A number of climate models have discussed possibilities of major shifts in coastal and ocean current systems, which may produce complex and profound changes across the planet. Although the evidence remains equivocal, there is some concern that the increase in frequency of the El Niño Southern Oscillation events over recent decades may be linked to anthropogenic climate change. There is also evidence for the possible weakening or 'switching off' of the North Atlantic Gulf Stream. The example of seabirds in the California Current gives some ideas of the sorts of impacts which are already occurring in the world's oceans. At smaller scales, wind plays a critical role in mixing the surface layers of the ocean. There is a very real concern that warming may increase the stratification of the ocean surface, reducing this surface mixing and hence the supply of nutrients to the all-important planktonic communities which lie at the base of the oceanic food-chains.

Global warming is increasing the volume of water in the oceans in two ways. Firstly, as water warms it expands in volume ('thermal expansion'). Secondly, rising air temperatures are causing land-locked ice in glaciers and ice-caps to melt at increasing rates and this water is being added to the water already in the oceans. These changes are complicated by local changes in the level of the land (isostatic changes) which occur in many areas. Rising sea levels will impact coastal regions in three broad ways: the inundation of coastal lands, the salinisation of water tables or natural aquifers, and increased erosion of coastlines. Natural ecosystems have adapted to such changes in the past, however such adaptation may be hindered by patterns of human land-use immediately surrounding such systems. The example of coastal marshes in the UK clearly illustrates the problem, but shows a potential solution. Natural systems may be important in reducing the rate of change and in protecting against coastal erosion.

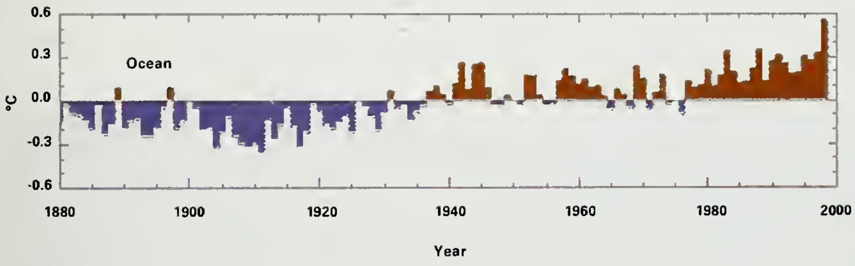


Figure 1. Increase in ocean temperatures over the last 120 years. Data are January to May global surface mean temperature anomalies (1880–1998), taken from National Oceanic and Atmospheric Administration.

Changes in seabird communities of the California Current, 1987–1999

Richard R Veit and K David Hyrenbach

Changes in the relative strength and routing of ocean currents are widely predicted consequences of climate change, although the exact shifts in particular localities are more difficult to predict. Any such changes will influence regional ecology, as changing temperature and nutrient supplies alter productivity and ecosystem structure throughout the food-chain. Seabirds provide a critical indicator of such fluctuations. They are highly dynamic and may well move as conditions shift. They are also readily observed and identified at sea without complex technologies. Seabird populations off southern California show changes in both abundance and community composition in response to short and long-term variability in ocean temperature. Warm-water species increase during warming episodes, while cold-water taxa decrease. It is likely that these fluctuations represent changes in distribution, as populations of mobile seabirds redistribute themselves to exploit changing environmental conditions and prey distributions.

Seabirds have been censused seasonally off southern California as part of the California Cooperative of Oceanic Fisheries Investigations (CalCOFI) programme since May 1987. Since this time, over 70,500 km and over 159,000 birds have been censused. These surveys have revealed drastic fluctuations in seabird abundance, which can be attributed to major physical, chemical and biological changes in the California Current. Sea level and ocean temperature off California have increased drastically during the period 1949–1993, while zooplankton biomass in the upper 200 metres of the water column has dropped dramatically (by about 70%). From a bird's perspective, this means that food is much scarcer, and is likely to be found much deeper in the water column.

The clearest sign of a changing avifauna off southern California is the drastic decline of overall seabird abundance. A 40% decrease in seabird numbers was reported between 1987 and 1994. Continued surveys have shown continuing low seabird densities during periods of El Niño and La Niña conditions, suggesting that longer-term factors are overriding inter-annual fluctuations. This declining trend is associated with a decrease in ocean productivity, gradual and persistent changes which have occurred concurrent with an increase in ocean temperature and a drop in macrozooplankton biomass.

In addition to declining overall abundance, ornithologists have documented changes in the makeup of seabird communities, which can be closely allied to the northward shifts in particular oceanographic conditions and water mass boundaries predicted as a result of global warming. Simultaneous declines in the

Sooty Shearwaters at sea. *Photo: E & D Hosking, FLPA*

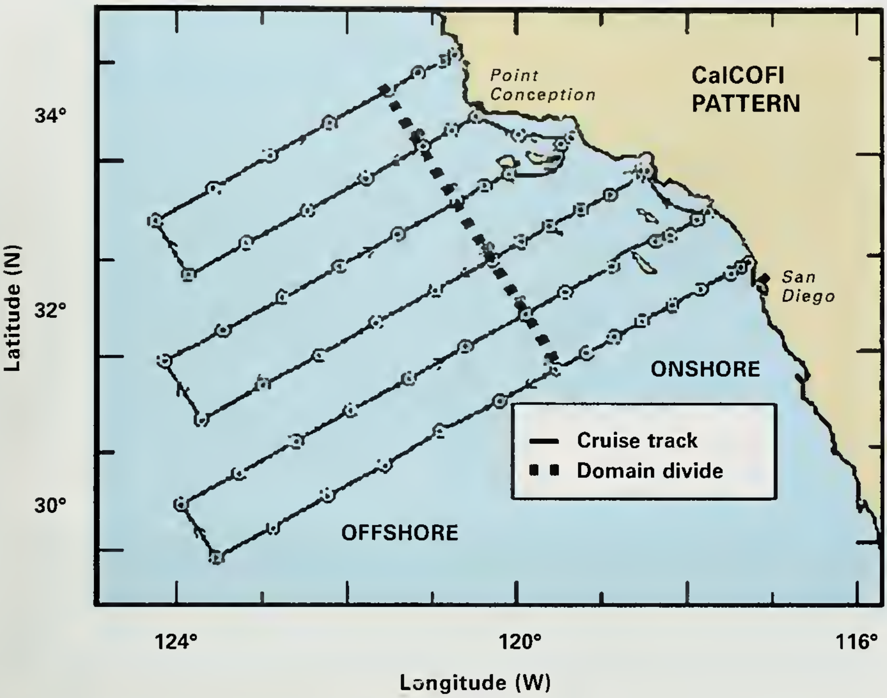


Figure 1. Study area off southern California showing the transect lines repeatedly surveyed seasonally between May 1987 and September 1998, and the two domains ('onshore' and 'offshore') used in this analysis.

Sooty Shearwater. *Photo: Kim Westerskov, RSPB Images.*

dominant coastal species (Sooty Shearwaters) and other cold-water taxa (Cassin's and Rhinoceros Auklets), and increases in the dominant offshore seabird (Leach's Storm-petrel) and other warm-water southern species (Black-vented Shearwaters) were recorded off southern California between 1987 and 1994. The magnitude of these changes are exemplified by the plight of the Sooty Shearwater. This far-ranging summer visitor, once numbering over five million birds and by far the most abundant seabird off California, has declined by 90% during the period 1987–1994.

Using these, and more recent data, we have further examined the impacts at the level of the wider seabird community. Data from the early years (1987–1990), were compared with recent observations (1995–1998) to determine whether there had been changes in the patterns of species dominance and abundance through time. Overall, we compared observations collected during four seasons (winter, spring, summer, fall) and within two spatial domains (onshore and offshore, Figure 1). The results are shown in Table 1. Changes in the dominant species were observed in four instances, while the overall composition of the community had changed in three. Overall, only three out of the eight comparisons we attempted showed no changes in either species dominance nor community composition.

Short-lived eruptions of southern, warm-water species are common during warming episodes off southern and central California. In 1992, a major El Niño event caused a transient climatic deviation similar to the overall changes observed over the 12 year period of this study. Our observations during 1992 showed changes (in comparison with the 1987–1990 data) in community structure roughly equal to the long-term comparisons described above. The Sooty Shearwater was replaced as the dominant species by the Black-vented Shearwater, while several southern species with affinity for warm water (ie, Pink-footed Shearwater, Black and Least Storm-petrels) increased in abundance during the fall of 1992.

Rhinoceros Auklet, Oregon Coast, USA.
Photo: E&P Bauer, Bruce Coleman.

Cassin's Auklet, Buldir Island, Alaska.
Photo: Lon Lauber, OSF

Domain	Season	Dominant species (1987–90)	Dominant species (1995–98)	Correlation coefficient (r_s)	Probability level	Result
Onshore	Winter	Cassin's Auklet	California Gull	0.340	$0.50 < p < 0.20$	Low correlation
	Spring	Phalaropes	Phalaropes	0.529	$0.50 < p < 0.02$	Significant correlation
	Summer	Sooty Shearwater	Sooty Shearwater	0.666	$0.01 < p < 0.005$	Significant correlation
	Fall	Sooty Shearwater	Pink-footed Shearwater	0.567	$0.05 < p < 0.02$	Significant correlation
Offshore	Winter	Phalaropes	Leach's Storm-petrel	0.629	$0.02 < p < 0.01$	Significant correlation
	Spring	Phalaropes	Phalaropes	0.641	$0.02 < p < 0.01$	Significant correlation
	Summer	Leach's Storm-petrel	Sooty Shearwater	0.502	$0.10 < p < 0.05$	Low correlation
	Fall	Leach's Storm-petrel	Leach's Storm-petrel	0.382	$0.20 < p < 0.10$	Low correlation

Table 1. Results of the analyses of changing seabird community composition between the beginning (1987–90) and the end (1995–98) of our time series. The correlation coefficient is a measure of agreement between the two time periods in the ranks of species abundance. Low correlation coefficients indicate a large change in the relative abundance of species in the bird community.

The avifauna off California consists of locally-breeding species as well as far-ranging visitors from both hemispheres, so it is likely that seabird communities off this coast respond to both local and remote physical changes. Ocean-wide seabird distributions in the North Pacific are known to respond to shifts in the location of water masses and current systems. Additionally, the abundance of far-ranging species may be affected by changes in ocean climate at their breeding colonies, far away from the California Current. Thus, it is likely that some of the fluctuations in seabird communities we have described off southern California have occurred in response to distant or larger-scale fluctuations in the atmospheric forcing and the circulation of the Pacific Ocean. At the same time, however, the changes in the California Current described here are representative of similar larger-scale shifts in the chemistry, physics and biology of the North Pacific Ocean. The properties of at least five pelagic ecosystems (the California, Peru and Kuroshio–Oyashio Current systems, the Central North Pacific Gyre, and the Subarctic Pacific) changed in response to a major disruption of basin-wide atmospheric and circulation patterns sometime in the mid 1970s.

Our analyses show that long-term (one year to decades) shifts in oceanic climate impact seabird communities, but that these impacts can be easily predicted for individual species. The 'community level' changes that emerged from our analyses involved species already identified in the past as having shifted their abundance: namely, the Sooty Shearwater, Cassin's Auklet, and Leach's Storm-petrel. A shift in the dominance and the structure of an assemblage of upper trophic level consumers such as seabirds, likely reflects profound changes in the wider oceanic ecosystems and in the physical processes underlying them. Similar changes have been reported for lower-level consumers in the California Current including euphausiids (krill) and juvenile Rockfish.

Pelagic seabird communities are actually loose assemblages with varied responses to environmental change. Their distributions can shift to exploit improved foraging opportunities elsewhere, or their populations can fluctuate in number due to changes in mortality and reproductive success. It is likely that the response of different seabirds is mediated by their particular life history characteristics (ie foraging behaviour, diet, energetic cost of locomotion, migrations). Thus, the declines in the abundance of resident (Cassin's and Rhinoceros Auklets) and visiting (Sooty Shearwaters) cold-water species likely mean very different things, namely the emigration of the far-ranging shearwaters out of the California Current as compared to real decreases in the global abundance of locally-breeding species. There is strong evidence that the reproductive success of seabirds breeding along the California coast decreases when ocean temperature increases and prey availability drops. Thus, locally-breeding seabird populations will likely decline if the warming of the California Current continues. However, it is difficult to predict the demographic impacts of such a warming trend on far-ranging visitors such as shearwaters and Kittiwakes that breed elsewhere.

The difference between behavioural and demographic responses to climatic change is particularly problematic for far-ranging species, since researchers in one part of the species range cannot ascertain whether local fluctuations in abundance are driven by re-distributions or by changes in the size of their populations. For instance, co-ordinated surveys off southern and central California, and Washington State have revealed concomitant declines in the abundance of the dominant resident (Cassin's Auklets) and visiting (Sooty Shearwaters) cold-water taxa across the west coast of North America (2,000 km). Ultimately, whether Sooty Shearwater populations have declined, have shifted their summer foraging grounds to the Central Pacific, or now 'overwinter' somewhere in the southern hemisphere remains unknown. However, recent population estimates off New Zealand have revealed that the breeding population at the Snares Islands has dropped by 30%. This decline was likely caused by years of bycatch at high-seas gillnet fisheries and large-scale decreases in ocean productivity.

Long-term multinational studies across the Pacific Ocean are essential to interpret changes in pelagic seabird communities off California. Particularly, evidence of out of phase variability in the physical properties of the eastern and western North Pacific, makes co-ordinated studies of seabird communities along both margins of the basin imperative. Additionally, population estimates and demographic studies at the southern hemisphere breeding grounds of far-ranging shearwaters and petrels will help place our observations off California in perspective.

Further reading

Hayward, T L (1997) Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. *Trends in Ecology and Evolution* 12(4):150–154.

Roemmich, D and McGowan, J A (1995) Climatic warming and the decline of zooplankton in the California Current. *Science* 267:1324–1326.

Veit, R R, Pyle, P and McGowan, J A (1996) Ocean warming and long-term change of pelagic bird abundance within the California Current system. *Marine Ecology Progress Series* 139:11–18.

Veit, R R, McGowan, J A, Ainley, D G, Wahl, T R and Pyle, P (1997) Apex marine predator declines 90% in association with changing oceanic climate. *Global Change Biology* 3:23–28.

Climate-related changes in the intertidal community

Raphael D Sagarin

One of the most diverse marine environments is the intertidal zone, which is the area along the coast that cycles from exposure to air to immersion in sea as the tides ebb and flow. The many plants and animals that live in this area are excellent study systems for investigating the effects of environmental change because the majority are very numerous, easily studied in the field, produce many offspring in a range of generation times, occupy many ecological niches, and are sensitive to environmental conditions, especially temperature.

In order to assess the effects of environmental change on the intertidal community during this century, we repeated an extensive survey of intertidal fauna first conducted from 1930–1933 at Hopkins Marine Station in Monterey Bay, California, USA. Looking at the precise study area used in the original survey (Figure 1), we observed that wide-scale changes have occurred in the abundance of many marine invertebrate species over the last 60 years. About half of the 60 species we looked at increased in abundance while half decreased in abundance. The overall diversity of the site is similar to the diversity in the 1930s. However, when species are divided into categories based on their known geographic ranges, a striking pattern emerges in which southern species mostly increased in abundance and northern species mostly decreased in abundance (Figure 2). This pattern is what we would expect to see at a single location if warmer temperatures were driving species' distributions northward.

Indeed, these changes occurred during a period of gradual warming of nearshore sea temperatures. Shoreline water temperatures have been taken every day by hand at Hopkins Marine Station since 1920. From this record we see that despite considerable year to year variation, temperature has increased by about 1°C since the time of the original survey in the 1930s. This amount of warming is consistent with many other studies that have shown warming temperatures during this century. Notably, summer temperatures in recent years have been significantly warmer than summer temperatures in the years preceding the original study. If certain vital stages in an animal's life history are linked to the summer months, these warmer summers may have played a key role in the changes we observed.

The changes we observed occurred sometime during the 60-year period between surveys, and can only be seen in a long-term comparison. In shorter-term studies we have done, in which changes are compared over a three year period, no pattern of change is apparent, and the changes in abundance are much smaller than over 60 years. With so much time between studies and so many species interacting with each other, many factors could contribute to the changes. Thus, we considered many alternative hypotheses to explain the pattern of change we observed.

El Niño events, which might also favour southern species, occurred with similar frequency and intensity before each study

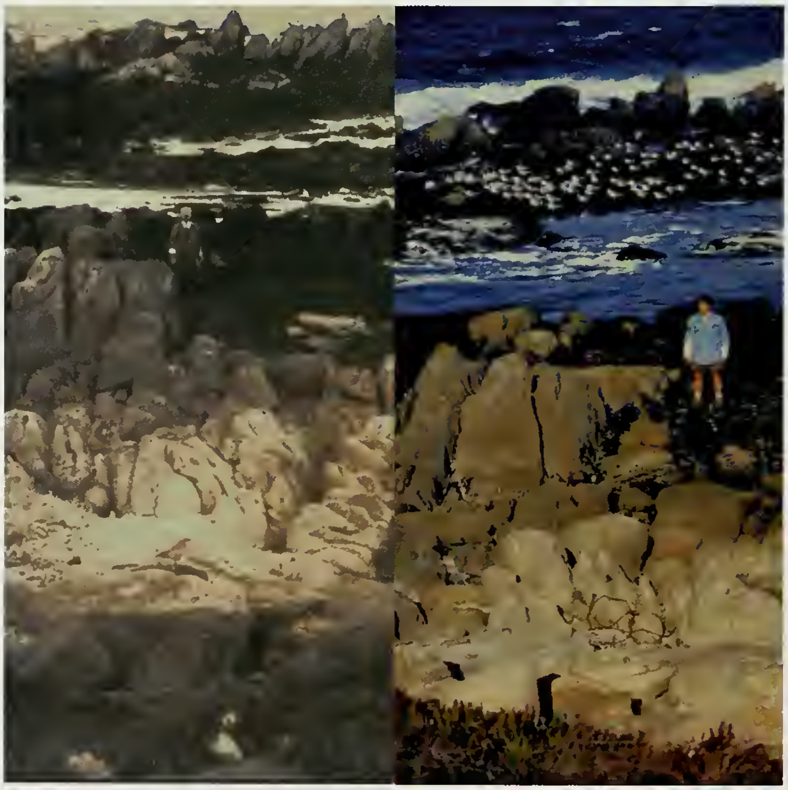


Figure 1. Right: W G Hewatt on his intertidal transect, c. 1932. Far right: R Sagarin in the same location, 1998.

making it difficult to claim that El Niño events, and not the gradual increase in temperature, are responsible for the changes we observed.

Using historical records and studies conducted by other investigators, we also considered the roles of human impacts, the reintroduction of Sea Otters and Black Oystercatchers, and the impacts of larger Harbour Seal populations, which haul-out to rest on the intertidal rocks. In all cases, we concluded that these agents could have had some effect on some of the species we studied, but they could not explain the strong range-related pattern of change we observed.

We also used surveyor's tools to ensure that the relative tidal height of the study area hadn't shifted due to earthquakes or sea level rise, and we compared the current substratum to historical photos and detailed maps to ensure that significant erosion hadn't occurred. We concluded that the physical environment of the study area was similar enough that the large changes we observed could not have been caused by seismic activity, sea level change, or erosion.

We should caution that this study does not identify specific mechanisms that would drive species to respond to temperature changes in the observed manner. In other words, it shows correlation, but not causation. Understanding mechanisms by which species will respond to climate change is an important next step in our scientific understanding of climate change.

This study is among a small, but growing number of investigations which show evidence of plant and animal populations responding in the current century to changes in climatic factors. Such studies are an important complement to earlier works that have predicted shifts in species' numbers and distributions in response to various climate change scenarios.

Finally, the study illustrates the importance of designated habitat refuges, such as the Hopkins Marine Life Refuge, in providing not only pristine habitat for plants and animals, but suitable study sites for long-term research. Long-term monitoring programmes will be essential if we are to understand how species are responding to climate change in the present, and how they will respond in the future.

Further reading

Barry, J P, Baxter, C H, Sagarin, R D, and Gilman, S E (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267: 672–675.

Lubchenco, J, Navarrete, S, Tissot, B N, and Castilla, J C (1993) Possible ecological responses to global climate change: nearshore benthic biota of northeastern Pacific coastal ecosystems. In: Mooney, H A (ed) *Earth system responses to global change: contrasts between North and South America*. Academic Press, inc., San Diego, pp. 147–165.

Sagarin, R D, Barry, J P, Gilman, S E, and Baxter, C H (1999) Climate related changes in an intertidal community over short and long time scales. *Ecological Monographs* 69: 465–490.

Southward, A J, Hawkins, S J, and Burrows, M T (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* 20: 127–155.

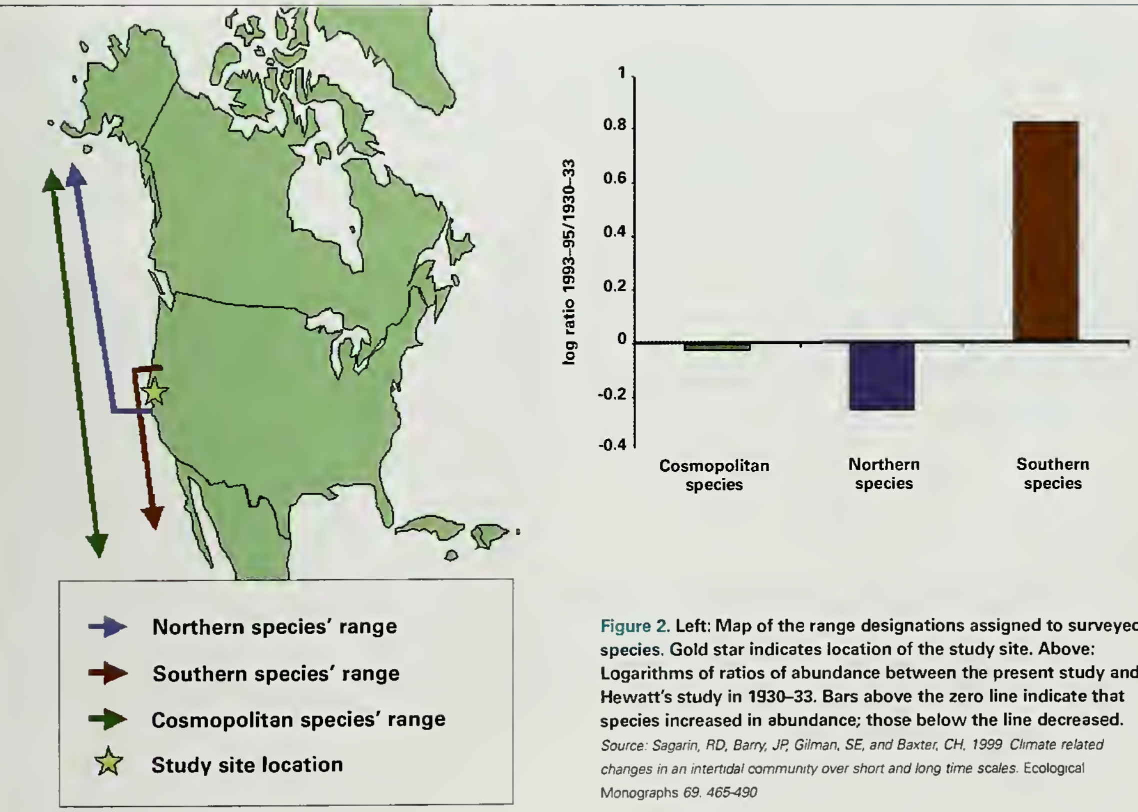


Figure 2. Left: Map of the range designations assigned to surveyed species. Gold star indicates location of the study site. Above: Logarithms of ratios of abundance between the present study and Hewatt's study in 1930–33. Bars above the zero line indicate that species increased in abundance; those below the line decreased.

Source: Sagarin, RD, Barry, JP, Gilman, SE, and Baxter, CH. 1999 Climate related changes in an intertidal community over short and long time scales. Ecological Monographs *69. 465-490*

Climate change and coral bleaching

Mark Spalding, Kristian Teleki and Thomas Spencer

Coral reefs are a critical global resource, both biologically, and in socio-economic terms. They are the most diverse marine habitat, with an estimated one million different species. They are also widely used by coastal communities as a source of food and as the basis for a major tourism industry, providing both a livelihood and foreign exchange earnings for many communities and developing nations.

Coral reefs are also highly sensitive to climatic influences and appear to number among the most sensitive of all ecosystems to temperature changes, exhibiting the phenomenon known as coral bleaching when stressed by higher than normal sea temperatures.

Coral bleaching is the term used for a loss of colour in reef-building corals and the subsequent visibility of the underlying (white) skeleton. Reef-building corals are highly dependant on a symbiotic relationship with microscopic algae (a type of dinoflagellate known as zooxanthellae) which live within the coral tissues. The bleaching results from the ejection of the zooxanthellae by the coral polyps and/or by the loss of chlorophyll by the zooxanthellae themselves. This reaction of corals has been widely observed for many years: corals usually recover from bleaching but they can die in extreme cases.

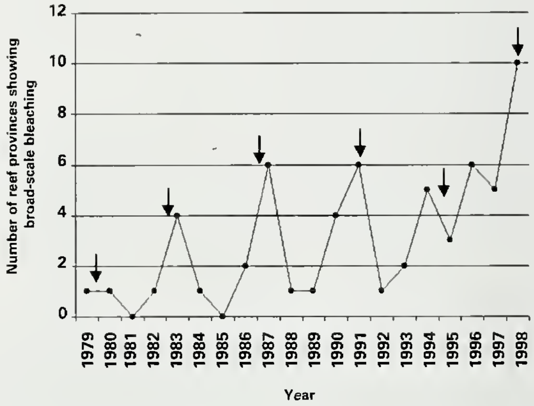
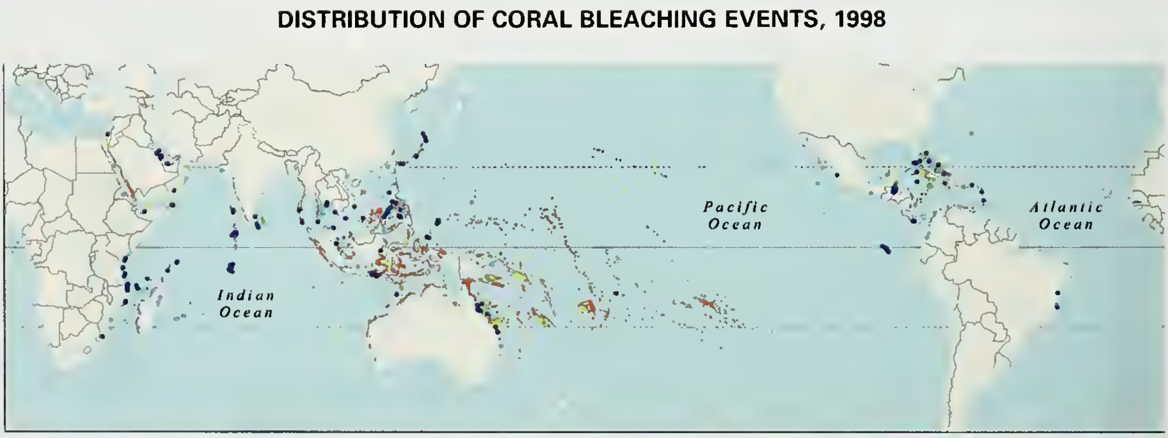


Figure 1. The number of reef provinces exhibiting moderate to severe bleaching since 1979. The arrows show the timing of the major El Niño years. Re-drawn from Hoegh-Guldberg (1999).



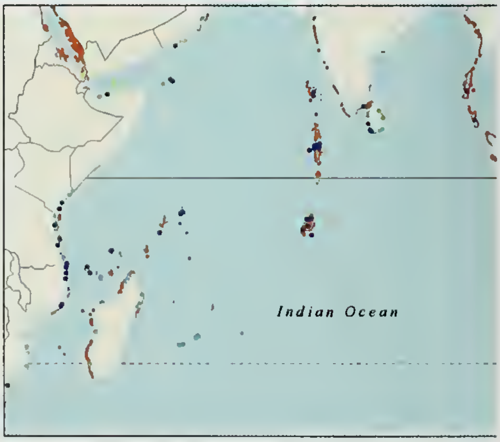
Severity of bleaching
- 0 (low)
- 1
- 2
- 3 (high)

🟥 Coral reef

Data sources
Bleaching events
Reefcheck; NOAA; GCRMN; CORDIO
Coral reefs: UNEP-WCMC Global Coral Reef Dataset Version 6.0

Map compiled by Corinna Ravillious.
© UNEP-WCMC, 2001

Figure 2. Records of coral bleaching events during 1997/98, plotted against a global map of coral reef distribution. Map shows some 550 separate data-points (with considerable overlap in some areas). This information is largely derived from expert records sent in to the NOAA/Coral Health and Monitoring Programme, together with information from the Global Coral Reef Monitoring Network and the global surveys conducted by Reefcheck. Intensity of bleaching has been classified into a semi-quantitative three-point scale of intensity. Records of 'zero bleaching' scoring a zero are marked in yellow. The global spread of this event is immediately apparent, as is the high intensity of the event on Indian Ocean reefs (detail right).



Bleaching is caused by various types of stress, including temperature extremes, pollution and exposure to air. It is temperature related stresses, however, which have been most widely reported, and which are of particular concern in relation to climate change. On any particular coral reef, the normal range of sea temperatures throughout the year is narrow – usually within 4°C – though the range of temperatures tolerated by reef-building corals world-wide is much wider (16–36°C). It would appear that corals in individual regions and localities have become highly adapted to these narrow temperature regimes. Studies have shown that temperatures of only 1–2°C above the normal range (threshold temperatures) for a few weeks are sufficient to drive a 'mass-bleaching' event (where a significant proportion of corals across the reef are bleached).

Reports of coral bleaching have increased greatly since 1979, with all records of mass-bleaching occurring after this date. The number of coral reef provinces (geographic divisions) in which mass bleaching has been reported varies widely between years, but shows a close correlation with El Niño events, as shown in Figure 1. The most significant mass-bleaching event to date was associated with the 1997–1998 El Niño, when there were records from all 10 reef provinces. Data have been compiled at the UNEP World Conservation Monitoring Centre for over 500 independent reports of bleaching during this period, and have been broadly classified based on the extent of impact. These data are presented in Figure 2. In certain areas, most notably the central Indian Ocean, this event was followed by mass-mortality, where up to 90% of all corals died over thousands of square kilometres, including virtually all reefs in the Maldives, Chagos Archipelago and Seychelles. Although new coral growth has been observed in most of these areas, full recovery from such an event will take many years or decades, while there is some concern that mortality on such a massive scale could lead to local disappearance of certain species, driving a loss in diversity and changes in community structure.

Although there are no clear records of mass-bleaching events prior to 1979, it is possible that such events could be rare but recurrent phenomena that reefs have recovered from in the past. However, the extent of coral bleaching observed during recent El Niños provides a clear indication of the wider long-term impacts of rising sea surface temperatures. Although such events are largely driven by El Niños at the present time, most climate models predict that the threshold temperatures which currently drive mass-bleaching events will be reached on an annual basis in 30–50 years.

At both the regional and local scale, certain corals have adapted to warmer, or more variable, temperature regimes. These include some of the same species which have been observed to be highly sensitive to temperature variations in other areas. Such adaptation is clearly seen in the reefs of the Arabian Gulf, where temperatures fluctuate over relatively wide extremes every year. Largely un-quantified observations in the central Indian Ocean in 1998 showed similar local-scale survival of corals in reef flat and lagoon areas. These are likely to be subject to more extreme temperatures on a regular basis, from the reduced water circulation and exposure to solar insolation and/or cold conditions in these areas. It remains to be seen whether coral larvae from these corals can recolonise reefs where more sensitive corals have died, or whether there is indeed sufficient genetic resilience within these species to adapt to the continuing increases in temperatures predicted under current models.

Further concerns compound the problems from rising sea surface temperatures. Corals may be placed under additional stress by the projected increases in atmospheric CO_2 concentration. It is believed that the concentrations of aragonite in surface waters will be reduced by such increases. Aragonite is an important component of the coral skeleton, and lower concentrations will reduce calcification rates and skeletal strength. This may lead to reduced rates of reef growth and weaker skeletal structures. All reef development is the result of coral growth out-pacing natural processes of erosion, from bioeroding organisms and also physical processes such as storms. Slower coral growth rates and weaker skeletal structures may shift the balance of many reefs from that of gradually accreting structures to that of gradually eroding structures, and this change will be further compounded by increasing rates of sea-level rise.

The 1997–1998 mass-bleaching event is providing a critical model of potential future impacts of climate change on coral reefs globally. Mass-mortalities were largely unpredicted and the wider ecosystem impacts, together with the potential for recovery and adaptation remain largely unknown.

Bleached coral, including darker patches which have recently died. Southern Seychelles, April 1998.
Photo: Mark Spalding.

Further reading

Burke, L, Bryant, D, McManus and J, Spalding, M (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, International Center for Living Aquatic Resources Management, World Conservation Monitoring Centre and United Nations Environment Programme, Washington, DC.

Glynn, P W (1996) Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* 2:495–509.

Hoegh-Guldberg, O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50: 839–866.

Kleypas, J A, Buddemeier, R W, Archer, D, Gattuso, J-P, Langdon, C and Opdyke, B N (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–120.

Managed realignment of sea defences and the re-creation of saltmarshes in south-east England

Iris Möller, Angus Garbutt, and Mineke Wolters

Together with tropical mangrove swamps, saltmarshes are considered to be among the most important and widespread coastal wetlands in the world. In many areas they play a critical role in natural coastal defence; they provide a habitat for numerous species, including very large numbers of birds; they provide feeding and nursery areas for a number of important commercial fish species; and are highly productive, exporting nutrients to surrounding areas. The physical and ecological processes that maintain these habitats are delicately adjusted to sea level. As a result, climate change and its effect on global sea level can have serious consequences for the ecological evolution of these intertidal systems.

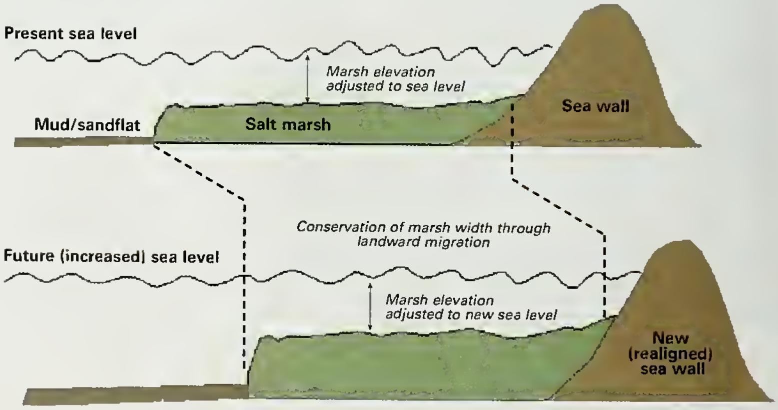
In England and Wales, saltmarsh has been estimated to cover 20% of the intertidal estuarine and coastal areas (Figure 1), although prior to reclamation, the area of saltmarsh is estimated to have been considerably larger. 80% of these marshes have been designated as Sites of Special Scientific Interest (SSSI). These saltmarshes are floristically rich habitats supporting a large number of invertebrate and bird species, many of which are found exclusively in these habitats.

Climate change induced sea-level rise provides a potential threat to these habitats as it may lead to an increase in the occurrence and depth of tidal inundation, and the subsequent 'ecological drowning' of the marsh. Recent 'best estimates' predict a rise in global mean sea level of 50 cm by 2100. On subsiding coasts, the effect of such global sea-level rise is exacerbated. This is, for example, the case on the south-east coast of the UK, where rates of relative sea-level rise are estimated to be of the order of 2–4 mm per year.

Saltmarshes can only continue to exist if they are able to migrate landwards (and 'upwards') in response to increasing sea levels (Figure 2), so that the relative number of tidal inundations per year remains below a critical ecological threshold and wave heights remain low and do not erode the marsh surface. This adjustment is only possible in conditions of continuous sediment supply and deposition and where low-lying land is available for colonisation landward of the existing saltmarsh.

Figure 1. Active saltmarshes around the UK coast are marked in black (after Burd, 1989).

Figure 2. A conceptual model of saltmarsh adaptation to sea-level rise. It will only be possible to maintain the same total area of marsh if sufficient sediment is available and conditions are favourable for marsh surface sedimentation, and if unrestricted landward migration of the saltmarsh is possible.



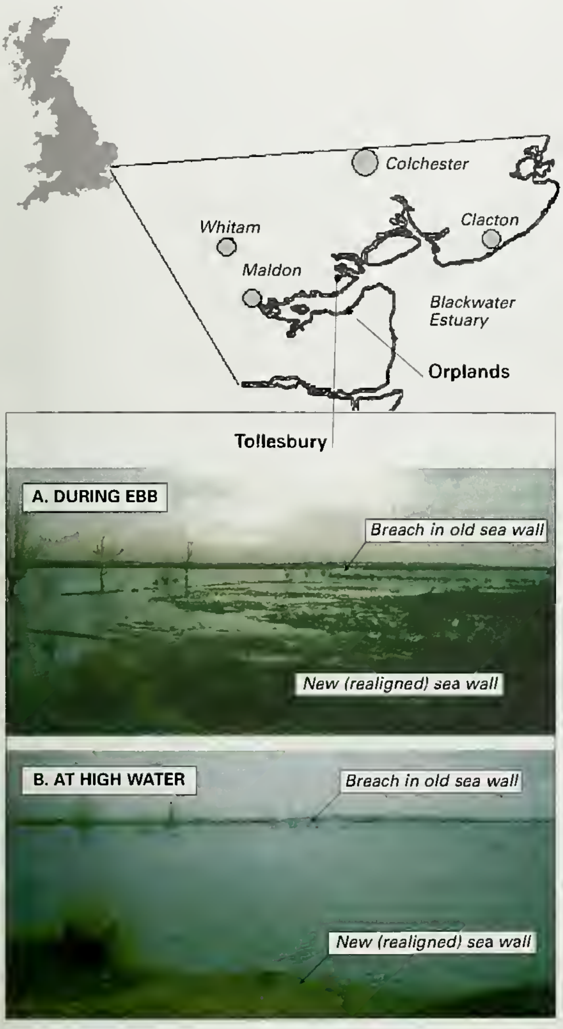


Figure 3. Location of the managed realignment sites at Orplands and Tollesbury in the Blackwater Estuary, UK.

Frequently, intertidal habitats are not able to migrate landward as they front fixed structures such as sea walls. In such cases, sea-level rise may cause net surface area losses due to marsh edge erosion. In Essex, on the UK east coast, less than 1 km out of a total of 440 km of saltmarsh coastline is not backed by embankments or sea walls. As a result, most marshes have been undergoing net erosion from their seaward edge for many decades (in some cases by several metres per year since the mid-20th Century). In the 15-year period from 1973 to 1988 total marsh erosion in south-east England exceeded 1,116 ha, or 20% of the 1973 total area. A scenario of accelerated sea-level rise may thus lead to further significant reductions in saltmarsh habitat over the next 50–100 years.

In several locations throughout the UK, the deliberate breaching of existing seawalls and/or the realignment of sea walls to a more landward location has been implemented to counteract these losses by re-creating saltmarsh from formerly reclaimed land. Such artificial managed realignment of sea defences for the purpose of saltmarsh creation as a coastal management strategy was pioneered in the early-mid 1990s. Two notable examples are located at Tollesbury (implemented in August 1995) and Orplands (implemented in April 1995) on the Blackwater estuary (see Figure 3)).

At Tollesbury, the initial colonisation of the new intertidal area by saltmarsh vegetation was much slower than anticipated. Recent results from the continuous monitoring of vegetation by the Institute of Terrestrial Ecology (now the Centre of Ecology and Hydrology) indicate that, in the first year after the sea wall was breached (1996), only a few plants of Common Glasswort colonised the site. However, species diversity increased significantly in subsequent years (Figure 4). Sediment that was deposited on the existing saltmarsh or lost to the estuary before the sea wall was breached, is now being deposited inside the managed realignment site. This deposition is increasing the elevation, allowing more of the site to become suitable for colonisation by plants. Perennial species like common Sea Lavender and Sea-purslane are already colonising the highest parts of the site. The nationally scarce plant, Golden Samphire, is also observed to be growing on the new sea wall. This plant, which is found on the adjacent Tollesbury marshes, is potentially endangered because of the erosion of the saltmarshes.

There has been rapid colonisation of the lower areas of the site by intertidal invertebrates, which provide prey for over-wintering wading birds such as Knots and Dunlins. Other

Sea Lavender in salt marsh habitat.

Photo: Chris Knights, RSPB Images

Knots over saltmarsh. *Photo: David Broadbent, RSPB Images.*

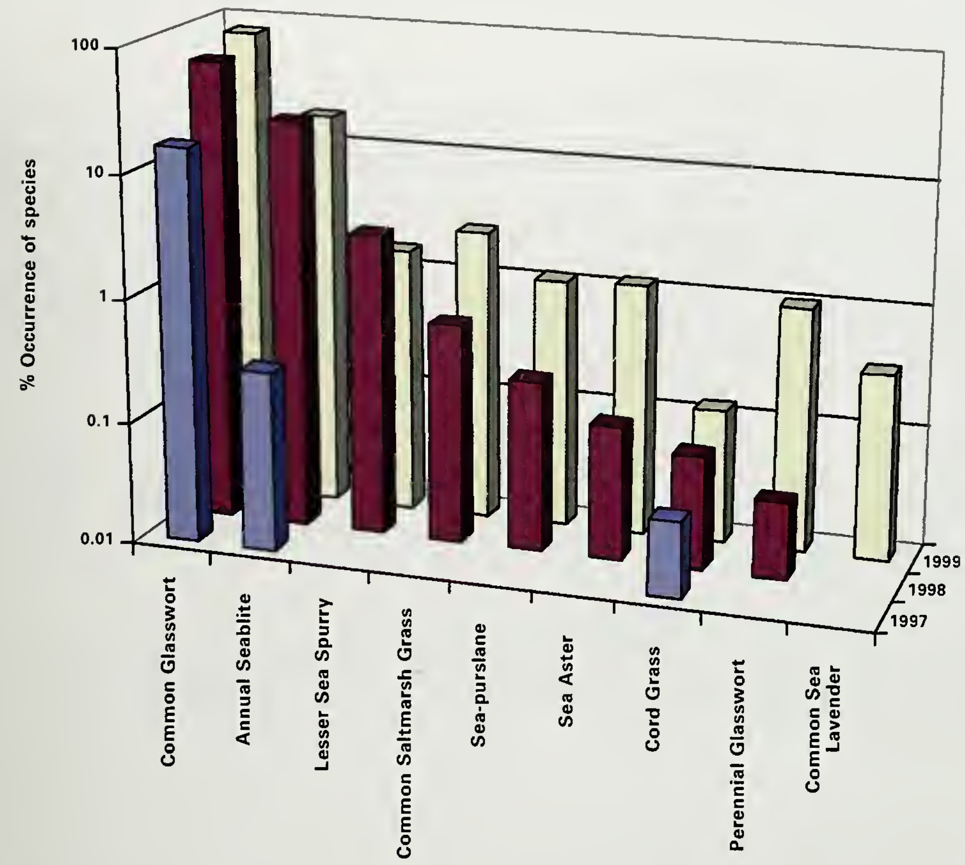


Figure 4. Plant colonisation of the managed realignment site at Tollesbury, Essex, between 1997 and 1999. Bars show the percentages of quadrats in which each species occurred (log scale) in each year after the sea wall was breached in 1996.

species such as the Avocet, Redshank and Curlew (all of which are protected species) have been recorded on the site. The site also provides a regular roost for a flock of Golden Plover, protected under the Wildlife and Countryside Act 1981, EC Birds Directive and the Berne Convention.

Although much knowledge on the ecological effects of managed realignment has been gained, our scientific understanding of saltmarsh sedimentation and vegetation colonisation needs to be improved to provide guidelines for the sustainable design of managed realignment schemes. In addition, there is a need to address socio-economic issues, such as compensation for landowners, before this strategy of adaptation to sea level can become a large-scale policy option. The present shortfall in annual expenditure needed to ensure the Environment Agency's inland and sea defences are maintained or restored to meet required standards, however, is estimated at £30–£40 million. In this context, managed realignment may be an attractive alternative to traditional 'hard' engineering methods. Most importantly, more effort needs to be made to involve the public in the process of planning and implementation of such schemes from the outset and to educate the public to a high level on the conservation and coastal management issues and options available.

Coastal areas around the world are typically densely populated and sea-level rise will become a major problem which will require management in many areas. How this is done will have a significant bearing not only on human populations and economic development, but also on biodiversity. This paper provides a clear example of how innovative adaptive approaches may be brought to bear on climate change related problems in coastal environments. If the above issues are addressed and considered when designing future managed realignment schemes, the potential benefits could be considerable, not only in economic terms, but also for the conservation of critical coastal habitats.

Further reading

Doody, J P (1992) 'The conservation of British saltmarshes'. In: Allen, J R L, and Pye, K (eds) *Saltmarshes. Morphodynamics, Conservation, and Engineering Significance*, pp. 80-114. Cambridge University Press, Cambridge.

Burd, F (1995) *Managed retreat: a practical guide.* English Nature, Peterborough.

French, P W (1992) *Coastal and estuarine management.* Routledge, London.

Phenological events as indicators of climate change

Introduction by Arnold J H van Vliet and R S de Groot

Phenology is defined as the study of the timing of recurring biological events, the causes of their timing with regard to biological and non-biological forces, and the inter-relationship between events in the same or different species. The 'event' may be the date of first flowering or budbreak, unfolding of a first leaf, the first bird song of the season, or arrival of a first migrant. The timing of these events is very important as they have close associations with, for example, the length of growing seasons, frost damage, outbreaks of pests and diseases, water fluxes, nutrient budgets, carbon sequestration and food availability.

Phenology and climate

Scientific research has shown that the timing of biological events is clearly related to air temperature, precipitation, soil temperature, soil moisture, photoperiod, solar illumination and snow cover. However, these will vary from species to species, will cause species-specific phenological changes, and result in changes in reproduction and in competition and interaction between species.

Phenological changes in response to climate change have a wide range of environmental and socio-economic consequences, with impacts on wildlife, agriculture, forestry and human well-being. Phenological observations have been used by farmers for many years to improve agricultural practices and are beginning to be used as indicators of climate change. Such observations are often easy to make and easy to communicate to a wide audience.

Phenological monitoring networks

Many European countries have or, at least, have had phenological monitoring networks, some of which originated in the 19th Century. The scientists and amateur naturalists involved in these networks have produced long-term datasets which contain an enormous amount of information on how biological systems respond to changing climatic conditions. The value of phenological records in providing an indication of the sensitivity of natural systems to climate change, and in climate impact assessment, is now recognised and their use should be an essential component of all earth observation and global change monitoring programmes.

To improve the standards of phenological monitoring, and increase the value of phenological research and the use of phenological data in the context of global climate change, a Global Phenological Network is being established. The network will improve the integration and accessibility of data, discover under-utilised datasets, and forge better links between phenological studies and other disciplines. It will facilitate the sharing of data and knowledge on recording and analytical methods, will seek to demonstrate the many benefits of phenological research to society, and will involve end-users in impact assessment. The initiative has the support of a large number of local, national and international organisations and will provide much needed coherence to a potentially valuable resource.

Climate change and the phenology of European trees and shrubs

Annette Menzel and Peter Fabian

In temperate zones, the timing of seasonal events in plant growth and development (phenology), such as flowering and leaf fall, are mainly controlled by temperature and light, although biotic and soil factors, water supply and genes also have an influence. The timing of springtime events is particularly sensitive to temperature. Since plant phenology is highly sensitive to annual variations in climatic conditions, it is an easily observable indicator of changes in the biosphere. Woody plants in the forests of temperate zones have evolved many adaptations to seasonal cycles in sunshine, temperature and the availability of water. Many species show an alternation of growth and flowering during the summer, with rest or dormancy during winter. Future climate changes may lead to the phenology of a particular species being less well-matched to local conditions. For example, an increased risk of damage from late frosts might result from an earlier onset of leaf growth or bud-burst caused by warmer average spring temperatures. Warmer winters might cause a delay of bud-break because species require cold conditions to break the dormancy of their buds. Mathematical models which represent the relationship between plant phenology and weather conditions allow the risks of shifts in the seasonal cycle under future climate scenarios to be assessed.

We first examined long-term records of plant phenology for evidence of trends that might reflect climate change. We then used statistical relationships derived from these studies to project likely changes in phenology in the near future. Finally, we used our recently developed model, which relates plant phenology to climate conditions, to simulate the onset of springtime growth, the length of the growing season and the risk of late spring frosts under climate change scenarios.

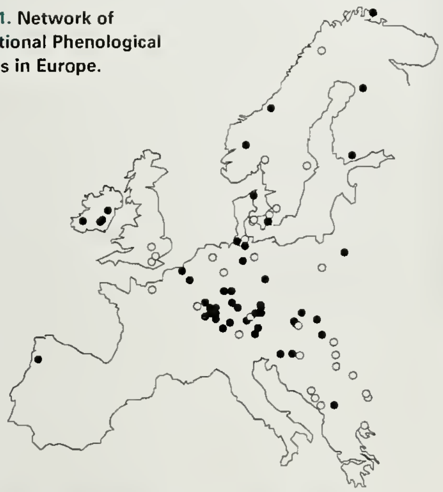
Trends in the phenology of trees and shrubs in the International Phenological Gardens in Europe

There is a network of International Phenological Gardens, spread widely across Europe (Figure 1), in which genetically identical clones of many species of trees and shrubs are grown. The timing of growth and development events of these plants has been recorded annually for more than 30 years. We calculated the linear trend in the date on which each event was recorded for each clone over the period 1959–1996 and made a separate set of analyses for each garden. This study produced hundreds of estimates of trends in phenological events during this period (summarised in Figure 2). Although the results for individual combinations of clone, species and garden are variable, they show a clear tendency for the average date of spring events, such as leaf unfolding, to have advanced. A typical spring event occurred about six days earlier at the end of a 30 year period than it did at the beginning. By contrast, a typical autumn event, such as leaf colouring, was delayed by about five days. When these two effects are combined, the growing season was about 11 days longer in the mid-1990s compared with the mid-1960s. The tendency for spring events to become earlier was greater in northern and central Europe than in the south-eastern parts of Europe, whereas the tendency for autumn events to become later was less in northern Europe than in central and southern Europe. The variation among years in the timing of spring events was strongly correlated with air temperature. Similar results have been found in regional studies of plant and animal phenology, but this example is unusual in providing a Europe-wide perspective. Remote-sensing studies of the annual cycle in plant cover, using satellites and inferences about the seasonality of plant activity from the annual atmospheric carbon dioxide cycle, provide the only other evidence of long-term changes in plant phenology at this spatial scale.

Changes in the phenology of Birch trees in Germany

Observations of various phenological phases, such as the timing of leaf unfolding and leaf colouring (prior to leaf fall), of Birch *Betula pendula* during the period 1951–1996 were taken from the phenological network of the German Weather Service. Linear trend analysis for trees at many sites showed a clear average tendency for leaf unfolding to become earlier during this period; leaf colouring became later, though this change was

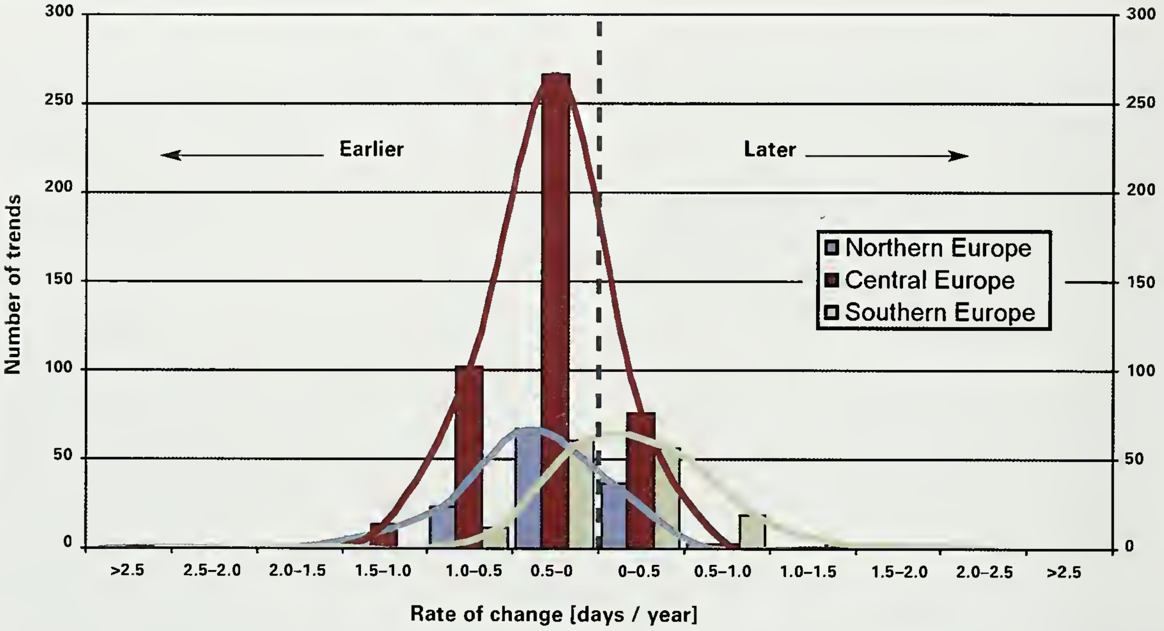
Figure 1. Network of International Phenological Gardens in Europe.



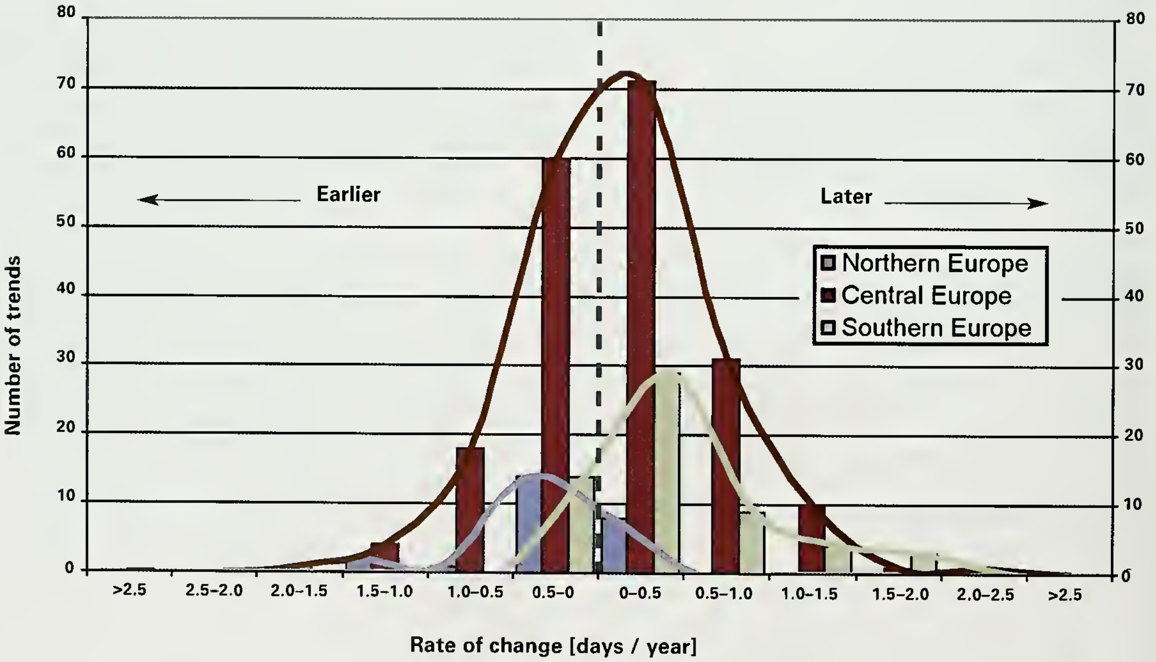
Species	Phases	Advances (days/°C)
Larix decidua	Leaf unfolding	5.0
Picea abies	May shoot	4.2
Betula pubescens	Leaf unfolding	4.3
Fagus sylvatica	Leaf unfolding	2.5
Prunus avium	Flowering	5.2
Quercus robur	Leaf unfolding	4.1
Sorbus aucuparia	Leaf unfolding	2.7
Tilia cordata	Flowering	1.9
Salix acutifolia	Flowering	4.8

Table 1. Rates at which the timing of developmental events of trees in International Phenological Gardens are becoming earlier expressed as days earlier per Centigrade degree of temperature change.

Spring



Autumn



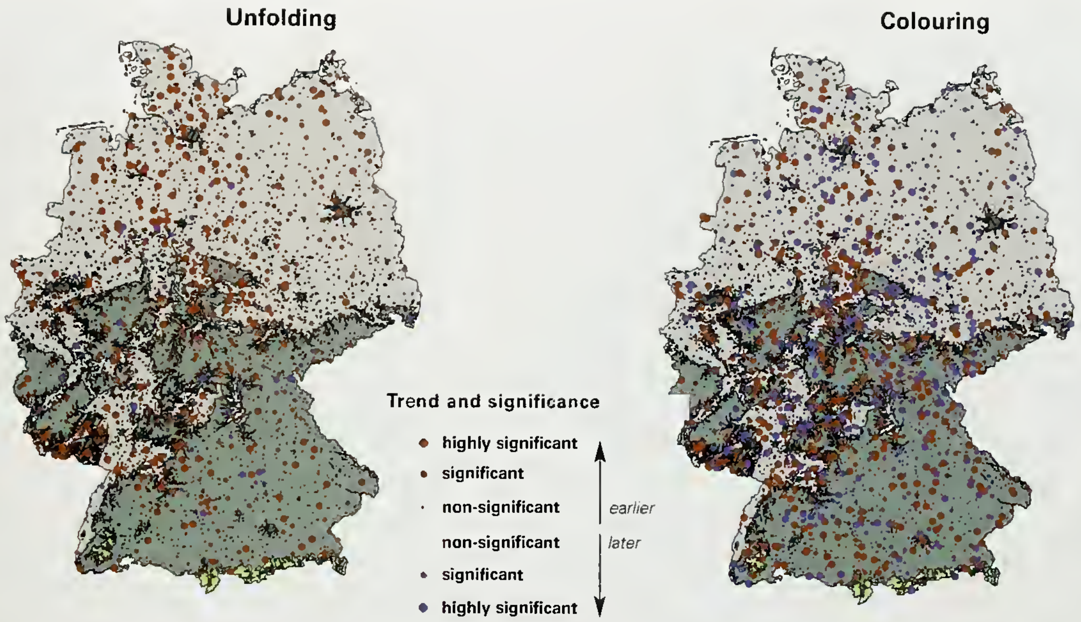
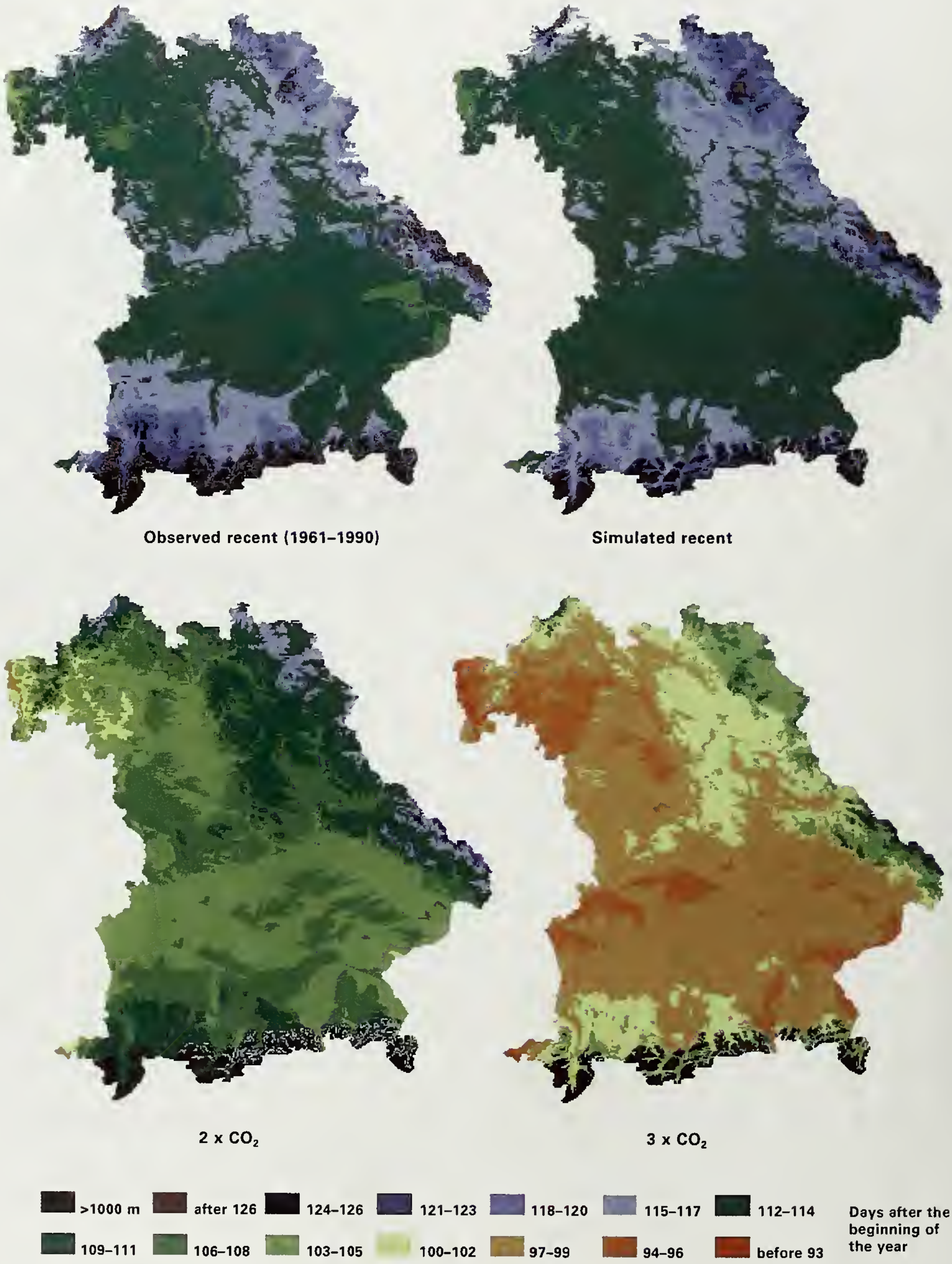


Figure 3. Linear trends in the timing of leaf unfolding (left) and autumn leaf colouring (right) of Birch *Betula pendula* in Germany. Data are from the phenological network of the German Weather Service and are for long observational series (20 years and more) during the 1951–1996 period. Each point represents a series for one place.

Figure 2 (left). Frequency distributions of long-term changes in the timing of woody plant phenological phases in spring (upper diagram: events such as leaf unfolding and flowering) and autumn (lower diagram: events such as leaf colouring and leaf fall) during the period 1959–1996. The columns show counts of trends for hundreds of combinations of plant species, clones and International Phenological Gardens, using only series of 20 or more years. Columns to the left of the vertical dashed line show trends for events which are now occurring earlier than they used to, whilst columns to the right show trends for events which are now occurring later. Each column shows the number of trends observed in each category of rate of change, which was measured in days earlier or later in the season per year. Results are shown separately for gardens in Northern, Central and Southern Europe. The averages of these large samples of trends indicate that spring events are occurring earlier (peak count to the left of the dashed line in the upper diagram) and that autumn events are occurring later (peak count to the right of the dashed line in the lower diagram) but with variation among regions.



Observed recent (1961–1990)

Simulated recent

2 x CO_2

3 x CO_2

Figure 4. Map of timing of leaf unfolding of Birch *Betula pendula* in Bavaria under different temperature scenarios (top left, observations of the 1961–1990 period; top right, simulation under present conditions; bottom left, 2 x CO_2 conditions; bottom right, 3 x CO_2 conditions) (Menzel 1997).

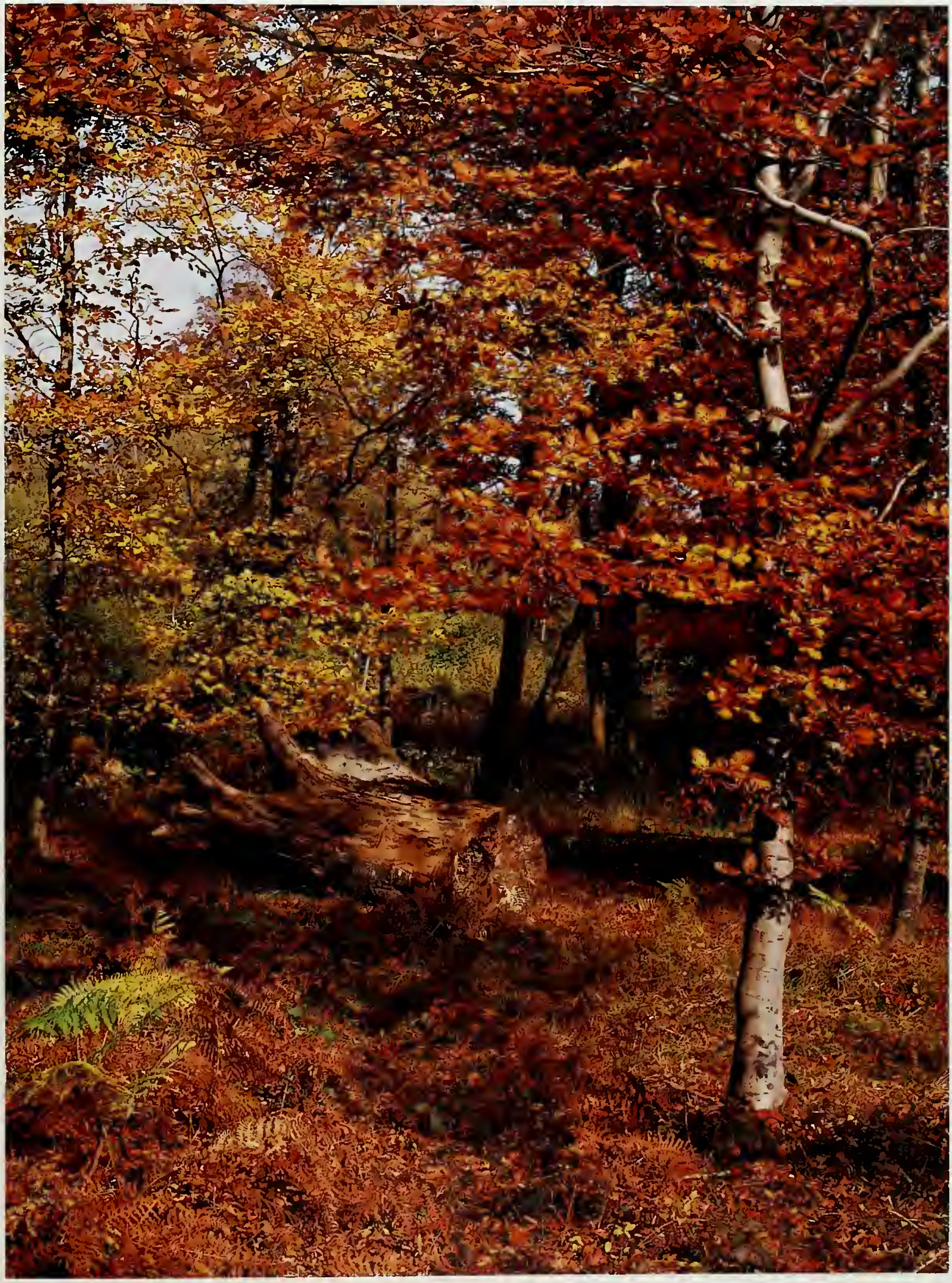


Figure 5. Birch trees. *Photo: Maurice Walker, RSPB Images.*

smaller than that in spring (Figure 3). These results are similar to those described above for the International Phenological Gardens and show that the observed lengthening of the growing season over the last decades is mostly due to an earlier start of the growing season. Moreover, these studies reveal that there is a strong spatial variability and variability among different phases, too.

Prediction of future changes in the spring phenology of trees

Most of the tree clones used in the study of changes in plant phenology in the International Phenological Gardens are of German origin, so the results are particularly appropriate for the assessment of impacts of climate change on the timing of development events in the native trees of Germany. Results for nine tree species indicate that the timing of leaf unfolding, May shoot and flowering is likely to become earlier if winter temperatures increase. However, the amount by which timing is expected to change varies considerably among tree species – from two to five days earlier for an increase of 1°C in mean winter temperature (Table 1). Phenological models developed using data from the International Phenological Gardens have been linked to maps of temperature simulated by climate models; these are being used to investigate likely changes in the spring phenology of trees throughout Europe as climate changes during the 21st Century. For a scenario in which the atmospheric concentration of carbon dioxide rises to twice the pre-industrial level, it is expected that leaf unfolding in Birch, a species which is very sensitive to spring temperature, would become six days earlier in central Europe. For Beech *Fagus sylvatica*, which is much less sensitive, leaf unfolding would be expected to advance by about two days only. If carbon dioxide concentration triples, then the changes predicted in central Europe are much larger (18 days earlier for Birch and 10 days for Beech). Simulated changes in western European countries, such as Ireland and the UK, are a few days less. Although these expected changes are large, the models do not predict that the risk of damage to leaves from late spring frosts will be much increased under either scenario.

Simulated phenological maps of Bavaria

Models of plant phenology can also be used to examine possible changes in phenology at much finer spatial scales. The phenological model for Birch was applied to simulate present and possible future spatial variation in leaf unfolding date under two scenarios of future climate change in Bavaria (Germany). The model was first parameterised to ensure a good fit between observed and modelled spatial variation in leaf unfolding dates. Then it was used to produce maps of the leafing dates expected if carbon dioxide concentrations double or triple (Figure 4).

Summary

For Europe as a whole, and for Germany in particular, the effects of increases in air temperature over the last four decades due to the anthropogenic greenhouse effect can easily be detected in long-term data on the phenology of trees. Results of phenological modelling reveal that the growing season of trees could be further lengthened in the future. The models do not suggest that the risk of damage from late spring frosts will increase.

Further reading

Menzel, A (1997) Phänologie von Waldbäumen unter sich ändernden Klimabedingungen - Auswertung der Beobachtungen in der Internationalen Phänologischen Gärten und Möglichkeiten der Modellierung von Phänodaten. *Forstliche Forschungsberichte* 164.

Menzel, A and Fabian, P (1999) Growing season extended in Europe. *Nature* 397: 659.

Fabian, P and Menzel, A (1999) Changes in phenology of trees in Europe. In: Karjalainen, T, Spiecker, H and Laroussinie, O (eds). *Causes and consequences of accelerating tree growth in Europe*. EFI Proceedings, 27.

Menzel, A (1999) Phenology as global change bioindicator. *Annalen der Meteorologie* 39: 41–43.

Climate change and phenology in the United Kingdom

Tim Sparks, Humphrey Crick, Ian Woiwod and Trevor Beebee

Phenology, the timing of natural events, probably represents the oldest *written* biological record. Within the UK, data exist from the first half of the 18th Century and extensive co-ordination of data continued until 1947. We are very lucky in being able to draw upon the Central England Temperature Record, which extends back to 1659, and can compare phenological events to temperature over a very extensive period. Where comparisons are possible, the current response of species to temperature is the same as it was historically. We can, therefore, use historical data to predict how we might expect species to respond to climate change.

In post-war years, the collection of phenological data in the UK has been less co-ordinated and tends to be taxa-specific. However, recording is still extensive. Many individuals continue to record events in their diaries and the length of these series are now becoming useful. Birds receive most attention, with information on migrant phenology available from county bird reports and from coastal observatories. Several of the British Trust for Ornithology's schemes, such as the Nest Record Scheme, can provide valuable phenological information. Data on invertebrates are available through institute-organised schemes, such as the Rothamsted Insect Survey, the Butterfly Monitoring Scheme, and the Continuous Plankton Recorder.

Statistical techniques are used to relate phenological data to temperatures. The estimation of the response of a species to temperature is improved by amalgamating data from many recorders or over larger geographical areas. A feature of phenological data is that, for a given number of recorders, plant phenology appears to have less variability than animal phenology. This may stem from the mobility of animals causing recording difficulties or be a consequence of fluctuations in population size.

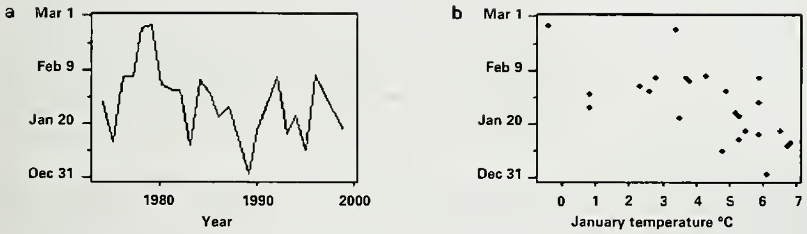


Figure 1. First flowering of Crocus *Crocus tomasinianus* in Norfolk, 1974–1999: (a) time series, (b) relationship with January temperature.

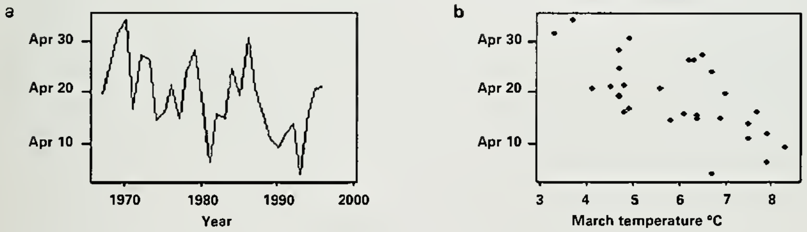


Figure 2. Average flight date of the Hebrew Character Moth *Orthosia gothica* from UK moth traps, 1967–1996: (a) time series, (b) relationship with March temperature.

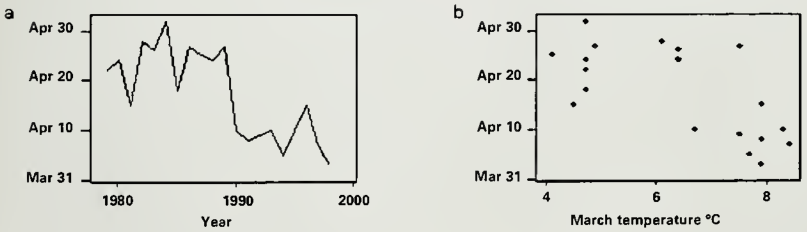


Figure 3. First spawning of the Natterjack Toad *Bufo calamita* in Hampshire, 1979–1998: (a) time series, (b) relationship with March temperature.

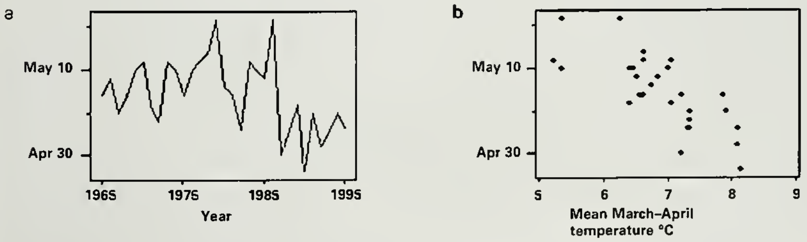


Figure 4. Average egg-laying date of the Chaffinch *Fringilla coelebs* in the UK, 1965–1995: (a) time series, (b) relationship with mean March–April temperature.

NB: All of the relationships shown are statistically significant. All temperature date used are from the Central England Temperature Record.

Organisms found in the United Kingdom for which the timing of events in spring and late winter has become earlier in recent decades and is correlated with temperature (see Figures 1–4). Clockwise from top left: Crocus, Hebrew Character Moth, Natterjack Toad, Chaffinch.

Photos clockwise from top left: GA Maclean, OSF; Peter Perfect, RSPB Images; Mark Hamblin, RSPB Images; Roger Wilmshurst, RSPB Images.

The 1990s was the hottest decade on record. The most marked changes were in the first quarter of each year, with mean temperatures for the 1990s being 1.3°C warmer than the 1980s. Not only do species respond to year-to-year fluctuations in temperature, but many are now demonstrating a response to this warming trend. In terms of phenology, earlier appearance has been observed in a range of plant, invertebrate and vertebrate species. There is now so much supporting evidence that there is little doubt that climate change has started to drive changes which may be quite fundamental to the ecology of species.

Plants

Much of the evidence of change in plant phenology comes from individual recorders with extensive data sets. Some show quite remarkable trends; for instance, a record of Winter Aconite *Eranthis hyemalis* from Norfolk shows that flowering has advanced by a month in a 35-year period. The trend and temperature relationship for the flowering of the non-native crocus *Crocus tomasinianus* is shown in Figure 1. Data from Surrey on tree leafing show that this was, on average, 10 days earlier in the 1990s than in the previous decade.

Invertebrates

Analysis of Butterfly Monitoring Scheme data over a 23 year period confirms how responsive butterflies are to temperature. Virtually all species respond to warmer springs and the majority show statistically significant trends towards earlier appearance. Many multi-brooded species have extended their flight period. The likely consequence for geographically restricted species is range expansion. These data also reveal, at least at the national level, a strong relationship between first appearance date and peak flight date.

Similarly, moth data from the Rothamsted Insect Survey show that many species are responding to warmer temperatures by having earlier flight periods. Figure 2 details the trend and temperature relationship for the flight data of the Hebrew Character Moth *Orthosia gothica*. Some insect pests, such as the Peach Potato Aphid *Myzus persicae*, have a huge response to temperature and would seem to benefit from warmer years.

Vertebrates

Recording the migration and spawning of amphibians are traditional phenological activities. Both features of the life cycle are highly sensitive to temperature. Figure 3 shows the trend and temperature relationship of the Natterjack Toad *Bufo calamita*. A similar pattern can be seen in some species of frog and newt.

A growing number of studies have demonstrated earlier migration of birds into the UK in spring. Arrival times are related to UK temperatures and probably also to temperatures along migration routes. A vast data set on bird nesting has revealed that this is also temperature related and that the majority of species have been nesting earlier in recent years. Figure 4 shows the trend and temperature relationship for Chaffinch *Fringilla coelebs*.

Conclusions

As we gather together a larger number of biological records, we are able to detect more and more effects which can be attributed to temperature. Despite the variability in biological records, especially those associated with animal phenology, the over-riding pattern is for earlier appearance with warmer springs. Observed changes are in keeping with climate warming in recent decades. Whilst there is still a need to identify changes in phenology, we now need to investigate what the effects of these changes will be on population dynamics and on community structure.

Further reading

Beebee, T J C (1995) Amphibian breeding and climate. *Nature* 174: 219–220.

Cannell, M G R, Palutikof, J P and Sparks, T H (eds) (1999) *Indicators of climate change in the UK*. DETR, London.

Crick, H Q P and Sparks, T H (1999) Climate change related to egg-laying trends. *Nature* 399: 423–424.

Future impacts of climate change on wildlife

Introduction by Mike Harley

There is little doubt that the Earth's climate is experiencing exceptional changes. The rate of warming during the 20th Century was the greatest in the last 1000 years, with the 1990s being the warmest decade and 1998 the warmest year. Average surface air temperatures are now between 0.4 and 0.8°C higher than they were in the middle of the 19th Century. This trend is likely to continue into the 21st Century. Climate models estimate that average global surface temperatures will increase by 3°C (within the range 1–5°C) by 2100. In the same time period, global mean sea level is estimated to rise by 0.5 m (within the range 0.1–0.9 m). These changes are largely attributable to human activities since the beginning of the Industrial Era; increasing concentrations of greenhouse gases in the atmosphere are having an unprecedented impact on the natural processes operating in the global climate system.

The previous chapters in this volume have described and discussed the recent impacts of climate change on wildlife, and demonstrated how ecosystems, and their component habitats and species, have responded to changing climatic conditions. The importance of good, multi-decadal data sets, recording changes in weather, climate, wildlife distributions and associations, and other environmental factors, is clearly exemplified in underpinning research in this field. However, the likely impacts of climate change on wildlife in the future has been clouded by uncertainties. Ecosystems are characterised by inherently complex relationships and feedbacks, which are further complicated when climate change scenarios are superimposed.

This chapter considers some contemporary research which aims to shed light on how wildlife might adapt in response to climate change in the 21st Century. The future management of wildlife, ecosystems, and protected sites and reserves, and the formulation of associated policies, requires the development of a predictive capability which can deliver scenarios for change. These may be derived from statistically validated simulation models and from carefully controlled field experiments, both of which are based on models for climate change. The studies described here are resulting in the development of some powerful tools and techniques, which can be used more widely by nature conservationists and environmental planners when making decisions about wildlife management in the context of global environmental change. It is important to understand how wildlife might adapt to changing climatic conditions, as contemporary mitigation measures to reduce greenhouse gas emissions and the impacts of climate change are unlikely to have much effect during the 21st Century.

Effects of experimental manipulation of climate on calcareous grassland plants and invertebrates

Gregory J Masters and Valerie K Brown

Calcareous grasslands are nationally important for nature conservation in the UK, being rich in biodiversity and containing many rare plant and invertebrate species. Furthermore, their area has declined dramatically over recent years, generally as a result of land use change. They are of great interest ecologically because of the diversity they support, while at the same time being vulnerable to management and/or environmental change.

In 1993, research began into the impacts of climate change on invertebrates and plants and the interactions between them. Field experiments consisting of manipulations of local climate are being used to model the impacts of climate change on these grassland ecosystems. The work aims to provide a means of predicting how grasslands in the UK and, indeed, in mainland Europe will change under a changing climate. The results provide valuable information for those involved with nature conservation and land management on not only the future appearance of grasslands, but also what lies behind the changes.

Experimental details

The experiments are located on an abandoned arable field (removed from cereal production in 1981) at Wytham, Oxfordshire. Manipulations of changes to local climate reflect predictions from climate change models for the UK. These include winter warming of 3°C during November to April, a complete summer drought (extreme event) during the months of July and August, and a supplementation of summer rainfall from June to September. These climate change simulations are applied singly, or in combination, to address two scenarios – warmer winters with increased or decreased summer rainfall. Manipulations began in early 1994, after a year of pre-treatment assessment. Plants and invertebrates have been monitored regularly over a six year period and the experiment is on-going. We use electric heating cables, laid on the soil surface, to provide an elevation of temperature of 3°C (± 0.1°C). Mobile rainshelters, controlled by rain sensors, move across the experimental plots at the onset of rain to imitate summer drought. Supplemented summer rainfall is provided by a carefully calibrated addition (20%) of deionised water to the average rainfall for the season.

Vegetation is monitored by recording plant species composition, relative abundance and structure. In addition to monitoring the abundance and general composition (order/family) of the invertebrates, key groups are identified

Above. The fenced site on Upper Seeds, Wytham. The white rainshelters indicate the five experimental grids, each with two shelters.

Top right. Winter warmed plot with a light snow cover. Snow has not settled on the 3 x 3 m plot.

Right. Droughted plot with the rainshelter in its parked off-plot position. The vegetation is dominated by flowering forbs with a lack of grasses in comparison with the surrounding vegetation.

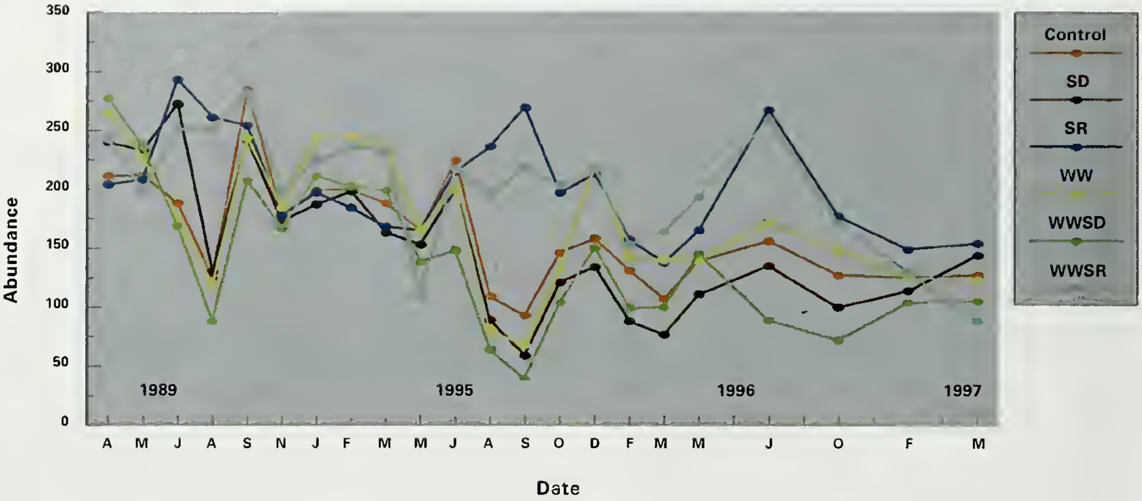


Figure 1. Vegetation dynamics represented as changes in abundance (cover or biomass), 1994–1997. The vegetation responds to soil moisture content; under supplemented summer rainfall (SR) abundance increases, particularly the grasses, and under summer drought (SD) abundance decreases. Winter warming (WW) has a transient effect; abundance is increased in early spring, but in late spring/early summer there is a great demand for soil water (to support the early flush of growth) and moisture levels run low, causing an early drought effect.

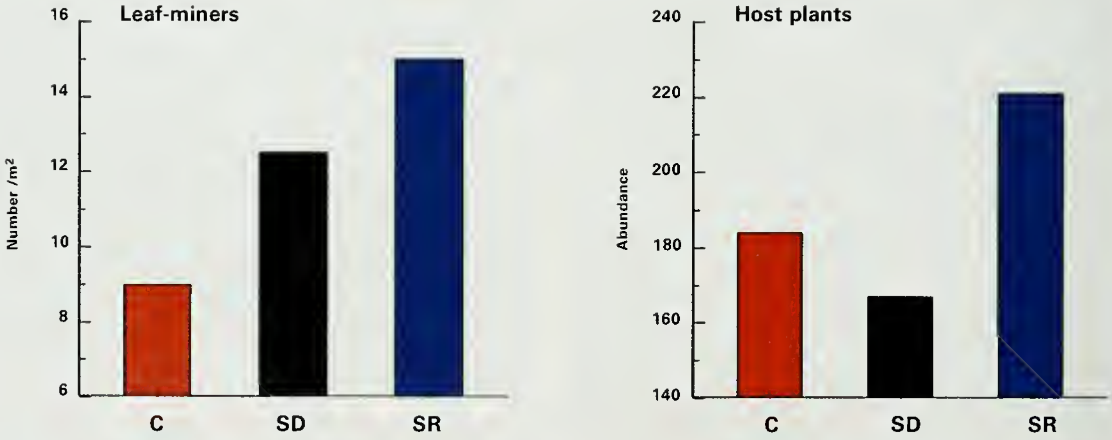


Figure 2. Leaf-miner and host plant responses to summer water manipulations. As in Figure 1, vegetation cover is promoted by supplemented summer rainfall (SR) and decreased by summer drought (SD) in comparison with the control (C). Leaf-miners would be predicted to respond in relation to the vegetation (as for SR), but under SD leaf-miner populations do not crash. Here, these insect herbivores are responding to changes within host plant physiology caused by drought stress, where nutrient levels increase leading to a better quality diet; their performance and subsequent populations therefore increase.

to species level for special study as potential indicators of climate change. Initially, three groups were chosen – two groups of plant feeding insects (leaf-miners and leaf/plant hoppers) and an important group of predators, the spiders. These groups are related to the vegetation in different ways; leaf-miners are closely related to plant species composition, spiders utilise plant structure for web construction and leaf hoppers are a 'half-way house' dependent upon species and structure. Once treatments began, we noticed clear responses of these three groups and of two further groups – the beetles and springtails. To date, we have identified over 300 species and have estimates of the relative abundance of over 60,000 specimens (38,500 identified to species level and a further 15,000 leaf-miner records).

Spittlebug nymph emerging from cuckoo spit. *Photo: Kim Taylor, Bruce Coleman.*

Hairy Violet. *Photo: C Mattison, FLPA*

Results and conclusions

After six years of manipulation, the treatments have significantly altered the grassland community. Water availability is central to the responses. Warmer winters promoted plant growth early in the year, resulting in an increased demand for limited soil water resources during the spring. This, combined with a naturally low rainfall in late spring, led to a drought, the effects of which were intensified by summer droughting (Figure 1). Deep-rooted herb species (for example, Wild Parsnip *Pastinaca sativa)* persist under such conditions, while shallow-rooted species (particularly grasses) have declined or indeed been lost from plots. In contrast, plots subjected to supplemented summer rainfall show an increase in grasses (for example, Yellow Oat-grass *Trisetum flavescens)* at the expense of annual herbs (for example, Smooth Hawk's-beard *Crepis capillaris).* However, in the short-term at least, perennial herbs (for example, Creeping Buttercup *Ranunculus repens)* have persisted alongside the vigorous grasses. Additionally, there have been individual plant developmental responses to the warmer winters (for example, Hairy Violet *Viola hirta* and Perforate St. John's-wort *Hypericum perforatum* had their phenology advanced by 21 days and 12 days respectively by the warmer conditions).

Invertebrate responses are, predictably, more complex, showing both direct and indirect (host-plant mediated) responses to climate manipulation. Generally, invertebrate groups track the vegetation responses, except under drought, where plant nutritional quality becomes important and can lead to population increases (for example, leaf-miner populations increase in droughted plots while their host-plants decline, Figure 2). Additionally, the timing of insect activity is modified (for example, the Spittlebug *Philaenus spumarius* (a froghopper) responded directly to warmer winters, with an earlier egg hatch (seven days) and consequent earlier development into adults).

This on-going work aims to provide a means of predicting how calcareous grasslands will be affected by climate change through establishing the mechanisms behind observed and predicted changes. Warmer winters may lead to spring droughts, which are strengthened by dry summers. Water is the key to the responses of the ecosystem; grasses dominate with increased rainfall, while deep-rooted herb species ('weeds') persist under drought. Invertebrates track these changes, except under drought, where plant nutritional quality is more important and insect populations show an increase instead of the predicted decline. The timing of insect activity is modified, as is the size of their populations – in the extreme, leading to insect outbreaks.

The research has added to our knowledge of how these important ecosystems will respond to climate change. The results are relevant to conservation, land management and agriculture. They enable prediction of the magnitude and direction of the changes that calcareous grasslands will experience under climate change and, through understanding the mechanisms of these changes, the management of existing and future grasslands can be planned. The technology involved in these field manipulations could also be applied to other habitats.

Further reading

Brown, V K, Masters, G J and Cheesman, O D (1999) Predicting the floral future of a warmer Britain. *Plantlife* Summer 1999, 15.

Brown, V K, Masters, G J and Clarke, I P (1998) Studies of the impacts of climate change on the structure and functioning of calcareous grasslands. *Bulletin of the British Ecological Society* 29: 3, 26.

Masters, G J, Brown, V K, Clarke, I P, Whittaker, J B and Hollier, J A (1998) Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). *Ecological Entomology* 23: 45–52.

Climate change, warblers and Spruce Budworms

Jeff Price

An important concern of researchers looking at the potential impacts of climate change on ecosystems is whether or not ecosystems will become 'decoupled'. That is, will the species within an ecosystem respond differentially to a changing climate?

To determine how the distributions of birds might change, it is first necessary to look at whether there is an association between their current distributions and climate. If an association exists, then the current climate can be projected into the future to see how distributions might change. Statistical models were used to describe the association between summer distributions of birds in North America and 18 climate variables, and were found to be highly reliable. The next step was to examine how bird distributions might change in relation to predictions for climate change. The Canadian Climate Center's General Circulation Model was used for this purpose. The modelled future climate was based on doubling the pre-industrial level of carbon dioxide in the atmosphere; this relates to a rise in average global temperature of 2°C, which could occur as early as the 2050s. The results were used to create maps of the projected summer distributions of many North American birds. Distributional models and maps have been developed for almost all song-bird species. While the results of the models cannot be used to look at the fine points of how the distribution of a given species might change, they can provide an impression of the direction and potential magnitude of the change (Figures 1 and 2).

Birds, Spruce Budworms and the southern boreal forest

Birds perform a number of valuable services for the ecosystems of which they are a part. These services include seed dispersal, plant pollination and predation on insect pests. Some ecosystems would likely break down if a number of birds and their accompanying services disappeared. Here I will focus on how the avian predation of insect pests might benefit the southern boreal forest ecosystem in North America, and how this system might decouple with a changing climate.

The Eastern Spruce Budworm *Choristoneura fumiferana* is a common, native insect of boreal forests in eastern North America. Its preferred foods include Balsam Fir *Abies balsamea* and several spruce species. Spruce Budworms are estimated to defoliate annually approximately 2.3 million hectares (ha) in the USA. The insect is usually present at low densities (<100,000 larvae/ha), but periodic outbreaks occur throughout the species range, with densities reaching 22 million larvae/ha. These outbreaks can extend over more than 70 million ha and last for up to 15 years, causing a greater than 80% annual loss of foliage on fir and spruce. This foliage loss will kill almost all of the trees in mature stands of Balsam Fir. Trees not killed by defoliation are often at risk from other plant-eating insects and pathogenic diseases, and standing dead trees increase the risk of fire.

While the exact mechanisms behind the beginning and end of outbreaks is unknown, weather is thought to play a significant

Changes in warbler species richness

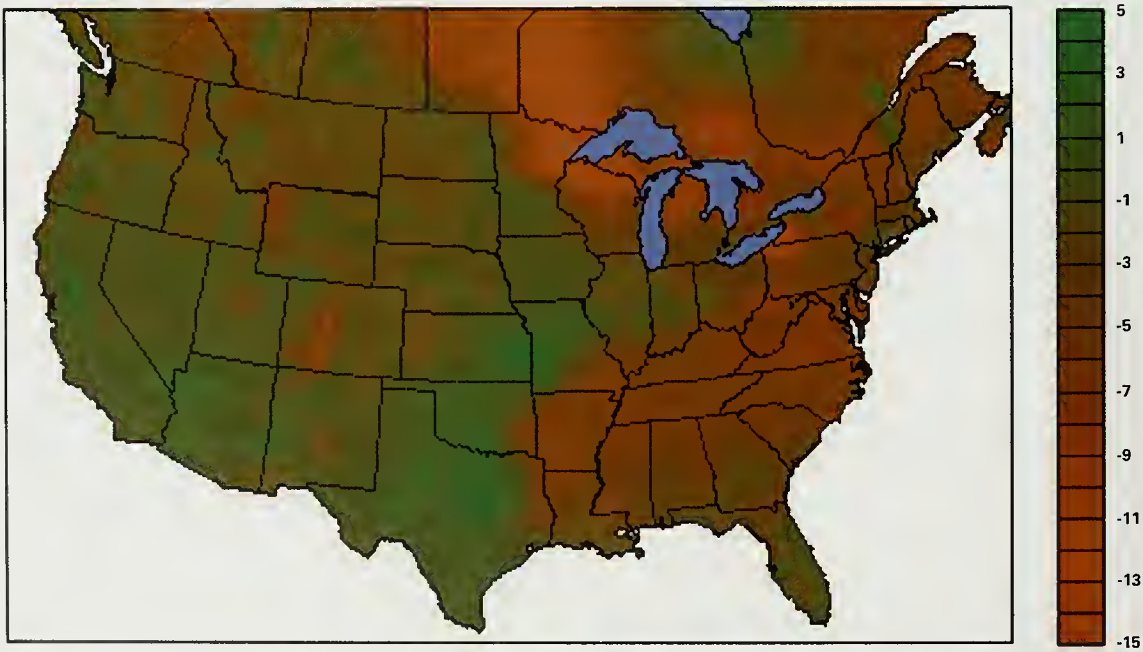
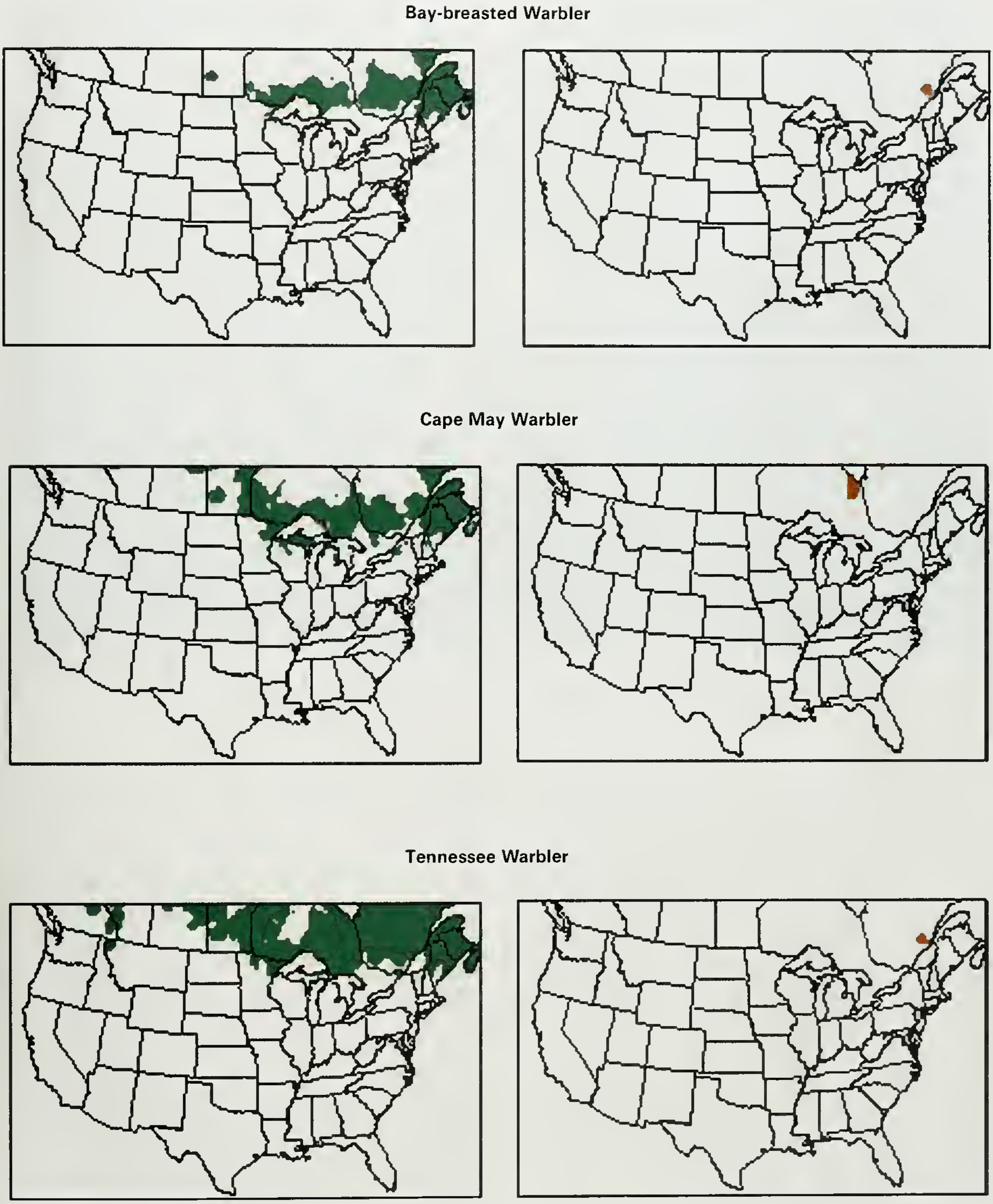


Figure 1. Net changes in the absolute number of warbler species in diferent parts of North America under a modelled future climate with double the pre-industrial level of CO_2. The map is made using expected potential distributions for individual species, such as those shown in Figure 2.



Bay-breasted Warbler

Cape May Warbler

Tennessee Warbler

Figure 2. Current (left panels, green shading) and expected future (right panels, red shading) distributions under a modelled future climate with double the pre-industrial level of CO_2 of three warbler species.

Cape May Warbler, Florida. *Photo: Gordon Langsbury*

role. Outbreaks frequently follow droughts and, in central Canada, tend to start in stands with high concentrations of mature firs flowering after hot, dry summers. Drought stresses host trees and frequently leads to a reduction in plant defence mechanisms; drought also changes the micro-habitat around plants. Insects feeding on drought stressed plants often have increased growth, survival and/or reproduction rates. Temperature also plays a role in regulating the number of eggs laid by Spruce Budworms; the number laid at 25°C is 50% greater than at 15°C. Drought and higher temperatures can also shift the timing of reproduction such that the insect may no longer be affected by some of its natural parasitoid predators. Weather may also play a role in stopping outbreaks; some outbreaks in central Canada were thought to be halted by late spring frosts killing the new growth on the trees.

The control of some populations of Eastern Spruce Budworm may be strongly aided by bird predators, especially some of the wood warblers. Several warbler species, including Cape May Warbler *Dendroica tigrina*, Bay-breasted Warbler *D. castanea*, Blackburnian Warbler *D. fusca*, Tennessee Warbler *Vermivora peregrina* and Nashville Warbler *V. ruficapilla*, are important predators. Many of these species, especially Bay-breasted Warbler, show functional responses to increases in Spruce Budworms; individuals move into the area and increase their reproductive output in response to increases in the insect's population. Birds consume up to 84% of larvae and pupae when populations are low (approximately 100,000/ha), and up to 22% when populations reach approximately 500,000/ha. However, once populations exceed 1 million larvae/ha, bird predation is unable to make an impact on numbers. These warblers, in concert with other predators (mostly predatory insects), are thought to be able to control populations of Spruce Budworms under normal conditions.

Climate change has the potential to impact on many of the components of this system. For example, the Spruce Budworm's northern range will likely increase with increasing temperatures. Currently, the distribution of this species is thought to be tied to whether larvae can complete development before autumn freezes begin. Increasing temperatures and an increased drought frequency could lead to more frequent, and possibly more severe, outbreaks. Increasing temperatures are also likely to reduce the frequency of late spring frosts in southern boreal forests, increasing the length of outbreaks in these areas.

A changing climate might also decouple Spruce Budworm population cycles from those of some of its parasitoid and avian predators. Distributions of most of the warblers that feed on the insect may shift significantly farther north. One set of models projected that three of the most significant predators, Tennessee, Cape May, and Bay-breasted Warblers, may disappear from below 50°N latitude (Figure 2). Indeed, the average latitude of occurrence of both Cape May and Bay-breasted Warblers has already shifted significantly farther north in the last 24 years.

This decoupling of predator and prey is likely to have the greatest impact on southern boreal forests. Replacing biological control mechanisms with chemical control mechanisms (pesticides) may ultimately yield a different set of problems. Besides the economic and social issues relating to large-scale pesticide application, some pesticides may not work as well as expected. Some insects are known to have reduced susceptibility to pyrethrins, DDT and some carbamate pesticides with increased temperatures.

The end result of these changes could be an increase in the rate of conversion from boreal forests to other habitat types (especially in southern boreal forests). The combination of increasing temperatures, drought conditions and insect damage will all increase the likelihood of major fires. As fire frequency increases, the successional pathway changes from fir/spruce to aspen/birch to grasslands. If the climate changes quickly, then some southern species may not be able to migrate into areas as fast as boreal species are lost. This could result in a habitat shift to grassland or grass/shrubland in areas that are currently southern boreal forest. This, in turn, could have impacts on both regional economies and on distributions of species using southern boreal forests.

Conclusion

Changes in bird distributions due to climate change could lead to disruptions in ecosystem services. Species within ecosystems have evolved together over time and depend on each other to various degrees for services such as food, protection or reproduction. Rapidly separating these species may cause detrimental changes. The example presented here is just one of the myriad of interactions taking place in ecosystems on a daily basis.

Humans could intervene to help prevent disruption of many ecosystem services, but the costs of such intervention could be large. For example, loss of predators may lead to the need to apply more pesticides. This will not only have direct monetary costs, but also indirect costs such as other ecosystem damage or possible human health problems. Over time, new predators might migrate into the ecosystem or the prey might become pesticide resistant. It is not necessarily the change itself that could cause problems, rather it is the rate of change. Unless all the components change at the same rate, the systems will decouple and the new systems may bear little resemblance to that which ecosystems managers are used to dealing with. More research is needed to determine not only how more of the pieces of the ecosystem work together, but also how they might move and at what rates relative to each other.

Further reading

Crawford, H S and Jennings, D T (1989) Predation by birds on spruce budworm *Choristoneura fumiferana:* functional, numerical and total responses. *Ecology* 70: 152–63.

Fleming, R A and Volney, W J A (1995) Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios. *Water, Air and Soil Pollution* 82: 445–454.

Jardine, K (1994) Finger on the carbon pulse: climate change and the boreal forests. *The Ecologist* 24: 220–224.

Mattson, W J and Haack, R A (1987) The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110–118.

Price, J, Droege, S and Price, A (1995) *The summer atlas of North American birds.* Academic Press, San Diego.

Potential impacts of global warming on pothole wetlands and waterfowl

Lisa G Sorenson, Richard Goldberg, Michael G Anderson, Terry L Root and Cynthia Rosenzweig

The pothole wetlands of the north-central USA and south-central Canada constitute the most important breeding area for waterbirds in North America. Known as the continent's 'duck factory', the Prairie Pothole Region accounts for only 10% of North America's waterfowl breeding habitat in area, but produces 50–80% of the continent's duck population. The region is characterized by gently rolling hills and millions of shallow ponds, called 'potholes'. These serve as a key breeding habitat for ducks, as well as a crucial feeding and resting area for millions of migratory birds and waterfowl that breed further north. The wetlands, and the birds that use them, are at risk if predictions of future climate change are accurate.

Shallow pothole wetlands are vulnerable to drought and computer models project that global warming will likely bring more frequent and severe droughts to the Prairie Pothole Region. Warmer temperatures increase evaporation and plant transpiration and, in turn, reduce the amount of water in soils and ponds. Even if global warming brings more rainfall, it may not be enough to offset the drying that is expected to occur under warmer temperatures.

We recently conducted a study of the potential impacts of global warming on pothole wetlands and duck numbers in the north-central US portion of the region. We compared historical data on duck and pothole counts, provided by the US Fish and Wildlife Services's Migratory Bird Office, with the Palmer Drought Severity Index (PDSI) – a rating of the wetness or dryness of an area compared with normal conditions. Figures 1a and 1b show that fluctuations in the number of ponds counted in May and the size of the breeding duck population closely mirror May PDSI values over the period of record. We found strong correlations between the counts and the PDSI, indicating the utility of the PDSI as an index of climatic factors important to wetlands and ducks. These correlations, in conjunction with state-of-the-art climate model projections of future PDSI conditions, were then used to predict impacts on waterfowl and wetlands in a warmer world.

Our modelling shows that global warming could cause the number of prairie ponds in the north-central US holding water in the spring to drop from the current average of 1.3 million to just 600,000 – 800,000 by 2060. In this same time frame, the loss of habitat could reduce the average number of ducks settling to breed in this region from 5 million birds today to between 2.1 and 2.7 million. A second study on the Canadian portion of the region is still in progress, but findings for this area are similar to those for the USA. Significant reductions in wetland abundance

Canvasback ***Aythya valisineria*** **on overwater nest.** *Photo: Michael Sorenson.*

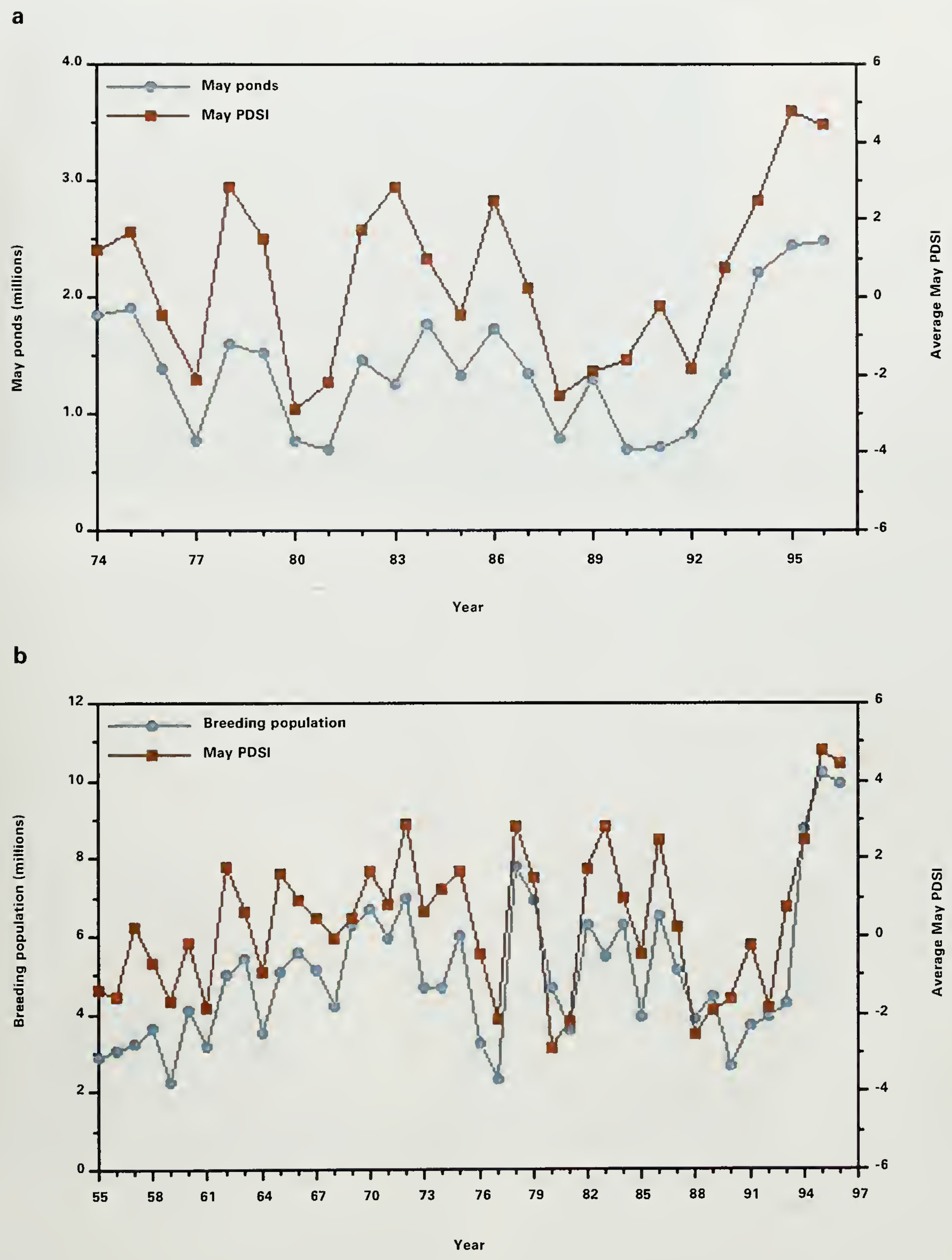


Figure 1. Number of May ponds (a) and May breeding duck population estimates (b) shown in relation to average May Palmer Drought Severity Index (PDSI) values for the north-central USA portion of the Prairie Pothole Region.

Aerial view of prairie pothole country in Manitoba.
Photo: Michael Sorenson.

and the numbers of ducks settling to breed in prairie Canada by the middle of the next century are projected.

Studies show that ducks breeding in the pothole region during drought years make fewer nesting attempts, have lower nest success and poorer duckling survival. The net result is fewer surviving offspring and declining population sizes if drought persists for several years. But ducks are adapted to changing conditions and periodic drought. When severe drought hits the prairies causing ponds to dry up, many species respond by flying farther north to nest in the parkland potholes of Canada, or even to boreal forest and tundra habitats. It is important to determine what happens to birds that respond to drought by moving to other areas – the answer to which may be different in the future than it is now. How climate change may effect these more northern habitats is not yet known. We think, however, that birds currently displaced northward by drought conditions from prairie to boreal forest and tundra habitat produce fewer young. In addition, our current research and a modelling study by Diane Larson, a researcher with the US Geological Survey's Northern Prairie Wildlife Research Center, show that Canada's parkland potholes may be even more susceptible to drying in a warmer climate than the prairie potholes. This suggests that the potential for ducks to find suitable alternative breeding areas in a drier future may be limited.

The future health of waterfowl populations is also tied to impacts on wetlands from changing agricultural practices. Warmer temperatures could increase pressure to shift farmland north, encroaching upon waterfowl habitat and the northern boreal forests. Changes in agriculture will also likely affect the amount of perennial grassland that surrounds pothole wetlands, another important determinant of duck breeding success. Finally, an increase in the frequency of droughts and floods in the region under global warming may make farming more difficult. Whether this results in pressure from farmers to bring more wetland habitat into agricultural production, or in farmland being abandoned, is presently unknown.

How can we protect waterfowl habitats from the potential impacts of global warming? We emphasise that the Prairie Pothole Region is unique; it is vast and there is no single conservation action that will have an effect on such a large area. Wetland conservation is crucial, however. As part of our ongoing work, we are currently identifying the least drought-sensitive areas of the Prairie Pothole Region so that these sites can be placed on the priority list for protection. We also recommend a re-doubling of current efforts to conserve wetlands, since they may be limited in the future, and more sophisticated annual monitoring of habitat conditions and waterfowl response to these conditions. Although conservation measures are important, ultimately, a large reduction in greenhouse gas emissions is the most important response society can make to preserve this ecologically and economically important area.

Further reading

Larson, D L (1995) Effects of climate on numbers of northern prairie wetlands. *Climatic Change* 30: 169–180.

Poiani, K A and Johnson, C W (1993) Potential effects of climate change on a semi-permanent prairie wetland. *Climatic Change* 24: 213–232.

Sorenson, L G, Golberg, R, Root, T L and Anderson, M G (1998) Potential effects of global warming on waterfowl populations breeding in the Northern Great Plains. *Climatic Change* 40: 343–369.

Projected direct impacts of climate change on the nature conservation resources of Britain and Ireland

Mike Harley and Terry Dawson

Climate change is an active natural process which has altered the dynamics of the Earth's physical and biological systems throughout geological time. Post-glacial palaeoenvironmental data based on greenhouse gas and aerosol signatures in ice cores, deep ocean and lake sediments, and peat deposits provides clear evidence of natural climate variability. Palaeoenvironmental data also supports evidence for the relationship between human activity and the huge increases in atmospheric greenhouse gases since the industrial revolution. In its Second Assessment Report (1996), the Intergovernmental Panel on Climate Change concluded that the balance of evidence suggests a discernable human influence on global climate to the extent that global and regional changes in temperature, precipitation and other climate variables are beginning to occur. Anthropogenically driven changes to climate are clearly being superimposed on the background of natural climatic variations, and together these are causing the changes to which we must respond in decades to come.

Ecological and geological processes are vulnerable to changes in climate, including the magnitude and rate of change, as well as to changes in climatic variability. However, the potential impacts of these changes on wildlife and natural (geological and geomorphological) processes are poorly understood. The UK Climate Change Impacts Review Group's *Review of the potential effects of climate change in the United Kingdom* of 1996 raised some important issues about the likely impacts of climate change on the UK's biodiversity, and this work informed the identification of priorities now being addressed by English Nature and other nature conservation organisations in the British Isles. An assessment of existing evidence of climate change impacts on habitats, species and natural processes, coupled with projections for future impacts, will allow judgements to be made about ecological and geological responses to perceived changes. This, in turn, will provide information to justify adaptation strategies, management options and mitigation measures, and to determine robust policy responses – particularly in relation to other key areas of nature conservation policy.

Nature conservation in Britain and Ireland follows a site-based approach, in which domestic and European legislation and international agreements provide protection to isolated features from development pressures and land use change. However, this approach does not adequately accommodate or, indeed, acknowledge the dynamics of global environmental change; nor does it recognise that, under such conditions, the maintenance of the current scientific interest of statutorily designated sites may prove difficult, or even inappropriate. Whilst such sites are likely to remain the best examples of semi-natural habitat, the species composition of these habitats may change in response to climate change. Landscape fragmentation and the potential for further climate-driven land use change, particularly in the lowlands, together with over-riding geological and physiographic constraints, will limit the potential for habitats and species to move in response to climate change. Nature

Figure 1. Maps showing the location of two of the 22 classes derived from the bioclimatic zonation of Britain and Ireland.

Class 17 is an upland / highland class characterised by a low number of growing degree days and low minimum temperatures. It is the most important class for alpine and boreal grasslands and montane heath.

Class 18 is an upland class characterised by being mild, wet and windy. It is the most important class for tall herb ledge communities and wet heaths.

conservation targets for the future will have to reflect this, particularly in the context of landscape modifications to link or buffer isolated sites.

A number of climate change impact studies of relevance to nature conservation have recently been carried out in the UK. These include a *Review of climate change implications for UK habitat and species conservation policy* undertaken for the Department of the Environment, Transport and the Regions (DETR) and the Ministry of Agriculture, Fisheries and Food (MAFF) and the *Regional climate change impact and response studies in East Anglia and North West England* (REGIS) funded by MAFF, UK Water Industry Research and DETR. Both studies fall under the broad umbrella of the UK Climate Impacts Programme (UKCIP).

To complement these studies and fill a particular niche within the UKCIP framework, English Nature, leading a consortium of 11 funding partners commissioned a major piece of research into the impacts of climate change on the nature conservation resources – species, habitats and natural (geological/ geomorphological) features – of England, Wales, Scotland and Ireland. The research is being carried out by a team led by the Environment Change Institute, University of Oxford, and including the School of Geography, University of Oxford, ADAS, ERM and the British Trust for Ornithology.

The study, named MONARCH (Modelling Natural Resource Responses to Climate Change), will provide a quantitative assessment of the likely direct impacts by considering how scenarios for climate change in the 2020s and 2050s will affect terrestrial, freshwater, coastal and marine environments. The work is focussing on protected site networks and UK Biodiversity Action Plan (and equivalent) habitats and species and is using a methodology which links established impact models to coherent climatological zones.

The zonation of the study area has been developed using statistical techniques to associate the key biodiversity elements (species, habitats and ecosystems) with climatic variables (Figure 1). An inventory of the key attributes of each climatological zone has been created, including protected site networks, important habitats and species, and significant natural features. This information was combined with the outputs from other ongoing research to identify a range of habitats, species and natural features to study with the impact models.

Existing impact models for predicting species distributions, water resources and sea-level change have been adapted, calibrated and validated for use within the climatological zones. Examples of preliminary outputs can be seen in Figure 2. Climate change impacts on the key nature conservation attributes are studied by applying the impact models to the range of UKCIP future climate scenarios for the 2020s and 2050s (1998). Significant driving forces, indicators of change and species/habitat vulnerability will be identified from this work.

Work on the project began in July 1999 and will conclude in April 2001. At the end of the study, the results will be reviewed along with the outcomes of complementary studies, particularly those within UKCIP, in order to make recommendations for further research and policy development. Significantly, this will be an important first step towards understanding the complex interactions between climate change and nature conservation and the types of response that may be needed to address the threats or, indeed, opportunities that future climates may present.

MONARCH funding partners

English Nature (lead) 1
Countryside Council for Wales 1
Environment Agency (England and Wales) 1
Environment and Heritage Service (Northern Ireland) 1
Joint Nature Conservation Committee (UK) 1
National Parks and Wildlife (Republic of Ireland) 1
National Trust (England, Wales and Northern Ireland) 2
National Trust for Scotland 2
Royal Society for the Protection of Birds 2
Scottish Natural Heritage 1
World Wide Fund for Nature-UK 2

1: Statutory agency
2: Non-governmental organisation

Further reading

Intergovernmental Panel on Climate Change (1996) *IPCC second assessment: climate change 1995.* Cambridge University Press, Cambridge.

UK Climate Change Impacts Review Group (1996) *Review of the potential effects of climate change in the United Kingdom.* HMSO, London.

UK Climate Impacts Programme (1998) *Climate change in the UK: the agenda for assessment and action.* DETR, London.

Figure 2. Change in the potential distribution of the Large Skipper butterfly *Ochlodes venatus* in Great Britain by 2050 under the UKCIP climate change scenarios, using the SPECIES model (courtesy of the REGIS project funded by MAFF and DETR): (a) current climate; (b) 2050s low scenario; (c) 2050s high scenario.

Conclusion

Rhys E Green, Mike Harley, Mark Spalding and Christoph Zöckler

An era of rapid climate change has begun. Scientific research is now underway to predict future changes and international efforts to reduce emissions of greenhouse gases are being formulated. However, we have not yet begun to slow the rate of change and, even if greenhouse gas emissions could be substantially reduced in the immediate future there would be a lengthy time lag before any discernible reversal in global climate trends commenced. The repercussions of climate changes on wildlife are likely to be considerable, yet they have received little attention. Natural ecosystems and wildlife are likely to be less adaptable than human systems to climate change, being already constrained by burgeoning populations and agricultural land-uses, and also threatened by other human activities.

Irrefutable evidence

This book provides clear evidence that climate change is already impacting on wildlife. Examples are given from Caribou in the Arctic and penguins in the Antarctic, and from tropical cloud forests and coral reefs in the low latitudes. Other examples focus on the temperate zones of Europe and North America. Despite this apparently broad coverage, the picture presented here is by no means complete, focussing on the few areas where most of the current research has been carried out.

The gaps in our knowledge remain considerable. We have little information about impacts over vast regions of the globe, such as South America and Africa, and in particular biomes and species. The work required to develop models and to understand changes is enormous. Not only do we have to contend with the uncertainties of climate modelling, but our efforts are compounded by the natural variations and complex interactions in ecological systems. Changes in climate may favour one species to the detriment of another and, through such a complex web of interactions, the overall impacts of such change may be buffered, or may be exacerbated, in the wider ecosystem. Furthermore, we cannot look at these changes in isolation. Around the globe, almost every ecosystem is under pressure from human activities, and much of our wildlife is already enclosed in protected areas with no place to go as climate regimes shift.

Where changes are observed, it is not always possible to tease out the importance of climate change as a driving factor. This is why some of the studies in remote and relatively pristine environments, such as the Arctic and Antarctic, are of particular importance, and also why many studies presented here look at multiple species over wide geographic areas.

Not every impact will be negative and, alongside the threats, there may be opportunities. Some species, such as the Caribou, may benefit from a warming climate, with the northern latitudes and their people also benefiting from an extended growing season. Elsewhere, changes in temperature and precipitation may have dire consequences. The coral bleaching observed in 1998 is a sobering reminder of just how far-reaching future changes may be, with impacts not only on single species but on entire ecosystems, and on the millions of people who rely on them.

What can be done?

The stories being told in this book are not all stories of high drama. Many portray subtle changes which may appear trivial, such as a shift in a butterfly's range or the earlier flowering of a particular plant. The underlying message is, however, simple – climate change is beginning to impact on the world's wildlife. We are moving from a period of crude scenarios to increasingly accurate models, supported by observations. While further research to fill the regional and ecological gaps in our knowledge will remain a priority for many scientists, we urgently need to address what more can be done.

International policies to reduce the emission of greenhouse gases are of critical importance, but essentially these focus on reducing the effects of climate change in the long-term. However, many impacts will occur over much shorter time-scales. Are we really prepared to adapt for the changes to come? Are there any ways that we might mitigate the impacts?

Nature conservationists urgently need to develop a new approach to their work. Traditionally, nature conservation policy has largely been based on maintaining the contemporary status of species and habitats and on static extrapolations of trends. In reality, nature is dynamic and climate change presents a yet more complex future which we must allow for.

Protected areas remain one of the key tools for conserving habitats and species, but as climatic conditions shift, species and habitats may also alter. It will be critical to allow for this, and to encourage the development of integrated and connected systems of protected areas to allow species and habitats to move as conditions change.

The identification of rare and endangered **species** is widely used as a means of campaigning for their protection. However, climate change is rarely factored into considerations about the future of such species. The Golden Toad may be the first species driven to extinction by climate change (the full explanation remains unclear), but many others, currently not endangered, such as the Emperor Goose, face an uncertain future as habitats shift and change.

Many modern approaches to nature conservation focus on the **sustainable use** of species and habitats, as most of the world's wildlife now lives in close proximity to humans and can sustain or even rely on a degree of utilisation. As the climate changes, these relationships may change, perhaps allowing for increased utilisation in some areas, but similarly threatening wildlife as these patterns of human use and landscape change.

We also may need to develop more innovative approaches to mitigate the impacts in certain areas. As sea levels inundate coastal lowlands, the concept of managed retreat may be an option in many areas, maintaining areas of coastal marshes at far lower costs than maintaining hard sea defences. Similarly, plans for increasing forest cover as a means of removing carbon dioxide from the atmosphere (carbon sequestration) might also be focussed on providing new areas for wildlife. These must be carefully planned so as not to compromise species relying on open landscapes, such as grasslands, bogs and wetlands.

At the level of international policy and law, there remains an urgent need to focus on the impacts of climate change on wildlife. The resilience of the human species has led to complacency among many that somehow we will adapt. For wildlife, however, the options are increasingly limited.

The Earth's climate is changing. The global average temperature has increased by about 0.7°C in the last hundred years and global average sea level has risen by 10–20 cm. There is a growing conviction among climate scientists that human activities, particularly the burning of fossil fuels, have influenced these changes and that warming and sea level rise are set to continue through the 21st Century and beyond. Biodiversity is already threatened by the huge increase in the proportion of the Earth's surface area and resources sequestered by the rapidly growing human population. Climate change will require plant and animal species to shift their geographical ranges or adapt to altered conditions, but habitat loss and fragmentation make this more difficult. This book is based upon an international conference on the impacts of climate change on wildlife and seeks to present the findings of some of the world's leading research scientists in this field in a way that is accessible to the non-specialist. The message is clear – climate change is already affecting wildlife.

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Insets left–right. Adélie Penguins (Michael Gore, FLPA), Red-breasted Goose (Tom Ulrich, OSF), Hairy Violet (C Mattison, FLPA), Speckled Wood butterfly (Hans Christoph Kappel, BBC), Golden Toad (Mike Linley, RSPB Images), Caribou (Joe McDonald, Bruce Coleman).

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