Monitoring Climatic Change With Dragonflies

Edited by

Jürgen Ott

BioRisk 5 (Special Issue)

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Preface

Over the last decades the discussion on the effects of climatic changes increased dramatically. Although there are some uncertainties about the reasons and their proportions, there is great evidence that green house gases are and will increasingly be the main factor causing climatic changes.

Beside habitat loss, fragmentation, globalisation, etc., climate change now is regarded as one of the major threats to biodiversity on Earth and here combined effects with the previously mentioned causes also have to be considered.

Innumerable studies have already been conducted - on observed phenomena as well as on potential effects, dealt with in the context of scenarios and models on future developments.

Here for the first time papers on one taxon – the damsel- and dragonflies – are compiled from different continents to give a vision on how this group has already been and will potentially be affected and what are the consequences for ecosystems, the services they provide, and nature conservation. Besides many examples of range expansions, also ecological effects are demonstrated - and without doubt this group may be regarded as a fantastic indicator for climate change impacts on biodiversity.

This book combines papers from two symposia of the World Wide Dragonfly Association (WDA) in Pontevedra (2005) and Swakopmund (2007) - which were compiled by the editor, as well as some additional contributions and a general view on biodiversity related climate change impacts from the EC funded ALARM project.

All the contributions show, that there are already and will be even more changes within dragonfly as well as general aquatic communities, leading to threats for many species, in particular the stenoecious ones.

We are far from general conclusions and understanding of all factors and effects, as still too many questions are open: e.g. i) whether adaptations of species to new conditions are possible, and if yes, to which extent, ii) what are long term and synergistic effects, and iii) whether there are management options to mitigate climate change impacts.

But already now it is clear, that there is an urgent need for action to reduce the effects of climatic changes (not only) for dragonfly habitats.

May this volume and the contributions therein be a source of information for scientists, students, practitioners, and decision makers and may it function as a mosaic stone to protect the endangered species of this charismatic insect group.

Jürgen Ott
Trippstadt, Germany
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EDITORIAL

BioRisk

Monitoring climate change with Dragonflies: Foreword

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Climate change has become a cold reality for the public, or a hot disaster for those who are suffering from extreme heat-related events such as the destructive fires in Australia in early 2009. The symptoms of climate change are no longer possible to ignore, with polar ice caps melting, glaciers receding, and the distribution of breeding birds steadily moving northward.

The combination of sound science, as illustrated through the regular reports of the Intergovernmental Panel on Climate Change (IPCC); the growing public awareness as illustrated by the Oscar-winning film, "An Inconvenient Truth" narrated by Al Gore; and the solid economic case made by the Report prepared for the British Government by former World Bank Chief Economist, Nicholas Stern, have been crucial in putting the issue squarely before the public.

And individuals, the private sector, and governments are all responding in various ways. Terms like "carbon sequestration", "carbon footprint", and "energy efficiency" are now part of the public vocabulary. All of this indicates that society at large may well be finally taking the issue seriously.

But despite all of this, our understanding of the dynamics of climate change remains surprisingly poor. But perhaps this is not so surprising, given the great complexity of the global climate system, and the diversity of its symptoms in various parts of the world. An effective means of providing solid scientific evidence for the changing conditions would be a boon to decision-makers, from an individual to a Head of State. **Monitoring Climate Change with Dragonflies** provides a novel and cost-effective approach, using dragonflies as a means of monitoring climate change. As the authors

of the various chapters have made very clear, dragonflies offer numerous advantages. They are relatively easy to identify; they are very sensitive to changes in environmental conditions, including climate; different species have different distributions, with a sufficient number of species to provide a rich source of data; they reproduce relatively quickly, so changes over generations are revealed in a timely manner; and research to date has indicated that the distribution of dragonflies is very sensitive to climate change. Added to these advantages is another important one in a time of economic distress: the monitoring process can be carried out on a regular basis on a very cost-effective budget. Dragonfly studies are not capital-or equipment-intensive activities. Further, the kinds of monitoring that are required can be done largely by students or interested amateurs, with appropriate leadership and oversight from qualified experts.

All of these advantages indicate that dragonflies, which play many important ecological roles in aquatic ecosystems, may become one of our most important allies in documenting the effects of climate change. They can help provide early warning, detailed evidence, rapid indication of changing climate patterns, and much else besides.

The rich flow of data that can come through a widespread collaborative network collecting regular information on the distribution of dragonflies in relation to climate change can also help provide insights into the responses that might be required to modify land use to the emerging climatic reality. **Monitoring Climate Change with Dragonflies** provides an important new tool for dealing with arguably the most important environmental challenge facing modern humanity. It provides a solid foundation on which subsequent research can be built, and can help ensure that responses to climate change are as appropriate as possible.

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EDITORIAL

Climate change impacts on biodiversity: a short introduction with special emphasis on the ALARM approach for the assessment of multiple risks

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How to study multiple risks: setting the scene

Climate change and human modification of the landscape are synergistic (Travis 2003), and affect biodiversity and the stability of ecosystems. This is because certain species will be favoured by changes, while others will not. However, as stated by Fanslow (2006), the simplicity stops here, with Samways et al. (1999) illustrating the differential impact of climate change events on a range of closely related species. It is relatively easy to test how increased temperature will affect an organism. We can isolate almost any organism, put it in a box and observe how it responds to environmental changes we can simulate in a controlled setting, such as a laboratory. We might find, for example, that warming benefits this isolated organism. But what if warming also benefits a

disease to this organism? What if temperatures become too warm for other organisms on which our hypothetical organism depends such as its prey when it is a predator or a pollinator of its host plant if it is a herbivore? What if warming benefits a competitor even more?

Once we step outside the small hypothetical box that defines just one organism, or some isolated parts of an ecosystem, and start to ask questions about how it will interact with other "boxes" in the environment, we are quickly inundated with uncertainty about how environmental change will reshape our world. Ecosystems are remarkably complex, which makes it exceedingly difficult to predict their behaviour (Walther 2010). In some cases, we may be able to understand how one species affects another species, but in a relatively simple hypothetical system of 50 species, for example, each species potentially interacts with 49 other species. This gives no less than 1,225 possible two-way interactions in a simple 50-species system. If then the frame of reference is expanded to larger areas with many more types of ecosystems, it is clear that even a large group of dedicated scientists could not study even a small percentage of the possible two-way interactions using traditional controlled experiments, much less the three- and four-way interactions that are often just as important.

Another challenging aspect to developing an understanding of interactions between components of a complex system is the matter of communication among scientists of different disciplines. The different scientific disciplines – which can be thought of as different boxes in which scientists work – have traditionally been viewed as distinct and have developed strikingly different languages. As a result, interdisciplinary collaboration tends to be rare because getting through language barriers with someone in a different discipline requires a lot of valuable time and energy for people who generally don't have a lot to spare.

When you want to understand processes in a very large scaled system, but cannot do experiments, modelling is a useful way to synthesize information gathered independently about components of a larger system.

One approach to understand environmental risks over large areas was followed by the EU funded research project ALARM, which had a scope matched only by the ambition of its acronym: "Assessing LArge-scale environmental Risks for biodiversity with tested Methods".

How to study multiple risks: the ALARM approach

The objective of the ALARM project (Settele et al. 2005, 2010; http://www.alarmproject.net) was to apply our best understanding of how terrestrial and freshwater organisms and ecosystems function and to use new ways to assess large scale environmental risks. The ultimate aim was to develop and test methods and protocols for such an assessment and provide information that can be used to reduce negative impacts on humans and, in turn, minimize negative human impacts – both direct and indirect.

Research was related to ecosystem services in the broadest sense including the relationships between society, economy and biodiversity. In particular, risks to biodiversity were assessed that arise from

– climate change,
– environmental chemicals,
– biological invasions and
– loss of pollinators

in the context of current and potential future European socio-economic development options and their respective land use patterns, for which scenarios were applied. Here, dragonflies are mainly and directly impacted by the first 3 factors, by the forth only indirectly.

Risk assessments in ALARM were hierarchical and examined a range of organisational (genes, species, ecosystems), temporal (seasonal, annual, decadal) and spatial scales (habitat, region, continent) determined by the appropriate resolution of current case studies and databases (compare Figure 1).

Socio-economics was a cross-cutting theme that contributed to the integration of driver-specific risk assessment methods, developed instruments to communicate risks to biodiversity end users, and indicated policy options to mitigate such risks.
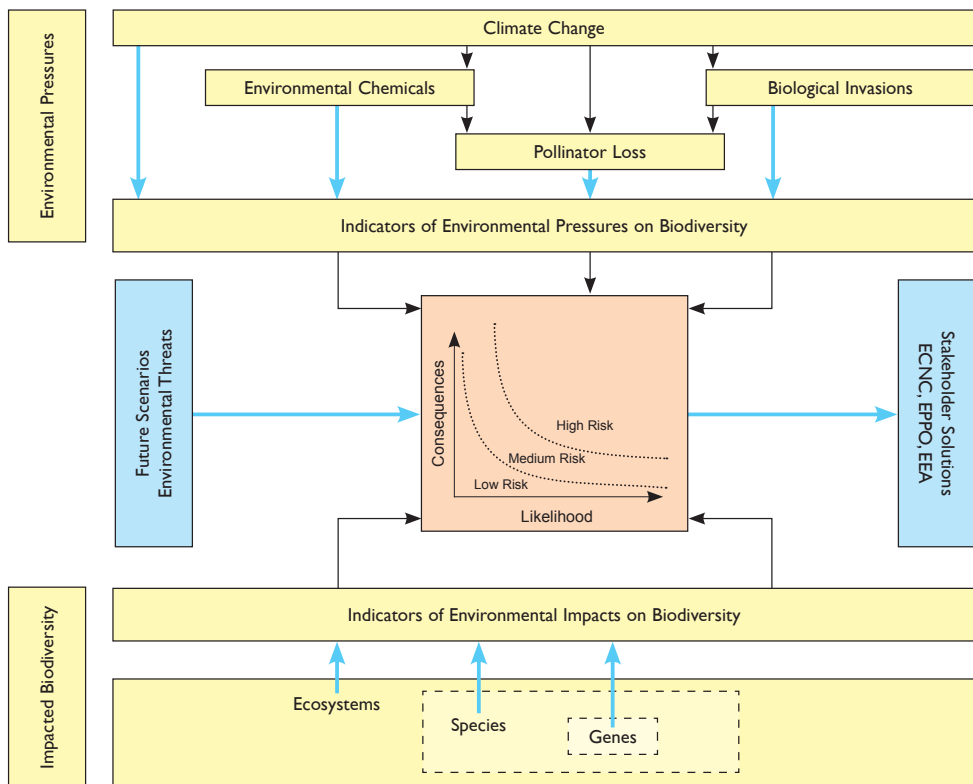
Figure 1. The ALARM research approach (from Settele et al. 2010)

So as to have a platform for practical interdisciplinary research, a field site network (FSN) was established within ALARM, where the different ALARM modules conducted joint research. All sites included freshwater as well as terrestrial habitats, including both lotic and lentic environments. The FSN covered most of European climates and biogeographic regions, from Mediterranean environments through central European and boreal zones to the subarctic (see Hammen et al. 2010a, 2010b, for further details).

The feature of ALARM that has set it apart from overly complex model exercises is that it made use of scientific narratives (or storylines) based on scientists' best understanding of the environmental systems they study (Spangenberg 2007a, Spangenberg et al. 2010, in press). ALARM puts these narratives together to paint a larger picture of how something as large and complex as the environment of a continent will react to different environmental and – interacting with them – socio-economic driving forces.

Just as challenging as reaching an understanding of how environmental change will play out, is translating that understanding into language that policymakers and the general public can understand.

To illustrate what we were trying to do through the ALARM project, we may contrast different forms of environmental storytelling: scientists tend to be reluctant to let a good story to distract attention from the facts, while journalists or activists can often be accused of ignoring facts for the sake of a good story. The goal of ALARM is to find a compromise between these ways of telling environmental stories and treat stories as the envelopes to carry facts, bearing in mind that facts are often the basis for a good story. For dragonflies the example of the expansion of the Scarlet Darter (*Crocothemis erythraea*, see Ott 2001, 2007b, 2010a, 2010b) is meanwhile well known and besides scientific papers also many popular articles or presentations start with this "success story".

After expanding its geographic reach in early 2007 by adding scientists and institutions particularly from outside the European Union, ALARM encompassed a total of more than 250 scientists from 68 institutions from 35 countries, with a total budget of more than 20 Mio. Euro (slightly more than 50% funded by the EU). The consortium was co-ordinated by the German Helmholtz-Centre for Environmental Research – UFZ. ALARM started in February 2004, and the EU funding lasted for 5 years until early 2009. It was an Integrated Project (IP) within the 6th Framework Programme of the European Commission (EC) within the sub-priority 6.3 - Sustainable Development, Global Change and Ecosystems.

In the following chapters we will detail some of the more climate related aspects of biodiversity conservation in general and of the ALARM approaches which are also relevant to dragon- and damselflies in particular.

Integrated long-term scenarios as a starting point for assessing biodiversity risks

Scenarios, narratives, models, and strategy development

Biodiversity is influenced by a combination of natural processes (e.g. evolution, succession, catastrophes) and anthropogenic pressures (e.g. land use, nitrogen deposition, climate change, alien species invasions). From a policy point of view, this situation constitutes an urgent need to identify the human drivers causing pressures on biodiversity, and to develop strategies and policies to mitigate the resulting impacts in order to minimise biodiversity losses (Spangenberg et al. in press).

Given that just like the environment, society and the economy are complex, developing (i.e. neither deterministic nor stochastic) systems, their future interaction and thus the development of biodiversity pressures cannot be predicted or expressed as quantified risks. However, since the system development is path dependant, such pathways can be evaluated by scenario techniques, with each pathway represented by a scenario narrative or story line, and some aspects of each illustrated by computer modelling. In turn, the modelling results have to be interpreted in the context of the narrative to integrate the qualitative elements into the scenarios and the strategy proposals derived from them. Such scenarios are means for the evaluation of potential risks, and policy strategies are the search for or the creation of bifurcation points in the trajectories.

Developing effective strategies for biodiversity conservation and management requires the transdisciplinary combination of capabilities, concepts, insights and tools of several disciplines (e.g. ecology, chemistry, economics, and political science) with non-scientific knowledge, and so does scenario development. A major challenge is to ensure that the assumptions used in the various modelling exercises are consistent (or at least their interpretation is), that the issues addressed are relevant and the assumptions made are plausible. The latter is the contribution of non-scientific knowledge and experience, realised in the case of ALARM by establishing a multi-stakeholder Consultative Forum, which had significant influence on the scenario formulation.

Regarding the contribution of quantified modelling, so far no comprehensive model has been developed integrating the diverse relevant ecological, economic, individual and societal processes (and even if it existed, it would not be too helpful). Instead, socio-economic, climate and biodiversity models exhibit a wide range of assumptions concerning population development, economic growth and the resulting pressures on biodiversity, and they deal with significantly different time scales and spatial framings.[1]

Therefore it is necessary to derive consistent assumptions and scenario interpretations from a comparative analysis of models and scenarios from several disciplines,

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[1]   Within ALARM, socio-economic, land use and nitrogen deposition models are run, one using the output of the other as input parameter, but land use and biodiversity models must be reconciled by interpretation on the basis of the storyline.

assessing their overlaps and the possible contradictions between the results of one and the assumptions of other scenarios. Within the ALARM scenario development process, this is done by interpreting the modelling results against the backdrop of a joint narrative. A complementary, cross-disciplinary knowledge base needs to be developed in order to support effective policy decisions and provide a basis for future modelling exercises on all levels. This requires the close cooperation within an interdisciplinary team of economists, climatologists, land use experts, biologists, modellers and policy experts. The three internally coherent but amongst them contrasting scenarios developed are one of liberal policies (GRAS), one of a continuation of rather mixed EU policies (BAMBU) and one of consequential sustainability policies (SEDG) (see chapter "Three basic scenarios.." below, for further details).

Usually, scenarios are based on rather linear extrapolations of past trends, which is a rather unrealistic assumption given the uncertainty inherent to the dynamics of evolving systems. Consequently, the effects of non-linear developments need to be taken into account (Walther 2010). Thus, complementing the rather linear scenarios underpinned by simulation runs, *shock scenarios* have been developed. They serve as sensitivity analysis for the basic scenarios, and although their probability of occurrence cannot be quantified, they illustrate how different future developments can and most probably will be from an extrapolation of past trends.

Given the interaction of the economic, social and natural systems, one illustrative shock to each of the systems is taken into account. The climate shock (collapse of the thermo-haline circulation, vulgo: the Gulf Stream) is conceptualised as a modification of the liberal GRAS scenario (as it provides the highest probability for such a shock occurring). The economic shock (Peak Oil: oil price quadrupling) and the societal shock (a pandemic) are applied to BAMBU, the current politics scenario, as they are not dependant on the policy changes assumed under both variants. Economic and social aspects, environmental impacts of the shocks and of the most plausible reaction of the political system to them are developed in the scenario narratives.

The scenarios and their interpretations have been presented to decision makers to support reflexive policy development efforts. They identify the most important drivers, show how they need to be modified, changed or abandoned in order to achieve a significant reduction of biodiversity loss, contributing to the new EU policy goals for 2020 and beyond. In this context, ALARM provides an up-to-date information base for decision makers which intend to ex ante evaluate policy strategies before implementing them. Thus, feedback circles, rebound effects and other system characteristics can be taken into account, supporting policies for effective protection of biodiversity

Three basic scenarios and three deviations (shocks)

GRAS (GRowth Applied Strategy): Deregulation, free trade, growth and globalisation are policy objectives actively pursued by governments. Environmental policies focus on

damage repair and limited prevention based on cost-benefit-calculations. No emphasis is put on biodiversity.

BAMBU (Business-As-Might-Be-Usual): Policy decisions already made in the EU are implemented and enforced. At the national level, deregulation and privatisation continue except in "strategic areas". Internationally, there is free trade. Environmental policy is perceived as another technological challenge.

SEDG (Sustainable European Development Goal): The sustainability of societal development is enhanced by integrated social, environmental and economic policy. Policy aims for a competitive economy in a healthy environment, gender equity and international cooperation. SEDG is a normative scenario with stabilisation of GHG emissions.

GRAS-CUT (Cooling Under Thermohaline collapse): Deregulation, free trade, growth and globalisation are policy objectives (as for GRAS) before a climate shock
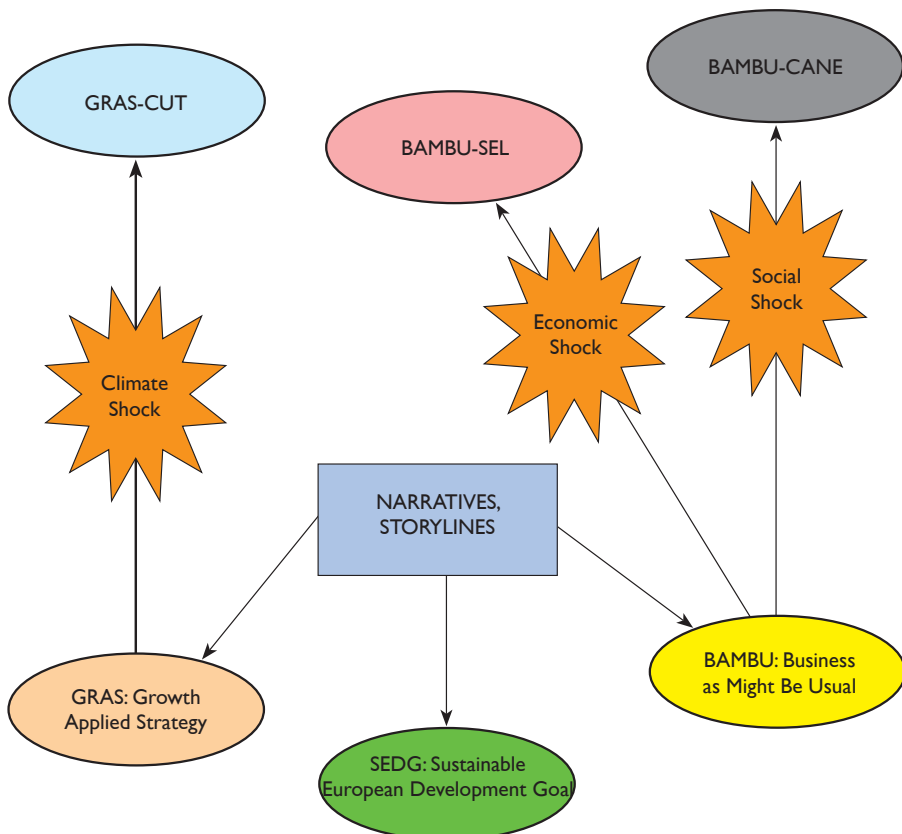
Figure 2. The ALARM scenarios (taken from Spangenberg et al. 2010).

(the collapse of the thermohaline circulation) in 2050. Alternative economic and environmental policies are then introduced in reaction to this shock.

BAMBU-SEL (Shock in Energy price Level): High prices for energy and high price volatility is to be expected, and absolute scarcities may occur in the near future - 2015. Alternative economic and environmental policies are then introduced in reaction to this shock.

BAMBU-CANE (ContAgious Natural Epidemic): A global pandemic in the near future - 2015, causes changes in population numbers, distribution and behaviour, with subsequent social and political implications. Alternative economic and environmental policies are introduced in reaction to this shock.

For all scenarios the impacts on biodiversity (species groups and ecosystems in different biomes) have been explored by deliberation methods, with the ALARM scientists serving as the expert base (Marion et al. 2010)

Observed and projected climate change in Europe

The Intergovernmental Panel on Climate Change (IPCC) estimates a 0.07±0.02°C per decade increase in global surface temperatures over the last 100 years (IPCC 2007). Temperature reconstructions present strong evidence that this magnitude has been the largest over the last 1000 years (Folland et al. 2001). Furthermore, the 1990s are likely to have been the warmest decade of the last millennium (Folland et al. 2001) with a continuation of the trend until 2009 (Jones and Moberg 2003 and updates[2]). 20th century annual mean temperature rise in Europe was 0.08±0.03°C, thus slightly larger than the global mean with the warming being more pronounced during winter than summer (Luterbacher et al. 2004).

Precipitation patterns are spatially and temporally more heterogeneous than temperature with some regions experiencing dryer conditions while others have become wetter. Due to the large variation, significant trends are generally more difficult to detect. Increases in temperature lead to increased water-holding capacity of the atmosphere, altering the hydrological cycle and thus also precipitation events (Treydte et al. 2006). Globally, observed annual precipitation records indicate a twentieth-century increase of about 9 mm over land areas (excluding Antarctica), although this trend is relatively small compared to the century-long variability (New et al. 2001). European trends in annual precipitation reveal a wettening in northern Europe while large parts of southern Europe show little change or drying (IPCC 2007).

Climate extremes are rare events that fall in the tails of the distribution of e.g. daily temperature or precipitation. In order to statistically detect any trends in the frequency and magnitude of extreme weather situations, longer observation time-series are required compared to changes in the mean climate. A global analysis with a large set of

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[2]   Source of updated values until 2009: http://www.cru.uea.ac.uk/cru/data/temperature (assessed: 21 September 2010).

indices of daily climate extremes such as a warm spell duration index, the number of frost days or the occurrence of very wet days was conducted by Alexander et al. (2006) for the period 1951–2003. They found significant increases in daily minimum and maximum temperatures throughout the globe and increases in precipitation extremes over many areas, although much less spatially coherent. Table 1 gives an overview of observed and projected changes in extremes and the level of confidence. Observed

Table 1. Change in extremes for meteorological phenomena over the specified region and period, with the level of confidence (Source: IPCC, 2007). In the IPCC terminology, "very likely" expresses a 90–99% chance and "likely" a 66–90% chance.

Phenomenon	*Change*	*Region*	*Period*	*Confidence*
Low-temperature days/nights and frost days	Decrease, more so for nights than days	Over 70% of global land area	1951–2003 (last 150 years for Europe and China)	Very likely
High-temperature days/nights	Increase, more so for nights than days	Over 70% of global land area	1951–2003	Very likely
Cold spells/snaps (episodes of several days)	Insufficient studies, but daily temperature changes imply a decrease			
Warm spells (heat waves) (episodes of several days)	Increase: implicit evidence from changes of daily temperatures	Global	1951–2003	Likely
Cool seasons/ warm seasons (seasonal averages)	Some new evidence for changes in inter-seasonal variability	Central Europe	1961–2004	Likely
Heavy precipitation events (that occur every year)	Increase, generally beyond that expected from changes in the mean	Many mid-latitude regions (even where reduction in total precipitation)	1951–2003	Likely
Rare precipitation events (with return periods > ~10 yr)	Increase	Only a few regions have sufficient data for reliable trends (e.g., UK and USA)	Various since 1893	Likely (consistent with changes inferred for more robust statistics)
Drought (season/year)	Increase in total area affected	Many land regions of the world	Since 1970s	Likely
Tropical cyclones	Trends towards longer lifetimes and greater storm intensity, but no trend in frequency	Tropics	Since 1970s	Likely; more confidence in frequency and intensity
Extreme extratropical storms	Net increase in frequency/intensity and poleward shift in track	Northern Hemisphere (on land)	Since about 1950	Likely
Small-scale severe weather phenomena	Insufficient studies for assessment			

changes in the frequency of temperature-related extremes show generally increases in heat events and decreases in cold events.

The projected warming until the end of the 21st century is 1.1 – 6.4°C in global mean annual temperature (IPCC 2007)[3]. Global annual precipitation is projected to increase by 1.3 – 6.8% until the period 2071–2100 according to simulations under the SRES A2 scenario (IPCC 2001). Projections for Europe show wetter conditions in northern Europe mainly during winter and drier conditions in southern Europe for the summer (Ruosteenoja et al. 2003). Still, observed increase in atmospheric CO_2 over the past decades was mostly above the mean (but within the 95% confidence intervals) of the extreme A1FI scenario (Le Quere et al. 2009).

One of the main objectives of the ALARM project was to study the risks of climate change to biodiversity in Europe. Both historic information about climate as well as climate scenarios projecting changes into the future are needed for this. Historic climate datasets on a regular grid system developed by the Climatic Research Unit (CRU) at the University of East Anglia, UK, provide high-resolution information for key climate variables in monthly time steps throughout the 20th century (New et al. 2002, Mitchell et al. 2003). The datasets consist of six variables: mean surface temperature, diurnal temperature range, precipitation, vapour pressure and cloudiness.

Coupled atmosphere-ocean global circulation models (AOGCMs) are the most sophisticated tools currently available for simulating responses of the climate system to increases in greenhouse gas concentrations. Projected changes in climate variables from AOGCMs were used to construct the core set of ALARM climate scenarios for Europe that continues the historic dataset into the 21st century (Fronzek et al. 2010). For the scenarios, labelled GRAS, BAMBU and SEDG, narrative storylines have been developed (see previous chapter) and also other drivers of biodiversity change were quantified to allow a multi-pressure assessment.

For the BAMBU basic scenario, simulations from three different AOGCMs were selected covering a wide range of climate model uncertainties to represent the scenario. Simulations from one AOGCM, the HadCM3, have been used to represent climate changes in all three ALARM scenarios. The range of temperature and precipitation changes is summarized in Table 2.

The spatial pattern of simulated changes in temperature and precipitation are shown below for the GRAS scenario with the HadCM3 AOGCM. For the five ALARM climate scenarios described here, this scenario gives the strongest warming by the end of the 21st century. In this scenario, winter warming until the period 2071–2100 (relative to 1961–1990) shows a gradient from south-western to north-eastern Europe with the smallest increases of *c.* 3°C over the Iberian peninsula and the largest increases of more than 10°C in northern Finland (Figure 3, left). Summer warming is strongest in the Mediterranean countries (Figure 3, right).

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[3] Estimated change by 2090–2099 relative to 1980–1999 with a 90% likelihood for six alternative scenarios of greenhouse gas emissions.

Table 2. Simulated changes in annual mean temperature (°C) and annual precipitation by 2071–2100 relative to 1961–1990 averaged over Europe for the ALARM scenarios.

Scenario (SRES)	Climate model	Temperature change (°C)	Precipitation change (%)
BAMBU (A2)	NCAR-PCM	3.0	3.8
BAMBU (A2)	CSIRO2	4.6	5.8
BAMBU (A2)	HadCM3	5.0	0.1
SEDG (B1)	HadCM3	3.3	-0.8
GRAS (A1FI)	HadCM3	6.1	-0.8
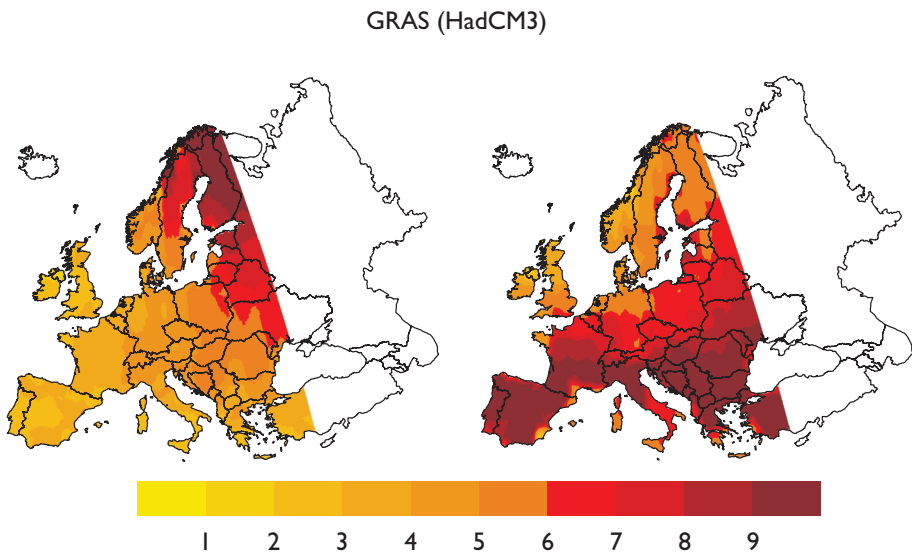
Figure 3. Change in air temperature (in °C) between the periods 1961–1990 and 2071–2100 in winter (December-February, left) and summer (June-August, right) for the GRAS scenario using the HadCM3 AOGCM with the A1FI emission scenario (taken from Fronzek et al. 2010).

The CSIRO2 model expects a similar temperature increase by 2100 (4.6° as compared to 5.0°), whereas the NCAR-PCM model results in a lower increase (3.0°) for the same scenario. The pattern of stronger warming in winter in North-East Europe and in summer in Southern Europe is consistent among all five climate scenarios (Fronzek et al. 2010).

The pattern of winter precipitation changes for the same scenario, again with the HadCM3 AOGCM, shows wetter conditions over nearly all of central and northern Europe and dryer conditions in southern Europe (Figure 4, left). Summer precipitation in this scenario decreases over large part of Europe with the only exceptions being Fennoscandia and parts of the Baltic countries (Figure 4, right). Averages for Europe shown in Table 2 do not convey these regional differences. Precipitation changes projected by the NCAR-PCM and CSIRO2 models show wetter conditions compared to the HadCM3 scenario (3.8% resp. 5.8% as compared to 0.1% increase averaged for Europe).

GRAS (HadCM3)
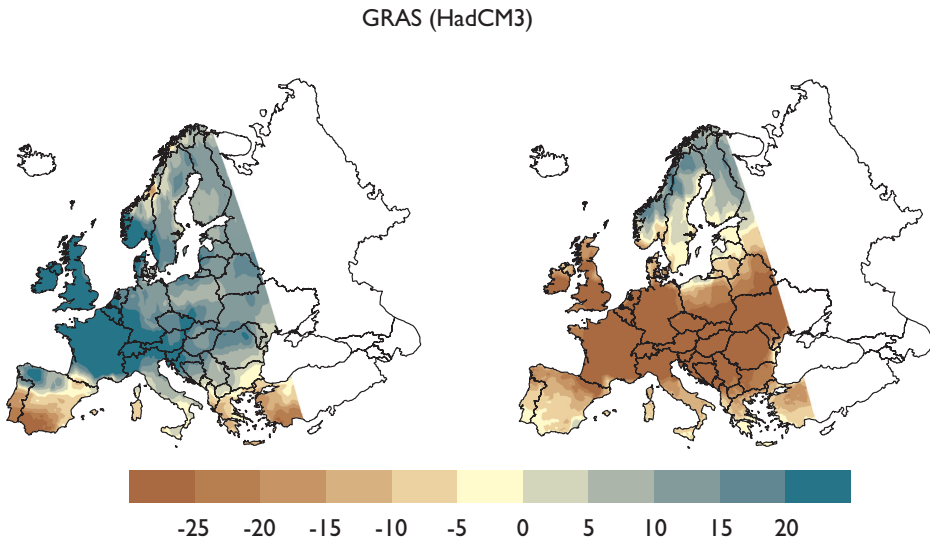
Figure 4. Relative change in precipitation (in %) between the periods 1961–1990 and 2071–2100 in winter (December-February, left) and summer (June-August, right) for the GRAS scenario using the HadCM3 AOGCM with the A1FI emission scenario (taken from Fronzek et al. 2010).

A further climate scenario (labelled GRAS-CUT) explores the impacts of a sudden collapse of the North-Atlantic thermohaline circulation (THC) that would cause a major cooling over north-western Europe.

Climate change impacts on biodiversity at large – with particular reference to ALARM results

Impacts of climate change on plants

A changing climate modifies the conditions which shape the physiological behaviour, the productivity and the ranges of many plants and thus, is expected to induce manifold reactions of climate sensitive species and ecosystems (e.g. Huntley et al. 1995, Sykes et al. 1996, Kappelle et al. 1999, Theurillat and Guisan 2001, Thuiller et al. 2005, Pompe et al. 2008). In recent years, an increasing number of ecological "fingerprints" of climate change impacts (Walther et al. 2001, Parmesan and Yohe 2003, Root et al. 2003) provide ground-truth data of observed changes in the behaviour and distribution of plant species (Walther et al. 2010). While a European scale analysis yielded strong impacts especially on Mediterranean and high mountain plant species (Thuiller et al. 2005, Rickebusch et al. 2008), a regional analysis from Germany showed specific vulnerability of plant species in the North-East and South-West of Germany due to increasing droughts (Pompe et al. 2008). Using this data and assigning the species to

their habitat specific species pool (Pompe et al. 2010) found that the species pools of tall herb communities, bushes, and turfs near or above the treeline were most sensitive, followed by dwarf shrub communities below alpine areas. The species assigned to forb communities, forest grassland ecotones and tall herb slopes outside floodplains, plant cultures, and urban, commercial, and industrial areas were least negatively impacted by climate change.

On the basis of long-term phenological records, trends in the response of living organisms to climatic changes can be tracked. Evidence that events in spring have been happening earlier in recent decades arises from a wide range of species and across a wide range of geographic locations. Despite some inconsistencies in the numeric values of the data, an overall trend of 2.3 days per decade towards an earlier onset of spring has been documented (Parmesan and Yohe 2003). Fewer phenological data are available for the fall season. However, the few data sets that include phenophases in both spring and autumn reveal a trend towards a prolongation at both ends of the season and thus, an extension of the growing season (Walther 2004). The observed lengthening of the growing season is based on terrestrial phenological data records with satellite observations of leaf area index anomalies over the past two decades (e.g. Lucht et al. 2002).

In addition to phenological changes, climate warming is also expected to shift the margins of species ranges or boundaries of biomes (e.g. Huntley et al. 1995, Sykes et al. 1996). Evidence for species range shifts has been reported from various habitats (Walther et al. 2010). The period of milder winter conditions since the 1970s for example is in temporal synchrony with a major phase of spread and establishment of thermophilous evergreen broad-leaved species on sites with former deciduous forest vegetation south of the Alps (Walther et al. 2002, Walther and Berger 2010).

In analogy, the partial replacement of neighbouring altitudinal belts is reported by Penuelas and Boada (2003) from north-eastern Spain. This upward shift of vegetation belts is ascribed to the rising annual temperature of 1.2–1.4 °C during the last 50 years with the main increase in the last 30 years. In the Arctic, Cornelissen et al. (2001) suggest a climate-induced change in species composition of arctic plant communities with declining macrolichen abundance as a consequence of the increased abundance of vascular plants. An analogue process of increasing species number and frequency is found at the altitudinal margin of plant life. In the Alps, e.g. Hofer (1992) and Grabherr et al. (1994) provide data on increasing species abundance and richness of plants on high mountain tops showing the overall trend of an upward shift of the alpine-nival flora, which is attributed to the observed warming in climate in these areas. A recent update of the flora of high mountain peaks in the Swiss Alps based on the Hofer (1992) revealed that the trend of increasing species numbers in the summit areas continues and might even have been accelerated in the last decade (Walther et al. 2005b).

The biotic response to thirty years of enhanced global warming has become perceptible and substantial. An overwhelming number of studies provide evidence for climate change impacts on species, communities and ecosystems (Hughes 2000, McCarty 2001, Walther et al. 2002, Root et al. 2003, Parmesan 2006, Walther 2010; for

plants see also Walther 2004). In the long-term perspective, the biotic implications of climate change and its evolutionary consequences depend on both the magnitude and rate of global warming as well as on the development of other human influences on biological systems such as habitat conversion, overexploitation and pollution (e.g. Leemans 2001, Travis 2003). It is the combination of these influences that also determines the full extent of the impact of climate change on plants.

Of particular relevance for dragon- and damselflies are studies on climate change impacts on aquatic plants, as these are the core resources for oviposition. Heikkinen et al. (2009) present the northern spread of the invasive aquatic plant *Elodea canadensis* in Europe, which is fostered by climate change effects. The expansion of this plant may favour the expansion of damsel- and dragonflies showing endophytic oviposition, and in fact in Scandinavian countries *Calopteryx* species show an expansion to the north (Ott 2010b).

On the other hand, the decrease of the water soldier (*Stratiotes aloides*) in northern Germany in recent years, which seems to be a combined effect of climate change and eutrophication, has an immediate impact on the populations of the endangered and protected Green Darter (*Aeshna viridis*), a dragonfly which lays its eggs only into this plant.

Impacts of climate change on animals

As for plants there is already strong scientific evidence of the impact of climate change on animals in Europe. During the 21st century rapidly shifting climate zones and rising sea levels will put increasing pressure on species already under threat for other reasons. Among the many examples of climate change effects are: i) phenological changes such as earlier first appearances of British butterflies in the summer (Roy and Sparks 2000) or general changes in the phenology for dragonflies (Ott 2001), ii) northward expansion of many species (Parmesan and Yohe 2003), in particular for Mediterranean dragonflies (Ott 2001, 2010a, 2010b), iii) spreading of sea shell animals (e.g. the barnacle *Balanus perforatus*) from warmer seas around SW England 100 km eastwards up the Channel (Hiscock et al. 2004), iv) overwintering of migratory water birds from the Arctic along the North Sea coast rather than the milder western seaboard of Britain (Robinson et al., 2005), v) microevolutionary adaptations such as diet expansion of a butterfly in response to climate change (Thomas et al. 2001), vi) local extinction of low elevation butterflies in the southern parts of their geographical range (Hill et al. 2002), and (vii) changes in the structure of local bird and butterfly communities (Devictor et al. 2008, Van Swaay et al. 2010), as well as for dragonfly communities (Ott 2007b).

One of several studies from within the ALARM project (Araujo et al 2006) has shown that projected climate change could trigger massive range contractions among amphibian and reptile species in the southwest of Europe. The authors projected distributions of 42 amphibian and 66 reptile species 20–50 years into the future under 4 emission scenarios proposed by the Intergovernmental Panel on Climate Change and

3 different climate models (HadCM3, CGCM2, and CSIRO2). The researchers found that increases in temperature are not likely to constitute a major threat to amphibian and reptile species in Europe. Indeed, a global cooling scenario would be much worse. However, increases in aridity could trigger contractions in the distributions of nearly all species occurring in the southwest of Europe, including Portugal, Spain and France. Impacts in these three countries are not trivial because, together, they hold 62% of the amphibian and reptile species present in Europe. The high proportion of amphibian and reptile species occurring in these three countries is due to the key role played by the Iberian Peninsula as refugia against extinctions during past glacial periods. With projected climate changes these hotpots of persistence might be at risk of becoming hotspots of extinction (see Araujo et al. 2006 for further details).

Just as amphibians, also dragonflies will of course show similar reactions and serve as an "indicator", as well as a "victim": higher temperatures during summertime and warmer winters (see chapter on climate change scenarios) will lead to many biological effects (e.g. change in the phenology, trend to an increased expansion, invasion of southern species, elimination of cold stenotherm species; see Ott 2001), weather extremes at a local or regional scale will lead to droughts in certain biotopes and eliminate all species of a water body or region or alter the communities (see Ott 2010b) and extreme storms can lead to long distance drifts of individuals and new areas may be readily occupied by a species.

In general all changes of the distribution of amphibians will alter also the dragonfly communities, as amphibians and dragonflies are prey and predators at the same time: dragonfly larvae prey on tadpoles and adult frogs prey on damsel- and dragonflies (Ott 2001).

In contrast, impacts of climate change on butterflies are projected to be more severe. Under an extreme GRAS scenario (climate corresponds to IPCC SRES A1FI) over 95 per cent of the present land occupied by 70 different butterflies would become too warm for continued survival. The best case SEDG scenario (A2) sees 50 per cent of the land occupied by 147 different butterflies would become too warm for them to continue to exist there. Many butterflies will largely disappear from where they are regularly seen now (Settele et al. 2008, 2009).

Butterflies are a typical prey for damsel- and dragonflies, but a decrease of butterflies will probably have only little effect on them, as butterflies will not in general be eliminated and dragonflies also can easily switch to other prey (e.g. Diptera).

In general, looking to the future, wild plants and animals will go extinct in some places unless they can keep pace with the rapidly changing climate. While some mobile species can do this, other, less mobile and stenoecious species, will find it much more difficult. There is also a concern that biodiversity may be affected in multiple ways because of other responses to climate change, such as increased demand for water, leading to drying out of rivers and wetlands.

The reactions of single species can have severe cascading effects on higher organisational levels of biodiversity. Since single species react individualistically to climate change, this will ultimately lead to the generation of novel communities (Walther

2010). These novel communities will be characterised by the disruption of currently existing species interactions and the potential of new interactions (Schweiger et al. 2010a). During the ALARM project Schweiger et al. (2008) showed that the future overlaps of climatically suitable areas of the monophagous butterfly *Boloria titania* and its larval host plant *Polygonum bistorta* may virtually disappear from where they presently co-exist and allow co-occurrence only in distantly located areas, whereby the ability to colonise these areas is questionable for both plant and butterfly. In a follow up study Schweiger et al. (2010b) showed that such mismatches are not the case for every species. In fact most butterfly species are supposed to be not limited by the distribution of their host plants and thus future mismatches are not an issue for them. However, there are several species which are to a certain extent limited by their host plants and for them future mismatches are indeed a serious issue. Of particular concern in this context are species that utilise range limited host plants.

Such mismatches of interacting species are not restricted to pairwise interactions but can expand to whole interaction networks as has been reviewed by Schweiger et al. (2010a). Although, the architecture of such networks and their redundancy and flexibility might impede cascading extinctions (Hegland et al. 2009, Memmot et al. 2004, Vilà et al. 2009), such buffer capacities are not unlimited and will not necessarily circumvent severe changes in species interactions and the consequent species extinctions (Memmott et al. 2004, Fortuna and Bascompte 2006). Further, changes in community composition and species interactions can, especially in combination with additional pressures (see below) lead to severe consequences for ecosystem services (Potts et al. 2010). This is in particular true for wetland ecosystems, where dragonflies are excellent indicators for the effects of climatic changes (Ott 2001, 2008b, 2010b).

Dragonflies only have a limited dependency on plants, but very much on waters, its quality and quantity. Alterations of the water level lead to changes of the dragonfly community (e.g. favour eurycious species and eliminate mooreland species, see Ott 2007b, 2010b) or could lead to invasions by Mediterranean species which previously did not inhabit these water bodies (e.g. by *Lestes barbarus* or *Ischnura pumilio*, see: Ott 2006, 2008a). If the water level recovers due to an increased precipitation the old dragonfly communities may recover as well and the new species may leave again, but it also could lead to an irreversible change and new aquatic communities (Ott 2010b, unpubl. data).

Multiple risks for biodiversity: Climate change in interaction with other pressures

In addition to climate change, global change creates many drivers that affect biodiversity (e.g., Potts et al. 2010, Schweiger et al. 2010). Among the most important drivers are land-use change with the consequent loss and fragmentation of habitats (Westphal et al. 2003, Tscharntke et al. 2005, Schweiger et al. 2007, Öckinger et al. 2010); increasing pesticide application and environmental pollution (Rortais et al. 2005, Dormann et al. 2007); alien species (Stout and Morales 2009, Walther et al. 2009, Vilá et

al. 2010); and the spread of pathogens (e.g., Cox-Foster et al. 2007). These drivers are often in conflict with desired ecosystem services. Sustaining pollination services, for instance, is for sure highly desired by both conservationist and farmers, but it is often decreased as a consequence of other demands such as increasing agricultural production. Habitat loss and fragmentation are generally thought to be the most important factors driving pollinator declines (Brown and Paxton 2009). In addition, increased use of insecticides can cause pollinator mortality by direct intoxication (Alston et al. 2007). Increased herbicide and fertiliser use can affect pollinators indirectly by decreasing floral resource availability (Gabriel and Tscharntke 2007, Holzschuh et al. 2008).

All these drivers act simultaneously and very likely synergistically on local communities (Tylianakis et al., 2008). So far, most studies have analysed specific drivers in isolation, and therefore evidence of interactive effects is scant. However, in a recent review within ALARM Schweiger et al. (2010) show that the effects of multiple interacting pressures can be contrasting. In the face of climate change, alien species can serve as additional pollen and nectar sources (Stout and Morales 2009) or pollinators (Goulson 2003). Such species can thus substitute otherwise lost functions. On the other hand, alien species can lead to reduced reproductive success and population declines of native pollinators by competitive displacement of native plants (Traveset and Richardson 2006) or by high levels of resource competition among native and alien pollinators (Matsumura et al. 2004, Thomson 2006).

Yet, knowledge about the relative contribution and the importance of interactive pressures is an indispensible precondition to understand current and to predict future changes in biodiversity and resulting ecosystem services.

New developments in relation to dragon- and damselflies

In the course of the project, ALARM was enlarged and partners from other continents have been included. With this expansion the ALARM approach had to be tailored for the respective regions, which in the context of dragon- and damselflies was particularly the case for research in Asia and Africa.

For Asian rice-growing systems a close collaboration with IRRI was started to analyse long-term trends in the biodiversity of natural enemies of rice pests, with a particular focus on parasitoids (by applying and adjusting the ALARM field site network approach, compare Grabaum et al. 2006). A further aim was to look into the options to develop appropriate sustainability indicators for rice growing systems, where in particular dragon- and damselflies might play a key role and where we have a direct field for the further application of the research results (Heong et al. 2010).

In southern Africa, there are many narrow range endemics that are at risk from the effects of global climate change. Among these are *Colophon* beetles (Samways 2005) and certain dragonflies. One species of dragonfly, only discovered in 2003, is *Syncordulia serendipitor*, which lives in primary high elevation streams (Samways 2008). With global change, it appears to have nowhere to go. However, genetic work has indicated

that this species diverged 60 million years ago (Ware et al. 2009), and it has seemingly survived climate changes in the past, some of which have been very rapid. This leads to the speculation that perhaps even some narrow range endemics are physiologically adapted to climate change. But then perhaps in the past the overall population size and hence genetic variation, was greater, enabling the species to survive climatically difficult times. There is some evidence for this among some other, more widespread, odonate species in southern Africa. There is remarkable elevational tolerance among some species, enabling them to survive at higher or lower elevations according to the prevailing climatic conditions (Niba and Samways 2006), even in the case of some endemic species (Samways and Niba 2010). Other species show great plasticity in their ability to expand their geographic ranges and colonize water bodies during wet phases of El Niño cycles, then shrinking back to predictably wet refugia in the dry phases (Samways 2010). As this is a common phenomenon, there appears to have been strong selection pressure on a whole range of species to survive stressful climatic conditions. These shifts in population presence can be so extreme, that in the case of one species, *Aciagrion congoense*, it appeared as a new national record to South Africa in 2000, apparently driven south by floods in Mozambique. It then became the dominant damselfly at iSimangaliso Wetland Park in 2001. However, a few years later, after an extended dry spell, it again disappeared from South Africa. The point here is that at least in this part of Africa, there is some evidence that odonate species are to some extent already honed to tolerate some anthropogenic climate change.

Within ALARM the effects on dragonflies were mainly studied in Germany and Europe: here the waters in the Palatinate (Germany) and the Gran Sasso area (Italy) were studied. It could be shown that the general trends for dragonflies (e.g. range expansion of Mediterranean species, alteration in the phenology, changes in the aquatic communities, decrease of stenoecious species, see Ott 2001, 2008b), which have already shown earlier, still continued and the expansion is an ongoing and European wide process (Ott 2010a, 2010b). In general biodioversity will increase, but in the medium term there will probably be a decrease, as stenoecious species, such as alpine and mooreland species, will decrease due to the negative effects on their biotopes. In the Mediterranean the lack of water, in particular in intensively used areas, will lead to the decrease and eventual extinction of many species (e.g. species of running waters).

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RESEARCH ARTICLE

Trends in occurrence of thermophilous dragonfly species in North Rhine-Westphalia (NRW)

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Abstract

Since 1996 the "Workgroup Odonata in North Rhine-Westphalia" ("AK Libellen NRW") has built up a data base including about 150.000 data sets concerning the occurrence of dragonflies in North Rhine-Westphalia (NRW). This data confirms an increase and spread of some thermophilous dragonfly species in NRW, and the effects of climate change evidenced by an increasing average temperature, are considered to be important reasons for this process.

The area

Covering 34.100 km² North Rhine-Westphalia (NRW) is one of the biggest federal states of Germany with the largest number of inhabitants (about 17 million people). The Rhine-Ruhr-area in the center of NRW is the largest and most densely populated area in Europe.

The country is mainly flat (65 % of its area is situated between 10 and 150 m a.s.l.). The southern parts are occupied by mountainous areas with altitudes up to

840 m a.s.l. The lowland is a mainly open landscape dominated by highly developed agriculture with several urban and industrial centers. The mountains are dominated by woodlands, nowadays the majority consisting of spruce forests (LÖBF 2005).

The climate

North Rhine-Westphalia is situated in a transition area of the atlantic and continental climate. The predominating western winds carry mainly wet air from the atlantic low pressure areas. Therefore NRW has a warm-moderate rain climate with mild winters and relatively cool summers (DWD 1989). Corresponding to the orography NRW is also climatically divided into lowlands and mountainous areas. The annual average temperature equates to more than 9°C in the lowlands and 5°C in the mountains respectively. As a region of even higher temperatures the conurbation in the Rhine-Ruhr-area is in an exceptional position.

The temporal distribution of precipitation has a summerly maximum in the lowlands and an additional winterly one in the mountainous countries. Effects of luff and lee in the mountains produce differences in the amounts of precipitation and intensify the differences of regional climates. So the precipitation remains below 750 mm in major parts of the Northwestern region "Niederrheinische Bucht" whereas it reaches more than 1.100 mm in the mountainous regions. Therefore NRW has a high diversity of regional climatic differences which for example also cause large amplitudes in the vegetation periods.

The inventory of waterbodies and its historical development

North Rhine-Westphalia is a country with abounding water. It is strongly marked by a dense net of river systems including the main rivers Rhine, Ems and Weser which contribute to the North Sea. Nevertheless especially in the lowlands only a few semi-natural rivers and brooks are left, the most running waters being regulated and paved.

The quality of water instead is much better today than it used to be some years ago, especially in the age of industrialization about a hundred years ago when this had been much worse. Also a growing number of projects restoring parts of rivers and brooks to its former natural conditions indicate a positive development of the running water bodies.

Natural lakes do not exist in NRW. The only particular exception is the "Heiliges Meer" in the North of the country. This area consists of a group of small lakes, resulting from erosion and the caving in of salty layers in the underground. The lakes are only some hundred years old, several are even younger. But since a hundred years ago a lot of artificial lakes have been constructed as reservoirs or gravel pits all over the country. They are mainly concentrated in the southern mountainous country called "Sauer-land" and within the alluvial floodplains of the rivers Rhine and Weser.

The mountainous areas are rich of springs and brooks. Here small water bodies exist e.g. man-made mill ponds or barrages. Until the 18th century a lot of swamps and bogs had existed in the lowlands, but only small rests have remained until today. The ground water level has decreased nearly everywhere and the diversity and density of small water bodies of the historical landscape does not exist any more. Although construction of new ponds and wetland areas is often practiced, these water bodies are subject to an accelerated succession due to eutrophication (in a high amount caused by air pollution) and also influenced by higher temperatures.

The "Workgroup Odonata North Rhine-Westphalia" (AK Libellen NRW)

In 1996 this honorary working group was founded to work on the protection and investigation of Odonata in NRW. The AK organizes annual meetings for all collaborators giving new information and exchanging experiences with the participants. Circular letters and mailings also offer recent information to every member. In every summer a weekend-meeting is organized to investigate dragonflies and collect data in areas which have not been well-investigated yet.

Active collaborators can choose between two ways of ascertaining data: first by observing only a few selected water bodies intensively and continuously to get a close image of the entire inventory of dragonflies autochthonous in these water bodies. They have to undertake several excursions (at least 5) in a year for 2–4 years in a row. The second way is trying to cover a larger area and observing numerous water bodies but undertaking only a small number of excursions (1–3) to each of them. Despite of this all data is welcome.

Information is also available from our homepage (www.ak-libellen-nrw.de) containing dates of meetings, recent news of interesting dragonfly-records, a download of the recording manual, the current red list, a bibliography as well as distribution maps of all known dragonfly species in NRW.

The AK organizes training courses on exuviae and adult dragonflies. It supports dissertations and other works on dragonflies. There is also an exhibition available to be rent for presentations in order to give information on dragonflies to a great public.

The AK is part of an efficient network together with the LANUV (the major governmental institution for ecology and nature conservation in NRW), the "Biologische Stationen" (institutions for nature conservation on the level of districts), the "GdO" ("Gesellschaft deutschsprachiger Odonatologen") and other fieldworking groups (e.g. the "Work Group on amphibians and reptiles", "AK Herpetofauna NRW").

Aim of this work is a publication about the dragonflies in NRW and the cooperation with other dragonfly-protection-groups all over the world.

Due to this intensive work on dragonflies in the last years interesting new knowledge could be attained but also new questions arose. One obvious result is the observa-

tion of positive trends in occurrence of several thermophilous species and other observations (such as a change in the phenology of some species) which indicate a warmer climate in NRW.

The climate change

The known global effects of the climate change are also visible in NRW. A report of regional climate scenarios for NRW (Gerstengarbe et al. 2004) shows the following results:

"Between 1951 and 2000 significant climatic changes could be observed in NRW. The most important changes are:
– an increase of temperature in the annual average up to 1,5 K
– a decrease of days with frost in average up to 20 days per year
– an increase of summer days (meteorologically: days with more than 25°C) in average up to 20 days per year
– an increase of precipitation in the annual average of more than 100 mm in some areas
– an increase of days with strong precipitation up to 8 days a year and a highly significant decrease of days (up to 40) with no or only small precipitation".

In respect to the climatic change in the near future (2001–2055) the report points to the following trends based on statistically solid proved probabilities:

"The temperature will increase for at least 2 K and therefore the number of meteorologically "cold days" (with frost) will decrease whereas the number of "summer days" will increase.

The precipitation will increase on a lower level.

The increase of water steam pressure will be overcompensated for the reason of increasing temperature and therefore the relative atmospheric humidity will decrease.

In connection with a clear increase of the air pressure the time of sunshine and global radiation will raise as well as the clouding will decrease slightly."

The database

Due to the almost complete interpretation of publications on dragonflies in NRW and other sources like unpublished reports, collections and the current data from the AK-observations a solid database with now about 150.000 data sets has been established. The spatial and temporal distribution of the acquired data is shown in the figures 1a and 1b. It reflects a nearly complete coverage of NRW and a very strong increase of data based on the intensive and systematical work of the AK in the last decade. The peaks before 1996 represent data from publications on dragonflies which summarize the knowledge about the species for certain periods of time (for example Le Roi 1915 or Kikillus and Weitzel 1981).
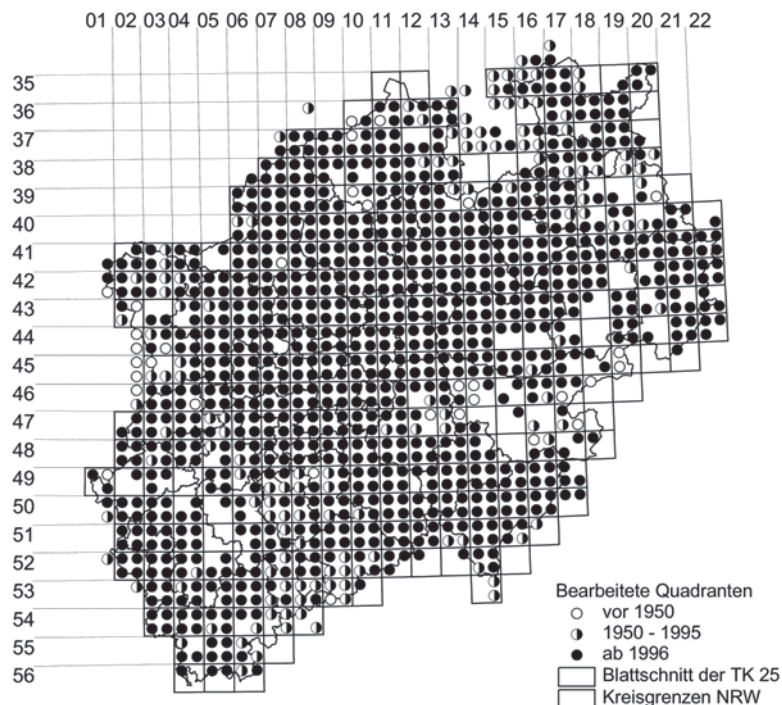
Figure 1a. The distribution of data on dragonflies registered in the data base of the AK Libellen NRW on the base of large scale map (1:25.000) (m) –quadrants, differentiated for three time periods (before 1950, 1950–1995, since 1996); one grid cell represents an area of about 5,5 × 5,5 km.

Nevertheless the fact of an increasing amount of data collected in the last decade has to be considered for the interpretation of any results. It is not always possible to determine whether the "increasing" of a dragonfly species results from climatic effects, other factors (f.e. offer of habitats or changing of habitats for example due to eutrophication) or only because of intensified observations.

The expansion of thermophilous dragonflies

Methods

The trends in occurrence of Odonata species in North Rhine-Westphalia were analyzed on the basis of the number of observations for each year and species. A data record corresponds to the observation of a species in an investigated area for each day, independent from number or autochthonousness of the species. To take into account the different intensity of this observation (the development of the number of observations is shown in fig. 1b) this number was set in relationship with the total number of
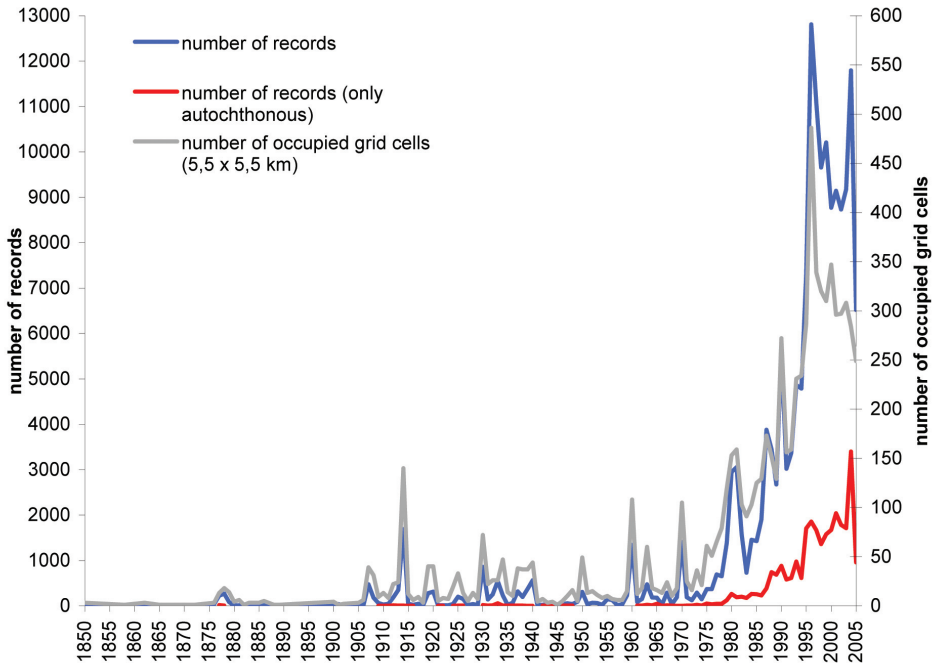
Figure 1b. Development of dragonfly observations for NRW in the last 155 years, differentiated for observations (blue), observations with proved autochthony (red) and coverage of quadrants of the large scale map "1:25.000" (m) (grey).

observations per year. So for each species the respective proportion was computed and its relative frequency was determined. With these annual portions an inventory trend analysis on the basis of the Spearman rank-order correlation coefficient (Spearman's rho) with the statistical program SPSS 11.5 was computed. The classification of areal types ("Faunenelemente") corresponds with St. Quentin (1960), Sternberg (1998) and Sternberg and Buchwald (1999, 2000).

Results

The results of trend analyses are given for some thermophilous species in table 1. In addition the below table (Table 1) refers to publications for their first records ("year") in NRW and current new works on their occurrence in our country.

Table 1 shows the currently known first records of some thermophilous species in NRW and its origins. It elucidates that apart from a few species (*Coenagrion scitulum*, *Crocothemis erythraea*, *Anax parthenope*) single observations of most of them have already been made in NRW since the 19th century. This indicates the dynamic distribution patterns of a very mobile dragonfly species and the influence that already a few years with favourable weather conditions could have.

Table 1. Year and referred publication of first records of thermophilous species in NRW and important new publications for the occurrence of the species, the Spearman rank-order correlation coefficient (Spearman's rho) and its level of significance for the trends of occurring for two regarded periods.

Species	Year of first record	Origin (reference)	Important new references	1850 – 2005		1980 – 2005	
Aeshna affinis	1913	KRIEGE (1914)	Bauhus (1996)	0,60		**0,56**	**
Anax parthenope	1983	Lempert (1984)	Böhm (2003)	**0,85**	**	**0,42**	*
Coenagrion mercuriale	1883	KOLBE (1886)	Conze & Göcking (2001), Müller (2003), Röhr (2006)	0,12		**0,54**	**
Coenagrion scitulum	1961	KIEBITZ (1962)	Grebe, Hofland & Rodenkirchen (2006)	0,25		**0,43**	*
Crocothemis erythraea	1977	FERWER (1989)	Bauhus (1996), Böhm (2003), Schmidt (2004)	**0,86**	**	**0,82**	***
Erythromma viridulum	1877	KOLBE (1878)	-	0,57		**0,58**	**
Lestes barbarus	1872	KOLBE (1878)	Schmidt (2004)	-0,37		0,38	
Orthetrum brunneum	1888	LE ROI (1915)	Krüner (2001)	0,16		**0,42**	*
Sympetrum fonscolombii	1872	KOLBE (1877)	Kordges & Keil (2000)	0,06		0,37	
Sympetrum meridionale	1930	KRABS (1932)	Böhm (2002)	0,23		**0,50**	**

Level of significance. **extra bold:** significant correlation ($P<0,05$)

*	$0,01<P<0,05$
**	$0,001<P<0,01$
***	$P<0,001$

But it also proves significantly the increase of thermophilous dragonfly species in North Rhine-Westphalia. Especially in the last 25 years the positive trend is at least significant for eight out of ten species. This development obviously is connected with the increase of average temperature in the same period of time. Furthermore the rapidity and intensity of the outspread of some species has been advanced by the change of habitat availability. Those developments have been observed f. e. for *Crocothemis erythraea* and *Erythromma viridulum* in the alluvial floodplains of the rivers Rhine and Weser, where many suitable waterbodies had arisen from the exploitation of gravel pits.

The occurrence of species in areas that were formerly not populated is also effected by climatic changes. For the first time populations of *Erythromma lindenii* or individuals of *Orthetrum brunneum* have been recorded in the mountainous parts of NRW in the last five years. In addition phenological changes have been observed for many species occurring nowadays much earlier and longer than in the 1980s. But additional factors may also influence the outspread and remain to be analysed in detail.

Comparison of groups of dragonfly species with different areal types due to their inventory development for the time span 1980–2005

Fig. 2 is a depiction of the differentiation between two groups of areal type (Mediterranean species / Eurasian, Westsibirian and Pontocaspian species) and displays the por-
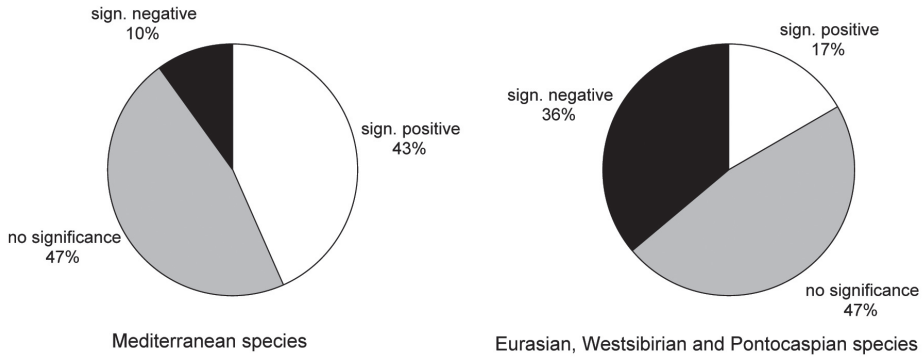
Figure 2. Portion of species with different significant trends in the „areal type groups" of the Mediterranean and the Eurasian, Westsiberian and Pontocaspian species (for the time span 1980–2005).

tion of the species with distinct trends of occurrence (significant positive, significant negative or not significant). In detail, 43% of species with significant increasing trends in their group "Mediterranean species" is clearly higher than in the group of "Eurasian, Westsibirian and Pontocaspian" which is 17%. However with "Eurasian, Westsibirian and Pontocaspian" 36% show a significant negative development. These trends underline a change in species' frequency within favour of the thermophilous species in North Rhine-Westphalia.
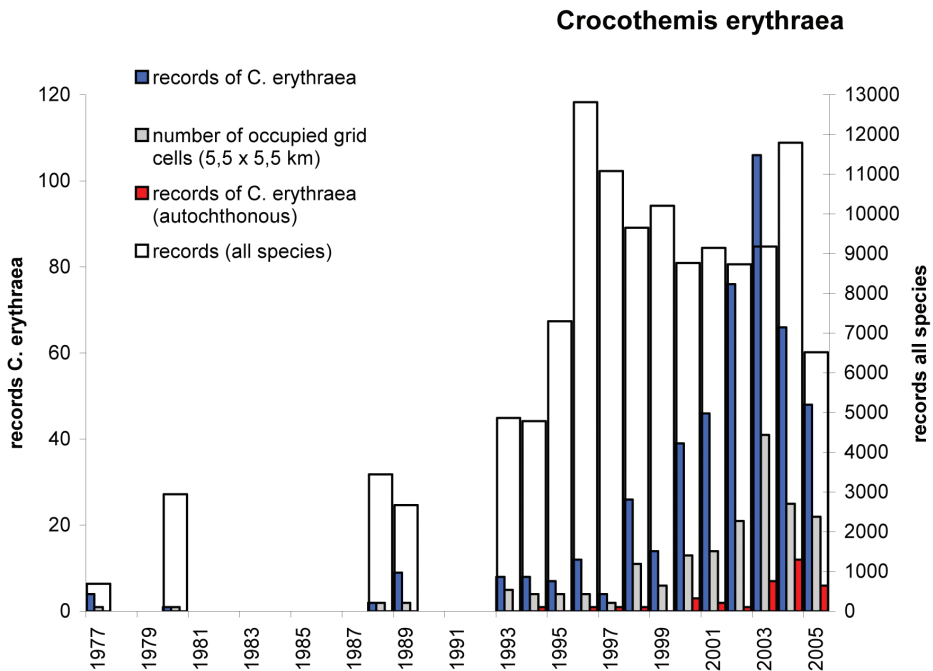
Figure 3. The inventory development of *C. erytrhaea* in NRW

Coenagrion mercuriale
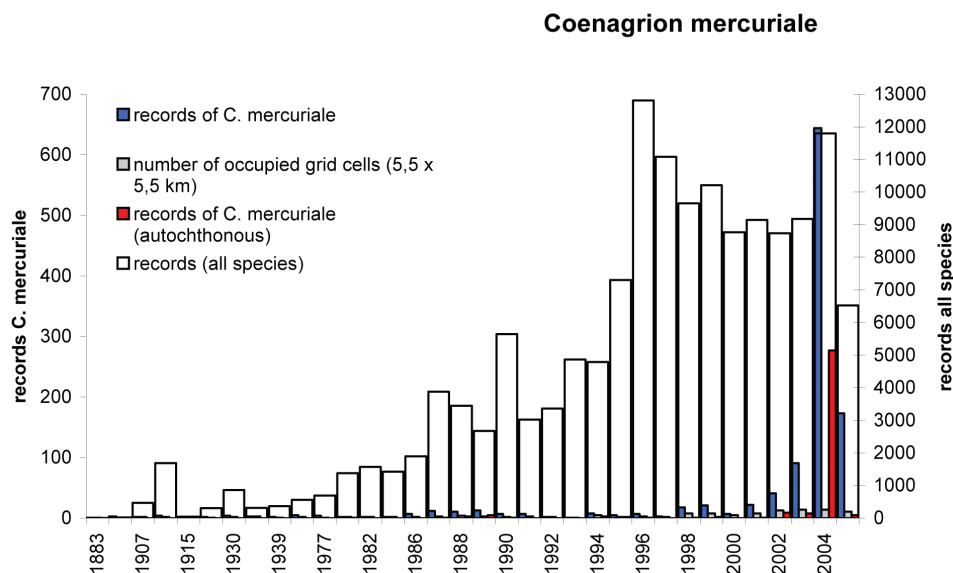
Figure 4. Inventory development for *C. mercuriale* in NRW (additional species-specific investigations in special protected areas started in 2003)

Different examples

A well documented example for the increase and spread of thermophilous dragonfly species is *Crocothemis erythraea* (Ott 1996, 2006, 2007). This species is now widespread in the lowlands of NRW, too. Autochthonous populations have been recorded from several places especially in the area of the Rhineland, where it occurs together with *Coenagrion scitulum* (Rodenkirchen 2004). Particularly this very conspicious and easily determinable species is a good indicator species showing increasing trends affected by climate change (see also figure 3).

The influence of systematic examinations and monitoring programs is shown in figure 4 for *Coenagrion mercuriale*. The erratically increasing numbers of observations in the last years are to be explained by special investigations in connection with the announcement of special protected areas for the "Natura 2000" network of the EU. On the basis of these investigations a thorough knowledge of this endangered species could be gained. But no "real" increase in the populations could be observed. In the Rhineland, an area with a higher average temperature, only one small and very isolated population could be observed. For a long time it has been found in a calcerous springbog. In the "Westfälische Bucht" several partially very large populations are to be found in systems of brooks and ditches. By searching for this species in its best flight period and at typical habitats known for the occurency of this species, some new populations have been observed here in the last years. But an increase of *Conagrion mercuriale* for the reason of climate change cannot be proved.

Figure 5. Different developements for Gomphus pulchellus in NRW and the upper valley of the River Weser ("Oberweser")

Regional aspects
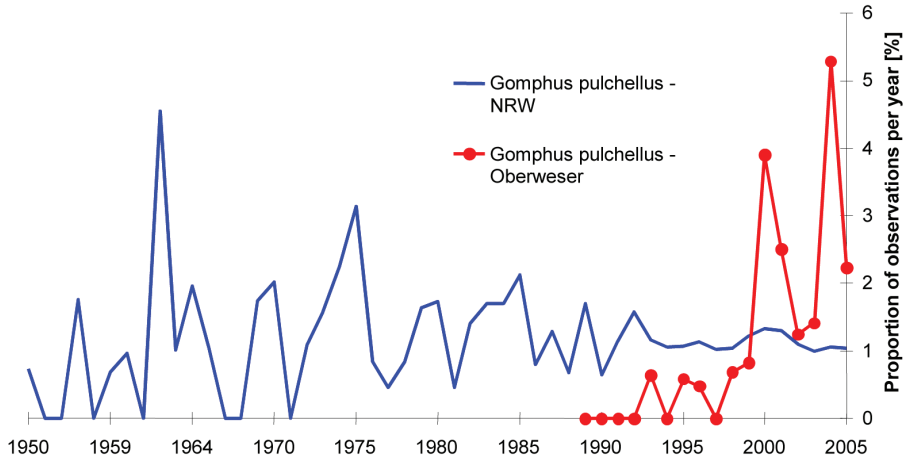
For some species the trends of occurrence on the regional level differ from those in the entire country. In Figure 5 different developments for *Gomphus pulchellus* in North Rhine-Westphalia and in the region of the upper River Weser valley ("Oberweser") situated in the east of NRW are presented. For the entire country this species does not show a significant trend in the regarded periods of time. But in the valley of the Weser the species has strongly increased by number of occurrences as well as number of individuals since 1995.

Conclusions

The analysis of trends statistacally tested and based on a large area and long period of time can only be carried out on the basis of extensive data collection. But often additional information and circumstances must be considered to explain trends in occurrence. Therefore the data base of the "AK Libellen NRW" is an important fund which has to be continued and further on interpretated closely in the next years.

The increase of thermophilous species in North Rhine-Westphalia can be proved on the basis of the collected data. The climate change is obviously the most probable reason for it. But there remain other aspects to be regarded, for example the effects of climate change on the whole species inventory (also on the base of regional landscapes), the inter- and intraspecific concurrence, the decrease of supposed "northern" species (for example *S. arctica*), the phenology and the local distribution of species. Therefore not only the data collection has to be continued but also special monitoring programs have to be developed and carried out including currently common species.

Another point will be the investigation of regional differences because these can elucidate the occasional factors.

Acknowledgements

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Appendix I

Year of first records of Odonata species in NRW, Spearman rank-order correlation coefficient (Spearman's rho) and its level of significance for the trends of occurring for three regarded periods. In addition the classification of areal types according to St. Quentin (1960), Sternberg (1998) and Sternberg and Buchwald (1999, 2000) is given.

	Year of first record[1]	1850-2005		1980-2005		1996-2005		areal type
Calopteryx splendens	1876	-0,08		**0,52**	**	**0,71**	*	pm
Calopteryx virgo	1872	**-0,75**	*	-0,10		-0,04		ea
Lestes barbarus	1872	-0,37		0,38		-0,58		hm
Lestes dryas	1850	**-0,76**	*	**-0,46**	*	-0,55		ea
Lestes sponsa	1876	0,03		-0,35		-0,36		ea
Lestes virens	1872	**-0,77**	*	**-0,48**	*	0,12		pk
Lestes viridis	1876	0,63		-0,20		**-0,73**	*	atm
Sympecma fusca	1876	**-0,83**	**	**0,41**	*	0,32		hm
Sympecma paedisca	1920	-0,55		.		.		ea
Platycnemis pennipes	1876	-0,13		**0,68**	***	**0,64**	*	pk
Ceriagrion tenellum	1883	**-0,82**	**	-0,34		0,13		atm
Coenagrion armatum	1881	-0,64		.		.		ea
Coenagrion hastulatum	1850	**-0,95**	***	-0,16		0,08		ea
Coenagrion lunulatum	1908	-0,32		**-0,58**	**	0,39		ea
Coenagrion mercuriale	1883	0,12		**0,54**	**	**0,94**	***	atm
Coenagrion ornatum	1986	**0,76**	*	0,29		-0,19		pm
Coenagrion puella	1876	**0,90**	***	**0,64**	***	-0,45		pm
Coenagrion pulchellum	1872	**-0,90**	**	-0,05		0,28		pk
Coenagrion scitulum	1961	0,25		**0,43**	*	0,54		hm
Enallagma cyathigerum	1850	**0,87**	**	0,32		0,27		ea
Erythromma lindenii	1876	0,33		0,20		-0,05		atm
Erythromma najas	1850	**-0,85**	**	-0,18		-0,24		ea
Erythromma viridulum	1877	0,57		**0,58**	**	0,39		hm
Ischnura elegans	1876	**0,87**	**	**0,49**	*	-0,32		ea
Ischnura pumilio	1883	-0,02		**-0,56**	**	0,62		pm
Nehalennia speciosa	1908	-0,55		.		.		ea
Pyrrhosoma nymphula	1876	0,53		-0,12		0,08		ea
Aeshna affinis	1913	0,60		**0,56**	**	0,21		hm
Aeshna cyanea	1876	**0,67**	*	**-0,42**	*	-0,33		pk
Aeshna grandis	1876	**-0,97**	***	**-0,51**	**	-0,03		ea
Aeshna isoceles	1850	**-0,94**	***	**-0,45**	*	0,16		atm
Aeshna juncea	1876	-0,17		**-0,58**	**	0,30		ea
Aeshna mixta	1850	**0,77**	*	-0,04		-0,55		hm
Aeshna subarctica	1926	0,54		**-0,72**	***	-0,30		ea
Aeshna viridis	1930	-0,51		.		.		ea
Anax ephippiger	1989	0,14		-0,02		.		hm
Anax imperator	1876	**0,90**	***	**0,55**	**	-0,52		hm

	Year of first record[1]	1850-2005		1980-2005		1996-2005		areal type
Anax parthenope	1983	**0,85**	**	**0,42**	*	**0,64**	*	pm
Brachytron pratense	1876	**-0,87**	**	0,01		0,31		pk
Gomphus flavipes	1914	0,50		**0,79**	***	0,52		pk
Gomphus pulchellus	1881	0,25		-0,32		-0,26		atm
Gomphus vulgatissimus	1872	-0,59		**0,82**	***	0,57		pk
Onychogomphus forcipatus	1872	-0,46		**0,48**	*	-0,37		pk
Ophiogomphus cecilia	1877	-0,53		**0,54**	**	0,38		ea
Cordulegaster bidentata	1850	0,20		0,10		**0,88**	***	adm
Cordulegaster boltonii	1849	**-0,67**	*	**-0,64**	***	0,35		pk
Cordulia aenea	1872	**-0,78**	*	0,33		-0,36		ea
Epitheca bimaculata	1872	**-0,77**	*	-0,23		.		ws
Oxygastra curtisii	1940	-0,52		.		.		atm
Somatochlora arctica	1908	-0,12		**-0,38**	(*)	0,04		ws
Somatochlora flavomaculata	1907	-0,33		-0,22		0,01		ea
Somatochlora metallica	1850	**-0,75**	*	-0,35		-0,12		ws
Crocothemis erythraea	1977	**0,86**	**	**0,82**	***	**0,88**	***	hm
Leucorrhinia albifrons	1941	-0,50		.		.		ea
Leucorrhinia caudalis	1888	**-0,76**	*	.		.		ws
Leucorrhinia dubia	1877	**-0,88**	**	**-0,74**	***	-0,30		ea
Leucorrhinia pectoralis	1877	**-0,95**	***	-0,32		0,06		ea
Leucorrhinia rubicunda	1849	**-0,85**	**	-0,21		0,22		ea
Libellula depressa	1876	0,62		**-0,56**	**	-0,43		pm
Libellula fulva	1907	0,42		0,18		-0,48		pm
Libellula quadrimaculata	1862	**0,67**	*	0,27		-0,21		ea
Orthetrum brunneum	1888	0,16		**0,42**	*	-0,21		hm
Orthetrum cancellatum	1876	**0,78**	*	**0,49**	*	-0,53		hm
Orthetrum coerulescens	1883	**-0,80**	**	0,09		0,52		atm
Sympetrum danae	1876	0,45		**-0,65**	***	0,24		ea
Sympetrum depressiusculum	1876	**-0,93**	***	-0,18		-0,54		ea
Sympetrum flaveolum	1876	**-0,77**	*	-0,36		-0,05		ea
Sympetrum fonscolombii	1872	0,06		0,37		-0,51		hm
Sympetrum meridionale	1930	0,23		**0,50**	**	0,25		hm
Sympetrum pedemontanum	1980	**0,73**	*	**-0,66**	***	-0,35		ea
Sympetrum sanguineum	1876	**0,87**	**	**0,48**	*	**-0,67**	*	hm
Sympetrum striolatum	1872	0,27		0,27		**-0,75**	*	hm
Sympetrum vulgatum	1850	-0,27		**-0,76**	***	-0,55		ea

[1] Year of first record; if not mentioned in the referred publication, the date of publication is given	Areal types
	adm adriatomediterranean
	atm atlantomediterranean
Level of significance	**ea** eurasian
extra bold: significant correlation (P<0,05)	**hm** holomediterranean
* 0,01<P<0,05	**pk** pontocaspian
** 0,001 <P<0,01	**pm** pontomediterranean
*** P<0,001	**ws** westsibirian

RESEARCH ARTICLE

Do climate changes influence dispersal and population dynamics of dragonflies in the western Peruvian Andes?

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Abstract

For nine dragonfly species (five aeshnids and four libellulids) all previous and verifiable data are related to the vertical climate zones and nature regions of the western Peruvian Andes and the Peruvian Pacific coast. Climate changes due to the El Niño and La Niña phenomena, as well as the global climate change have an influence on the different natural regions and also restrict aquatic biotopes. These changes influence the dispersal and behavior of some dragonflies and concern also loss of habitats as well as alterations of biotic and abiotic factors at and in water.

However new waters and habitats also are formed in most nature regions. Specialists like *Rhionaeschna peralta*, a species of high mountain regions and the Puna, are not able to react to habitat losses by adaptation, while other species such as *R. maita* and *R. marchali* do colonize new habitats also in higher altitudes. While the here represented aeshnids change their distribution ranges within the vertical nature regions of the west Andes, this is suspected for three of the four libellulids (*Orthemis ferruginea*, *O. discolor* and *Pantala flavescens*) as latitudinally respectively longitudinally immigrations and expansions of their areals.

For all species discussed, a seasonally earlier flight beginning is detectable, but for no species an extension of their flight time.

Altogether, the above named three libellulid do react more flexibly and faster to the alterations by climate changes than the majority of the five aeshnid species.

The influence of increased UV-B and UV-A radiation possibly affects also the site occurrence of some species in high altitudes of the Andes.

Keywords
climate changes, dragonflies, effects, biodiversity, biogeography, Peru, Andes

Introduction

Until a few years ago, climatology was in Peru exclusively limited to examinations of the El Niño events and the consequences for agriculture and fishery. With signing the Kyoto Protocol measurements and supervision of the CO_2-emmissions were also included as part of the responsibility (SENAMHI 2006). In 1994 the national environmental council CONAM (Consejo Nacional del Ambiente) was brought into being (Congreso de la República 1994), which in 2001 with the submission of the first report to the UN also fixed the subject of climate change as the main focus of its work (CONAM 2001). It was not until 2003 that studies of the effects of climate changes on the biodiversity were incorporated in the conceptual formulations (CONAM 2004) - though the term "biodiversity" referred exclusively to cultivated plants and economically useful animal species.

To the present day there are only a few studies to the biodiversity of the western Peruvian Andes, and these concern botanical recordings and research on a few zoological taxa such as mammals, birds and butterflies which allow some statements to species diversity. Within the scope of such investigations by North American and Peruvian biologists since the beginning of the 90s of the last century, Odonata were also increasingly collected and deposited with the Natural History Museum (Museo de Historia Natural de la Universidad San Marcos) in Lima. Wider samplings in the coastal regions to 1400-m height and the high andean ranges between 3000 and 5000 ms were carried out since 1989 in irregular intervals by the author (Hoffmann 1991, in prep). However these investigations are up to now limited, however, to a pure sampling activity without studies to Odonata coenosis and its ecology. These data and also the odonatological collections of the Natural History Museum in Lima, the University La Molina in Lima and the University of Cajamarca reveal for some species of the suborder Anisoptera changes in the dispersal behavior which is possibly caused of climatic changes within their distribution ranges.

Out of 481 dragonflies recorded in Peru (Hoffmann 2009), 46 species were sampled up to the present in the western Andes and the coastal desert. Some species from the families *Aeshnidae* and *Libellulidae* should be looked at more closely here, because at least enough data are available to be able to discuss changes due to climate change.

Definition and data

Ecological Regions

According to different authors, the division of the Andes into ecological regions is variably handled. For example Brack (1985) distinguishes four terrestrial ecological regions in the West Andes and coast. The Instituto Nacional de Geografía de Peru defines for the same area of Peru five regions (INGP 1989) and later with 14 subregions (in INRENA 1995). All three works are primarily based on precipitation and temperature data as well as plant communities. However, the subdivision into partly very small-flat subregions (exclusively guided by plant communities) is at least not partially when viewed objectively comprehensible.

A first division of the Peruvian Andes into nature regions was undertaken by Pulgar Vidal (1967) and was revised completely in the ninth edition in 1987. Pulgar Vidal divides Peru primarily in nature regions in accordance with:
– altitudinale zones
– relief
– climate
– vegetation
– fauna
– agriculture
– (historic) folklore

The nomenclature adapts the Indian population's original Quechua-names. The division of the West Andes (incl. coast desert) takes place accordingly in six regions (Table 1 and Fig. 1).

Climate and Weather Records

Generally the nature regions, as well as the ecological regions of the Peruvian West Andes are according to Pulgar Vidal (1987) and Brack (2000) related to climate gradients,

Table 1. Relation of natural areas in the westerns Andes to altitudinal zones

nature regions	altitudinal zones
Chala („coast")	0 – 500 m
Yunga („temperate valleys")	500 – 2.300 m
Quechua („Farm land")	2.300 – 3.500 m
Suni („narrow plain")	3.500 – 4.000 m
Puna („uninhabitable heights")	4.000 – 4.800 m
Janca („ice land")	4.800 – 6.768 m
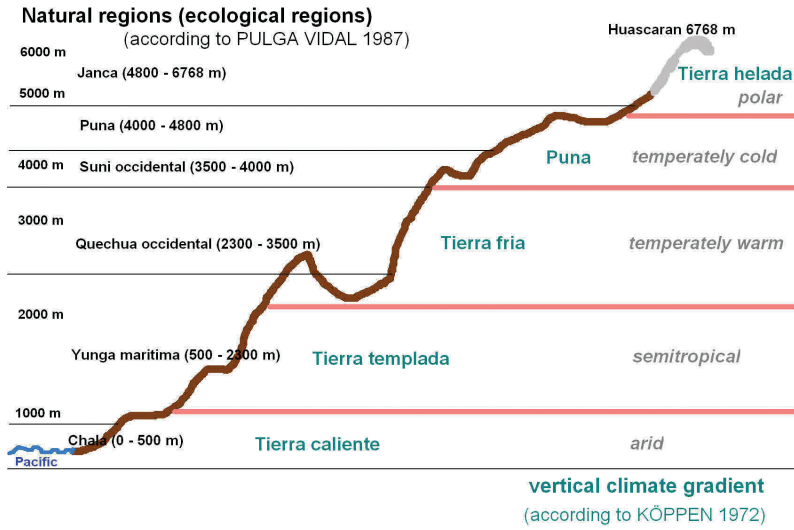
Figure 1. Schematized profiles of the westerns Andes with its natural areas and vertical climate gradients

as they are also applied to the vertical zonations of altitude zones of mountains (Fig. 1) according to the climate zonation by Köppen 1972.

Temperature decreases with rising altitude, the precipitations increase at first and then decrease also with sinking temperatures. This is very similar to the meridional course of the values of these climate elements in direction towards the pole (Table 2).

Long-term weather records in Peru before are only from few places and generally as from the 1980er years. Secular data series are only available from Lima.

The peculiarity of the mainland climate in the western part of the Andes is dictated by the Humboldt Current and El Niño events. The absence of the cold Humboldt Current is created by the El Niño event, which in turn causes a "natural" climate alteration of irregular intervals about Christmas time for several weeks occasionally. This ENSO-mechanism (El Niño / Southern Oscillation) stands in competition to the anthropogenic "greenhouse effect" (Arntz and Fahrbach 1991; Schönwiese 1995).

The El Niño event has the effect of producing hard showers in the coastal belt up to an altitude of 2.500 m (Quechua), while temperatures and precipitations at greater heights are influenced more weakly.

Meteorological data

It is very difficult to obtain weather records in Peru. The National Meteorological Institute (SENHAMI) functions under the auspices of the ministry of defense and weather data are provided only under certain prerequisites and then only against very high fees. Furthermore long-term series of measurements exist only from a few places. These are often interrupted for longer periods of time due to faulty measuring instruments.

Table 2. Relation of natural areas in the westerns Andes to altitudinal zones, precipitation and temperatures

nature regions	altitudinal zone	annual mean of percipitation	annual mean of temperature
Chala	0 – 500 m	90 mm	20° C
Yunga	500 – 2.300 m	170 mm	19° C
Quechua	2.300 – 3.500 m	500 – 1.000 mm	12° C
Suni	3.500 – 4.000 m	700 – 1.300 mm	10° C
Puna	4.000 – 4.800 m	1.000 mm	6° C
Janca	4.800 – 6.768 m	700 mm	1° C

The data used here were gathered predominantly from publications of SENHAMI, Internet presences and series of measurements by mining companies in the Andes. Older data were partly published in the "Atlas Del Peru" (Inst. Geogr. Nac. 1989). Rare weather informations which are also taken into account can be found in older odonatological publications (e.g. Calvert 1956).

With the beginning of the CCA project in Peru (Hoffmann 2006) diurnal data at the sample waters were recorded by a mobile weather station[1]. These however always represent only at hourly intervals values at a research locality for the duration of the stay. In addition to the weather data, the UV radiation (UV-A and UV-B) was also included.

Hydrological data

In 2006 all waters examined were analysed (abiotic factors), conductivity, pH, water hardness, temperature and oxygen content being measured. Unfortunately, the device for measuring oxygen already ceased functioning at the beginning of the examinations. For future measurments water level gauges were installed at the waters.

Water temperatures of some larger waters were often taken in the course of hydro geological examinations (e.g. CONAM 2005) and were taken from relevant publications. Other sources are found in publications of Peruvian limnologist and also among mine companies which from time to time measure water-levels of large lakes. Such data were provided by the national park office Huascaran.

Dragonfly data

In the present consideration literature data (Calvert 1956, Schmidt 1952, Ellenrieder 2003 and others) was used although only a very few publications take into account the odonata fauna of the western Peruvian Andes. The verification of localities proved

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[1]   The weather station were entrusted to the administration of the National Park Huascaran and remained for the purpose of long-term series of measurement at Pampacocha, a lake in the Puna (4,068 m of height).

to be very difficult. The description of species and the publication of species lists as a rule were not made by the collectors themselves or by scientists on the spot, but by odonatologists in Europe or the USA. Locality labels in many cases have been assigned, interpreted or read wrongly[2]. Records which could not be verified were not taken into consideration.

Data from the entomological collections of the universities of Cajamarca and La Molina (Lima), as well as the Natural History's museum in Lima formed an essential basis. These however required a thorough revision since more than 30% of the specimen from the western Andes had been wrongly identified. Since 1994 Günther Peters (Berlin) thankfully accepted the examination of the aeshnids.

Furthermore, since 1989 the author regularly collected in the Peruvian western Andes, predominantly in the departments of Ica, Lima and Ancash (Hoffmann 1991 and in prep). Current data on odonata exist from the "Climate Change and Aeshnids - Project" in January and February 2006, August and September 2006 as well as February and March 2007 (CCA, Hoffmann 2006).

Results

Climate

Since there is a historically natural influence on climate by the ENSO mechanism (El Niño / Southern Oscillation), this phenomenon will first be described.

El Niño / La Niña

As an "El Niño" is called the appearance of an unusual, non-cyclic, change of currents in the oceanographic-meteorological system of the equatorial Pacific.

When it occurs, the cold Humboldt Current decreases along the Chilean and Peruvian coast until it succumbs. This happens due to a shift of the wind zones through which the normal west flow of near-surface (warm) sea water flows back to the east. The Walker-circulation has reversed itself, with the consequence that the east Pacific heats up. Its roll in the global warming heating is discussed controversially. While

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[2] For example: for *R. elsia* is given by Calvert (1956) and later by Ellenrieder (2003; assumed from Calvert) a locality "Huanuco". Today this place (see distribution map in Ellenrieder) is the capital of the same named department in the eastern slope of the Andes at a height of barely 2000 m. An unusual locality for a strong "coastal dragonfly", which only occurs on the west side of the Andes. It must be assumed that there is a mistake in the later localization. Thus there is a small place called Huanaco on the coast in the department of Ancash and in the department of Arequipa likewise near to the coast a place called Huancan. From both places are collection records of *R. elsia*, as well as of other species.

el Niño is a natural climate phenomenon it is, nevertheless, supposed that it will be strengthened by the anthropogenic greenhouse effect.

A current study points out, that El Niño events, particularly big ones, can be predicted more exactly than was previously assumed (Chen et al. 2004).

La Niña is an extremely cold current in the equatorial Pacific in contrast to El Niño, the naming being based on what, so to speak, is an anti-El Niño.

La Niña usually follows an El Niño event being triggered by exceptionally high differences of atmospheric pressure between South America and Indonesia. This leads to stronger trade winds. The warm water is driven at the surface in the Pacific Ocean by the trade wind to South-East Asia. As a result cold water flows up from the depth of the Pacific on the coast of Peru. This upwelling water lies up to 3°C below the average temperature.

The consequences are not as strong as in the case of the El Niño, but La Niña nevertheless has a considerable influence:

– in the west Pacific the water at the surface is warmer,
– in South-East Asia La Niña brings rains and colder temperatures,
– in South America it rains less and the deserts dry up.

Altogether, less natural disasters occur, however, than during an El Niño.

The number of La Niña events has decreased during the last decades, that of the El Niño events has increased (fig. 2). The assumption exsists that the anthropogenic greenhouse effect is responsible for this situation. Up to now, this could however not be proved.

According to the data of the last 66 El Niño events, those of 1925, 1933, 1941, 1957, 1972, 1982–1983 and of 1997–1998 were the strongest and a group of ten (1932, 1939, 1943, 1953, 1965, 1987 and 1990–1995, additionally 2001, 2004 and 2006–2007) are estimated as moderate to weak (acc. to Woodman-Pollit 1998).

An El Niño event lasts for about twelve to eighteen months and has its acme between December and June. Indeed, there were – dependent on definition - two recent exceptions: one event lasted from the middle of 1990 to the middle of 1995 while the Niño of 1997/98 was clearly shorter (NOAA 2005).
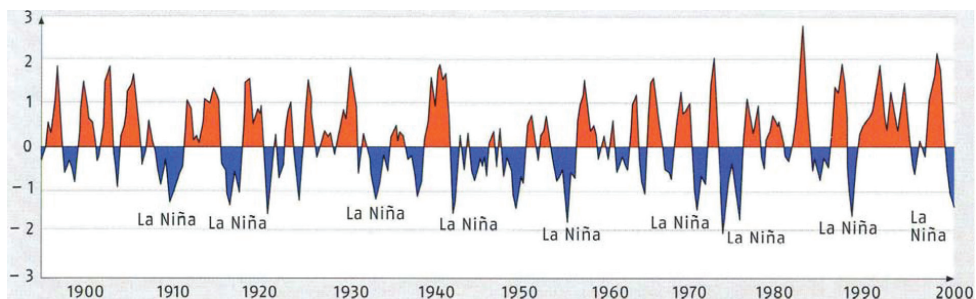
Figure 2. Sequence of El-Niño-and La Niña episodes in 1890–2000; temperature deviations (°C) are shown (acc. to Caviedes 2001)

An El Niño influences the weather predominantly on the coast up to the upper Yunga, has however, also an influence up to the uppermost elevated regions of the western Andes. Changes can only be perceived and measured during the events, but also influence the climate before and after event, though only to a slight degree. For example the El Niño event from November 1997 to April 1998 caused in Pisco (Pacific coast) maximal precipitations of 212 mm in December, while in January the amount of precipitation sank to 38.7 mm. On the other hand, the amount of precipitation in the Chala lay at about the level of the previous years while in the Puna however it lay under those of previous years (fig. 6). In May 1998 the amounts of precipitation lay in Pisco with 12 mm again in the range of the long-term averages.

Effects on the temperature development in El Niño years are noticeable up to the high regions (s. fig. 5, year 1998).

Climate changes

According to Hanson et al. (2006) the measured temperatures have increased in the annual global mean temperature since 1970 to 2005 by 0.6° C (fig. 3).

The increase in the global annual means of measured temperatures since 1985 till 2005 amounts altogether 0.5°C. This corresponds in the five-year means since 1990: 1990–1995 = 0,1°C, 1995–2000 = 0,2°C and 2000–2005 = 0,3°C.

The increase of the measured temperatures from 1985 to 2005 amounted to a maximum of 0.8°C in the western Andes (Puna) and a minimum of 0.2°C (Chala). With respect to all altitudes of the Peruvian western Andes the temperature increase since 1985 probably lies between 0.5°C and 0.8°C (no meteorological data are available from Yunga, Suni and Jalca). An increase twice as high as the global mean. The last five-years showed in 2000–2005 a smaller increase in the Puna and a slight decline in the Chala (fig. 4).
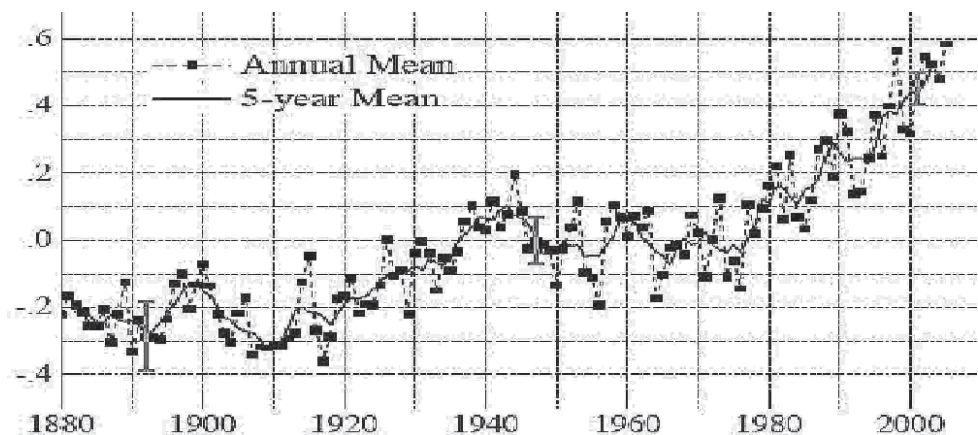
Figure 3. Global mean surface temperature anomaly (°C). Global annual surface temperature relative to 1951-1980 mean based on surface air measurements at meteorological station and ship and satellite measurements for sea surface temperature (from Hanson et al. 2006).
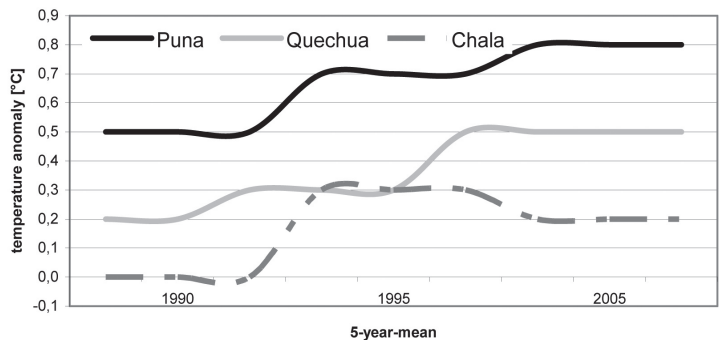
Figure 4. Altitudes-mean temperature anomaly (°C) in the nature regions Puna (4,000 m), Quechua (3,050 m) and Chala (60 m). Annual temperature mean based on surface air measurements at meteorological stations (source: SENAMHI 2006).
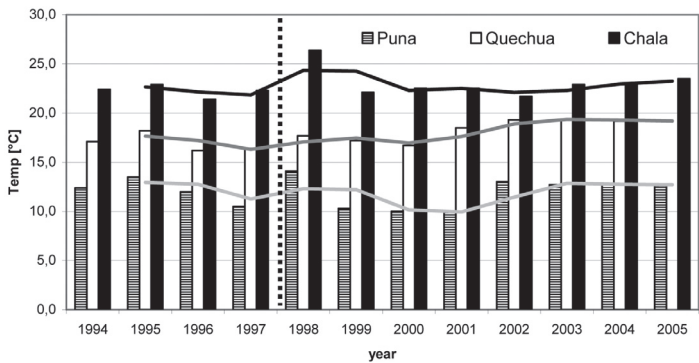
Figure 5. Average January temperatures in Puna (4,000 m), Quechua (3,050 m) and Chala (60 m) for a period of the past eleven years. Curves: gliding average for two periods; spotted line: occurrence of El Niño (source: SENAMHI 2006)
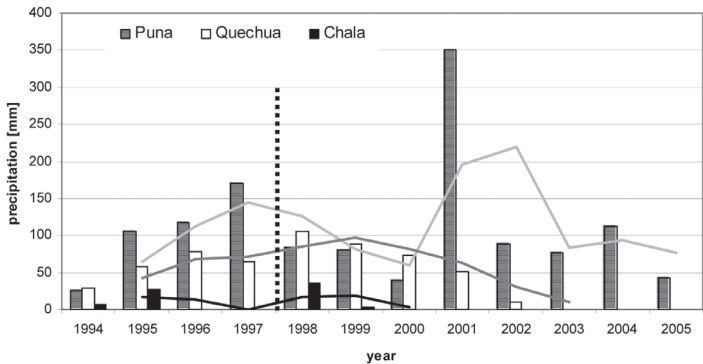
Figure 6. Average January precipitations in Puna (4.000 m), Quechua (3.050 m) and Chala (60 m) for a period of the past eleven years. Curves: gliding average for two periods; spotted line: occurrence of El Niño (source: SENAMHI 2006)

The average temperatures for January (midsummer) since 1994 are marked by a slight increase in the Quechua and since 2000 also in Chala and Puna. The increase of the temperatures primarily in the Chala could have been caused by the El Niño event 1997/1998 (fig. 5). The decrease of temperatures of 1999 and 2001 were accompanied by a La Niña event within these years (cf. fig. 2).

The amount of precipitation decreased continuously in Chala and Quechua since 1997 / 1998. The amount in the Puna is very irregularly, with a not interpretable peak in the year 2001 (fig. 6).

The relative atmospheric humidity in January is relatively constant in the Chala with an increase of only 3% on average over the last eleven years. In the upper altitudes of the Puna a continuous decline of more than 20% is remarkable, in the Quechua the values show great variations of up to 16% (Fig. 3–6).

Dragonflies (*Aeshnidae* and *Libellulidae*)

Interpretable data are available for the following species. It should be noted that *Rhionaeschna maita* is thought of as a good species in contrast to Ellenrieder (2003) who classified it as a synonym of *R. brevifrons*[3]:

Aeshnidae
   Rhionaeschna maita (Förster, 1909)
   Rhionaeschna absoluta (Calvert, 1952)
   Rhionaeschna elsia (Calvert, 1952)
   Rhionaeschna marchali (Rambur, 1842)
   Rhionaeschna peralta (Ris, 1918)
Libellulidae
   Erythrodiplax cleopatra (Ris, 1911)
   Orthemis ferruginea (Fabricius, 1775)
   Orthemis discolour (Burmeister, 1839)
   Pantala flavescens (Fabricius, 1798)

Two patterns (three time periods) were taken for the details on the phenology:

Records and information before 1956: Information from collections and literature; only of very few sources are available or collector activities must be estimated as very low.

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[3]   *Rhionaeschna maita* is represented here as a good species because there are some significant differences to *R. brevifrons.* Possibly a "wrong" lectotype was synonymized by Ellenrieder (2003), then the actually published photos by Geller-Grimm (2005) of the putative holotype de facto show *Rhionaeschna brevifrons* and do not correspond to the first description of *R. maita* by Förster (1909). Both Ris (1913) and Schmidt (1952) describe *R. maita* as closely related to *Rhionaeschna marchali,* to which resembles in many characteristics. All three species are sympatric in the upper Yunga and the lower Suni.
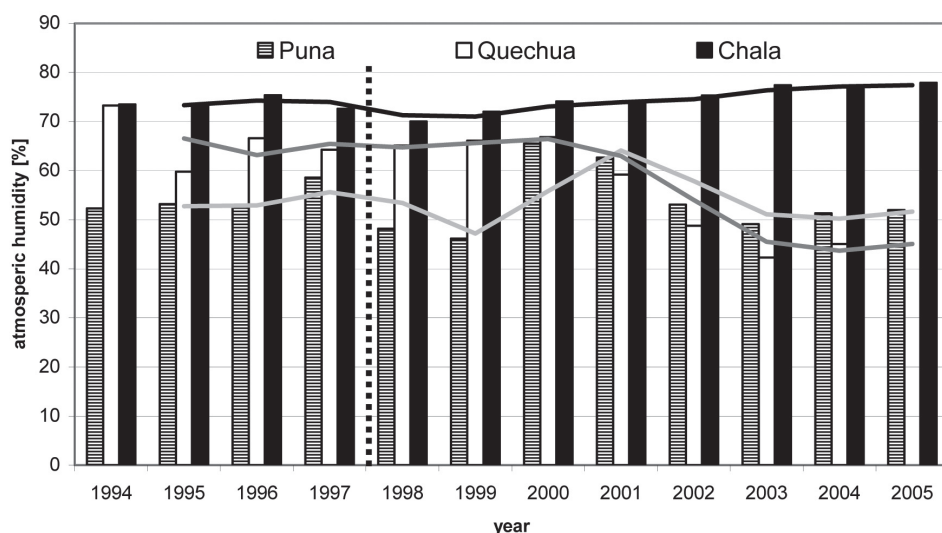
Figure 7. Average January atmospheric humidity in Puna (4,000 m), Quechua (3,050 m) and Chala (60 m) over a period of the past eleven years. Curves: gliding average for two periods; spotted line: occurrence of El Niño (source: SENAMHI 2006)

Records and information before 1996: at least from 1982 to 1996 data were regularly collected in complete annual courses, also in the western Andes and the coastal region.

Records and information after 1996: samples in irregular time periods, with some years not sampled at all.

Current results from the CCA project begun in 2006 (Hoffmann 2006) are presented separately.

Aeshnidae

Rhionaeschna maita (Förster, 1909)

Nature region: Until 2005 the species was recorded exclusively in Quechua and Suni at altitudes between 2,300 m and 3,900 m. Evidence is currently (2006) available from the Puna at 4,100 m. Some records from the Yunga and the lower Quechua must be ascribed to the sister species *Rhionaeschna brevifrons* on the basis of re-determinations of collection material.

Phenology: Obviously the flying time in the upper altitudes (more than 3,000 m) is from August to October, i.e. in the "andean spring" while at less than 3,000 m a second flight period from February to May ("andean autumn") is found.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Puna (4000–4800 m)									o	o		
Suni (3500–4000 m)		■						▨	▨	■	■	
Quechua (2300–3500 m)		▨	▨	⊠	■	■			▨	▨		
Yunga (500–2300 m)												
Chala (0–500 m)												

■ records before 1996	⊠ records before 1956 (Calvert 1956)
▨ records after 1996	o migrating specimens

Habitat utilization: Till now the species was found only at mesotrophic, predominantly slow running and not too cold (> 15°C) waters.

Rhionaeschna absoluta (Calvert, 1952)

Nature region: The main distribution of *R. absoluta* is in Yunga and Quechua. As the only species of the genus *Rhionaeschna* it was recorded also from the eastern high Andes at 3,800 m.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Eastside of the Andes	⊠											
Suni (3500–4000 m)												
Quechua (2300–3500 m)			⊠	⊠	■	■		■	■	⊠		
Yunga (500–2300 m)			⊠	⊠	■	■		▨	▨			
Chala (0–500 m)												

■ records before 1996	⊠ records before 1956 (Calvert 1956)
▨ records after 1996	

Phenology: The species shows two flight periods which are similarly to those of *R. maita* in the „andean spring" and "andean autumn". Records from the Yunga in the months August to October are available only since 1999, but then regularly.

Habitat utilization: Except at strongly flowing waters *R. absoluta* was found at all other types of waters. Eutrophic waters are preferred, oligotrophic waters avoided.

Rhionaeschna elsia (Calvert, 1952)

Nature region: Until now this species was found only in the arid coastal area of Peru. All findings until 1996 are up to 500 m above sea-level. In 2001 *R. elsia* was found for the first time in the Yunga at 900 m and in 2006 even at 1500 m.

Phenology: Obviously the flight times also have changed. Calvert (1956) indicates February to May as the period; later records (until 1996) cover a longer time from Oc-

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Yunga (500–2300 m)									▨		▰	
Chala (0–500 m)	▰	╳	╳	╳	╳	╳	▰		▨	▨	▰	▰

▰ records before 1996	╳ records before 1956 (Calvert 1956)
▨ records after 1996	

tober to July and more recent records (1996 onwards) cover the period from the end of August till the middle of July, indicating a phenological omnipresence.

Habitat utilization: Former records were taken exclusively in standing, mostly brackish waters (coastal lagoons and ponds). The records from the Yunga (900 m respectively 1,500 m) come from stagnant waters or temporary ponds in dry riverbeds. In 2006 imagos and larvae were also collected from a slowly flowing brook in the Chala at an altitude of 285 m.

*Rhionaeschna marchali (*Rambur, 1842)

Nature region: The main distribution of the species is in Yunga and Quechua between 1,900 m and 2,900 m. Currently (2006) *R. marchali* was also stated from the Suni between 3,500 m to 3,800 m. According to Calvert (1956) obviously the species also occurs on the eastern Andean slope. This, the only record from the 1930s could, however, not be verified.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Suni (3500–4000 m)								▨	▨			
Quechua (2300–3500 m)	▰	▰	▰	+	+	╳	╳	╳	▨	▨		
Yunga (500–2300 m)				╳			╳	▨	▰	╳		
Chala (0–500 m)												

▰ records before 1996	╳ records before 1956 (Calvert 1956)
▨ records after 1996	+ records before 1936 (Schmidt 1956)

Phenology: In the Quechua the species flies all the year round, except for November and December, the flight records for May to July having been taken before 1956. In Yunga and Suni the flight time is probably limited to the "andean spring".

Habitat utilization: Ellenrieder (2003) stated as habitats wet soils, crop pastures, muddy bottom pools, creeks, running brooks with aquatic plants and streams. Also according to current records (2006) the species occurs euryoeciously even in the Suni at 3,850 m, where water temperature of all waters sampled was between 15°C and 23°C.

Rhionaeschna peralta (Ris, 1918)

Nature region: A definite "mountain aeshnid" which occurs only above the Yunga (2,300 m) and which reproduces as the only aeshnid up to the lower margin of the

Janca (records at 5,000 m; see Corbet 1999). The main distribution of the species in the Peruvian Andes lies in Quechua and Suni, i.e. between 2,300 ms and 4,000 ms.

Phenology: *R. peralta* is phenologically omnipresent at heights between 2,300 m to 4,300 m (similar to *R. elsia* on the coast).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Janca (4800–6768 m)		▓	▓									
Puna (4000–4800 m)	▓	▓	▓					░	░	░		
Suni (3500–4000 m)			▓	⊠	⊠			░			⊠	▓
Quechua (2300–3500 m)				⊠	⊠	▓	▓		▓		+	+
Yunga (500–2300 m)												
Chala (0–500 m)												

▓ records before 1996	⊠ records before 1956 (Calvert 1956)
░ records after 1996	+ records before 1936 (Schmidt 1956)

Habitat utilization: The species occurs at wide brooks, permanent stagnant waters as well as mesotrophical ponds in riverbeds in Quechua and Suni. Sampling localities in the Puna were lakes, bog ponds and flood areas of artesian springs. In the upper Puna and lower Janca *R. peralta* was also found at stagnant areas of open thermal springs (temperature of emerging water 35°C, cooled down to 20°C at the outer edges). The temperatures of the water sample were between 16°C and 20°C; all waters being mesotrophic to oligotrophic.

Libellulidae

Erythrodiplax cleopatra (Ris, 1911)

This species shows ecologically similar characteristics to *Rhionaeschna elsia (*see above).

Nature region: *E. Cleopatra* occurs mainly in the arid coastal area, however, ascends infrequently also to altitudes of 1,000 m. Since 1996 records from more than 2,000 m are on the increase. Current records (2006) of *E. cleopatra* come from the lower Quechua at 2,500 m.

Phenology: In the Chala (arid coastal area) the species flies from October to May, i.e. with the exception of the winter month, for over eight months of the year. The

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Quechua (2300–3500 m)									░	░		
Yunga (500–2300 m)				+	+	+	+		░	░	▓	
Chala (0–500 m)	⊠	⊠	⊠	⊠	⊠				░	░	⊠	⊠

▓ records before 1996	⊠ records before 1956 (Calvert 1956)
░ records after 1996	+ records before 1936 (Schmidt 1956)

flight time at altitudes between 500 m to 2,500 m, i.e. in Yunga and Quechua, does not extend for more than five months, but beside this in August and September - in these months the species is missing in the Chala.

Habitat utilization: The majority of records in the area of the Chala and the lower Yunga is from stagnant waters and temporarily flooded ponds in riverbeds. In contrast to *R. elsia*, brackish waters with high salinity are obviously avoided. Current records from the upper Yunga at 2,000 m were taken exclusively from temporarily flooded ponds in riverbeds. In 2006 imagines and larvae were also obtained from a slowly flowing brook in the Chala at an altitude of 285 m.

Orthemis ferruginea (**Fabricius, 1775**)

This species was recorded for the first time in Peru also as reproducing within the scope of the CCA project in the second half of September 2006, the sampling locality being situated in the Yunga at 1,200 m. The site was a mesotrophical, permanent pond in the bed of the Rio Santa.

Orthemis discolour (**Burmeister, 1839**)

The species has its main distribution in Peru to the east of the Andes.

Nature region: Most records from the western Andes are from the northern Chala up to 350 m. There are a few records from the northern Yunga at 850 m and 1,900 m. Currently *O. discolor* was sampled also in the lower Quechua at 2,500-m, far to the south of older record localities in the Yunga.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Eastside of the Andes	■	■	■	■				■	■	■	■	■
Quechua (2300–3500 m)									▨			
Yunga (500–2300 m)					+	+						
Chala (0–500 m)	■	+	+	+	+	+	+			■	■	■

■ records before 1996	+ records before 1936 (Schmidt 1956)
▨ records after 1996	

Phenology: The flight time in the Chala extend for more than five months from the middle of October to the end of February. In the Yunga records are from May as well as from September and October after 1996. Currently (2006) the species was collected in September from the lower Quechua.

Habitat utilization: In the Chala *O. discolor* was recorded exclusively at mesotrophical to slightly eurotrophical standing waters, brackish coastal lagoons being avoided. The locations in the Yunga are mesotrophical standing waters in river beds

and backwaters. The records in the Quechua were taken at an oligotrophical to meso-trophical backwater in the upper reaches of a brook.

Pantala flavescens (Fabricius, 1798)

Nature region: West of the Andes the species is autochthonous only in the Chala up to 500 m. Nevertheless there were some records also from other nature regions above 4,000 m which before 1996 supported exclusively migrating specimens. Currently (2006) the species was sampled in the Yunga as well as in Quechua up to 2,800 m, in the Yunga already in 1999 autochthonous.

  Phenology: The species flies in the Chala (arid coastal area) from October to May, i.e. with the exception of the peruvian winter about eight months of the year. Up to

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Puna (4000–4800)											o	
Suni (3500–4000 m)												
Quechua (2300–3500 m)											o	
Yunga (500–2300 m)												
Chala (0–500 m)		+	+	+	+		+	+				

	records before 1996	o	migrating specimens
	records after 1996	+	records before 1936 (Schmidt 1956)

now records in the Yunga are only for November and December. In the Quechua *P. flavescens* was found exclusively in August and September (including reproductive records), i.e. at a time when the species does not fly in its main distribution area western of the Andes.

  Habitat utilization: In the arid coastal area *P. flavescens* is euryoecious and only avoids brackish waters with a high salinity and strongly running waters. A mass emergence in a swimming pool with several thousand specimens was stated from Tacna in February 1994 (Hoffmann 1998). In Yunga and Quechua the species could be found in mesotrophical ditches and temporary areas of standing waters in river beds.

Discussion and conclusions

Climate change and abiotic sequence effects

In what way global warming and the consequences of El Niño events overlap or mutually increase each other is not clear up to the present. It is noticable at least that the intervals between El Niño years become increasingly shorter, while the number of the Niña events is decreasing. Since the variations of the SST (sea surface temperature) have increased in the tropical Pacific during the last 100 years, and an accumulation

of El Niño events appeared, the question is whether a connection exists between El Niños and the anthropogenically caused greenhouse effect. In order to find this out, Timmermann et al. (1998) have calculated and analysed a greenhouse simulation with a globally coupled ocean atmosphere model. It turned out that the eastern Pacific will warm up until 2100 by about 3°C. On the other hand the west Pacific will warm up by only about 1°C. This would mean that in future, situations similar to El Niño would much more frequently appear if the emission of greenhouse gases (primarily of CO_2) is not limited or becomes reduced. Increasing interannuale variability overlaie the long-term warming trend.

Consequences of intensive El Niño events in Chala and Yunga (0–2,300 m) are documented adequately by state authorities in Peru, because these regularly impair the economy immediately and at short notice, particularly as far as the fishing industry and agriculture are concerned. Such documentations do not exist for the higher altitudes of the western Andes, possibly because the consequences do not play an important part here.

The climatic change due to global warming manifests itself much more strongly, although in El Niño years the change is hardly recognizable at the lower altitudes. Documentations of the consequences of the climate change are available only with regards to the melting of andean glaciers. The consequences although already recognizable and measurable, are shown merely as sequence scenarios.

In the mid 2006, a French-Peruvian project was started to now examine more intensely factors, progress and consequences of the gradual disappearance of the glaciers.

Analyses of satellite photos show for the Cordillera Blanca only, the largest tropical glacier massif, a reduction of the ice masses of 15% (corresponding to 13.5 km³) in the period 1970 to 1997 (27 years). During the last 35 years before 2005 (1970 to 2005) the reduction had accelerated and now, lies by 22% (CONAM 2005), an increasement of 7% during eight years. In subareas such as the Huascaran massif, this decline amounted even to just below 30% (CONAM 2001). According to UNESCO (2006) some smaller glaciers below a height of 5,000 m have already completely disappeared and others will be completely gone the latest by 2010.

The melting of the glaciers in parts of the upper nature regions from 3,000 m to 4,800 m (upper Quechua, Suni and Puna) has at first sight provided a greater available of surface water, however, on the other hand, also a loss of the water reservoir of 12% compared to present day.

The melt water are led away by the rivers to the Pacific, with the result that these show from May to September higher water levels in downstream regions, also during the dry times in the Andes, where 20 years ago these rivers still fell dry at this time of the year.

At the same time, the amount of precipitation and atmospheric humidity decrease continuously from 500 m to 4,000 m altitude, while on the long term in all nature regions a rise in temperature is to be registered.

Beck et al. (2006) indicate changes in the extend of the climate zones defined by Köppen as a consequence of climatic warming. Thus positive trends are to be noted in

South America for temperate climatic zones (average temperature of the coldest month between 3°C and 18°C) and tropical climates (the coldest month less than 18°C), while dry climates (no certain cycles nor summer nor winter rains) show a long-term decrease. Similar decreasing trends show the cold climates (average temperature of the warmest month below 10°C).

Habitat losses and formations of new habitats

The climate changes cause in part considerable habitat losses both at upper altitudes and in the arid coastal zone.

Glaciers melting leads to more permanent wettings in the Puna as well as flooding of upland bogs as well as artesian and thermal springs.

Thus *Rhionaeschna peralta* could not be recorded any more at such waters and even disappeared from the highest up now recorded reproductive waters in the Jalca at 5,000 m (cf. Corbet 1999). Also at many Puna lakes the species was not found any more after 2001. The reasons for this could be a noticeable increase of the water-level which led (apart from an anthropogenic use) to the loss of the Totora reed (*Scirpus sp.* and *Juncus sp.*) as oviposition and larvae habitats. However, at other lakes in which the water levels have fallen during the last years due to the increased melting of the glaciers supplying them with water the abundances appears to have increased (e.g. Lake Titicaca).

A further reason for the disappearance of species is possibly also the increase in water temperatures of some lakes in the Puna (e.g. in the Cordillera Negra). Thus a surface temperature (at a depth of 20 cm) of 21°C was measured in the Laguna Ututo (at 4,464 m) in 2006 (Hoffmann 2006). Here these waters were not or no longer fed by glacier waters. The centre of the distribution of *R. peralta* therefore lies at present between 2,300 m and 4,000 m in Quechua and Suni, in which the species apparently could profit in these regions from the formation of new habitats in form permanently water-bearing ponds and stagnant waters, for reasons of the steady melt water run-off in river beds profited, as long as these were mesotrophical.

For *Rhionaeschna maita*, with regard to the vertical distribution, the same applies as for *R. peralta*, with respect to their center of distribution in Quechua and Suni. While the latter appears to retreat, however, slowly from the Puna (see above), *R. maita* conquers at present waters in the lower altitudes of this region (up to 4,100 m). Apart from slowly flowing and mesotrophic run-offs of backwaters are preferred. As a rule, the temperatures of these waters do not lie below 15°C. Such waters appeared within the last few 10 -15 years. The species thus occupies a newly arisen niche, which *R. peralta* due to its ecological claims - up to now it has never been recorded from running waters in the Puna - obviously cannot taken up. With increasing warming and as long as a water surplus will be available, *R. maita* will possibly ascent to higher altitudes in future.

A further aeshnid which appears to profit from climatic changes is *Rhionaeschna marchali.* It has expanded its area of distribution from the Yunga and Quechua into the Suni and appears likewise to be euryoecious. Conspicuous for this species are mass appearances of the population, above all at standing waters in the Quechua, something that can possibly be explained due to increasing water temperatures (see below).

Similar trends in vertical distribution can also be ascertained in arid coastal region. Both *Rhionaeschna elsia* and *Erythrodiplax cleopatra* have extended their distribution into higher natural regions with *R. elsia* up to the middle Yunga at 1,500 m and *E. cleopatra* even up to the lower Quechua at 2,500 m. Both coastal species appear to profit from changed conditions, particularly with respect to suitable new habitats in the higher regions. On the other hand it is remarkable, that in particular *R. elsia* is no longer present at some coastal lagoons, but has recently appeared in slow running waters. Obviously the occurrence of this species is tied to the existence of slightly ionized waters (salts, conductivity values between 1.5 S/m and 3.9 S/m)[4]. Such condition of waters are at present increasingly full filled and areconverted into usable lands since particularly the need for agricultural products has increased and a permanent water regime of the rivers makes irrigation throughout the year possible as a result of the climate change. Furthermore it can be supposed that rising water temperatures and evaporation rates of the coastal lagoons also lead to habitat losses.

An example of a specie for which no changes in its vertical distribution can be ascertained is *Rhionaeschna absoluta.* The surprise is greater, because occuring exclusively in Yunga and Quechua– the species is considered as euryoecious and has been recorded up to now as the only species of the genus *Rhionaeschna* also in the eastern Andes.

Changes of water temperatures

Measurement series of the last 25 years of different types of waters prove a general increase of water temperatures of around up to 18% (max. 3.6°C) in the nature regions above the Chala and even up to 27.5% (max. 9.1°C) in a few small waters of the Chala. Some newly formed bodies of water by increased water effluents of the Quechua and Suni show temperatures of up to 25°C. In very small coastal lagoons of the Chala up to 29°C were measured. No dragonflies could be found in such waters.

Some species, in particular aeshnids, give up waters in the upper altitudes with temperature rises of more than 21°C. The only aeshnid which is an exception of this, and which appears to settle such waters is *Rhionaeschna marchali.*

On the other hand the majority of the species appears to profit from an increase in water temperatures in upper nature regions. Either they migrate due to changing conditions in their original reproduction waters to higher regions or they colonized new

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[4]   For comparison purposes: seawater shows a conductivity of approx. 5 S/m, natural incidences of dissolved copper salts up to 5800 S/m

habitats without giving up their original waters in the lower regions, as for instance *Orthemis discolor* and *Pantala flavescens.*

Phenological adaptation

For the majority of the species discussed here, a change of flight times is noticeable after 1996, compared with former data. All species have flight times during the southern summer season with a beginning in "late spring". According to the altitudinal zone this beginning is "brought forward" during the last years at the end of the winters. Species which started to fly formerly only late in the seasonal course can already be found in spring (e.g. *R. marchali* in the Quechua and *E. cleopatra* in the Yunga). In connection with this it has to be pointed, that "winter" and "summer" - particularly with the exception of the Chala - have to be defined over the amounts of precipitation, dry and respectively rainy season. While temperatures rise above the Yunga in the longter mean, precipitations decrease over the same period of time (cf. fig. 5 and fig. 6). Other species such as *R. elsia* in the Chala and *R. peralta* between 2,300 m and 4,200 m (Quechua to Puna) fly recently over the whole year and are phenologically therefore omnipresent. Most species above 1,000 m are not flight-active against this during the months in June and July, with the lowest precipitations of the year. There was one exception, however in July 2006, in a really dry summer with precipitations of less than 5 mm, already started in May (normally long-standing monthly means in May with 75 mm). This resulted in a mass emergences of *Rhionaeschna sp.* in the Quechua, with thousands of dragonflies appearing in the streets of Huaraz (3,048 m) for several days. Inquiries through the local press and local inhabitants showed that it concerned without questions aeshnids, presumably *Rhionaeschna marchali.* Obviously there was a mass emergence briefly before with following migration events, similar to described in Europe for *Hemianax ephippiger* (Peters and Günther 2000; Günther 2005) and currently for *Aeshna mixta* (Günther 2006). As a cause it is to supposed that early beginning dryness and relatively high temperatures (monthly mean of daily temperatures of 27°C instead of 24°C of a long-standing mean) led to a drying up of standing waters with a low water-level. Because *R. marchali* starts to fly very early in the year (according to older data of Calvert 1956, the complete wintertime could not be confirmed until, however), it possibly concerned the phenomenon of an emergency emergence of the last larvae instar. Moreover the species flies at least in two generations.

Currently, changes in the phenology have become known for some European species, even if they probably still represent the exceptions (e.g. *Sympetrum flaveolum*, Kunz 2006).

On the other hand such "prolongations" of flight times as reported by Busch-Nowak (2002) about the very late emergence of *Libellula depressa* in October in Baden-Wurttemberg (Germany) and by Hoess (2006) about very late flight times of *Coenagrion puella* in Switzerland are not ascertainable from the western Peruvian Andes in an analogous way up to now.

Immigration

Immigrations from distribution areas in distinct latitudinal climatic zones such as described by Ott (1996 and 2000) for *Crocothemis erythrea* are noticeable in the western Peruvian Andes at least for *Orthemis ferruginea*. Paulson (pers. comm. in Heckman 2006) considers *Orthemis discolor* as an own species and not conspecific to *Orthemis ferruginea*. He gives North and Central America as the distribution area of *Orthemis ferruginea*. Donnelly (1995) indicates that *O. discolor* has dispersed from South America along the Caribbean side to Florida whereas *O. ferruginea* coming from North America dispers along the pacific side to Costa Rica. Both species are sympatric in parts of Mexico and Costa Rica (fig. 8) and sometimes even occur at the same waters.

On checking the collection material from Peru, some years ago, it was discovered that all specimens (with one exception) determined as *O. ferruginea,* had to be reassigned to *O. discolor*. Merely a male from the northern Yunga collected in August 2001 belonged to *O. ferruginea.* Later an ovipositing couple was caught in September 2006 about 400 km south of the first location, also in the Yunga. Possibly the species is distributing along the Pacific coast in a southerly direction which means that it could also occur in Ecuador and Colombia. At present, the distribution of *O. ferruginea* still appears to be discontinuous.

Obviously the equatorial climatic zone extending for over 1,000 km from Costa Rica to Colombia has been up now a barrier which prevented dispersals to the south. Beck et al. (2006) show climatic changes in the pacific coastal areas, in that the equatorial climate is being taken over by a tropical climate. These changes possibly favour the immigration of *O. ferruginea* into western South America. At least here are climatic conditions at the locations in the Yunga similar to the main area of the species in the western Central America.

Possibly *Pantala flavescens* and *Orthemis discolor* take other ways of the immigration. The latter occurs in Peru predominantly east of the Andes in the equatorial climate zone and the changing tropical climate zones. *O. discolor* was, however, already recorded before 1936 in the northern and middle Chala, as well as after 1956 in the northern Yunga. The current records in Yunga and Quechua allow three options of dispersion: a longitudinal immigration from the northern distribution in the Yunga, a vertical dispersion from the Chala and thirdly immigration from its main distribution area east of the Andes. For an origin from the main distribution area speaks the fact, that *O. discolor* is stenoecious at the new locations, as it sometimes seems for some euryecious species at new settlements outside their eurytopic areas (Lattin 1967). This is not really to be expected with immigration from Chala and northern Yunga.

Pantala flavescens shows a similar dispersion pattern. The area of distribution of this species extends in South America up to the 20°C isotherms (annual mean temperature). Accordingly it occurs autochthony up to now only in the Chala and after 1998 also in the lower Yunga. Findings at high elevation sites of the Andes concerned exclusively migrating specimens. The current findings in the Yunga up to the Quechua
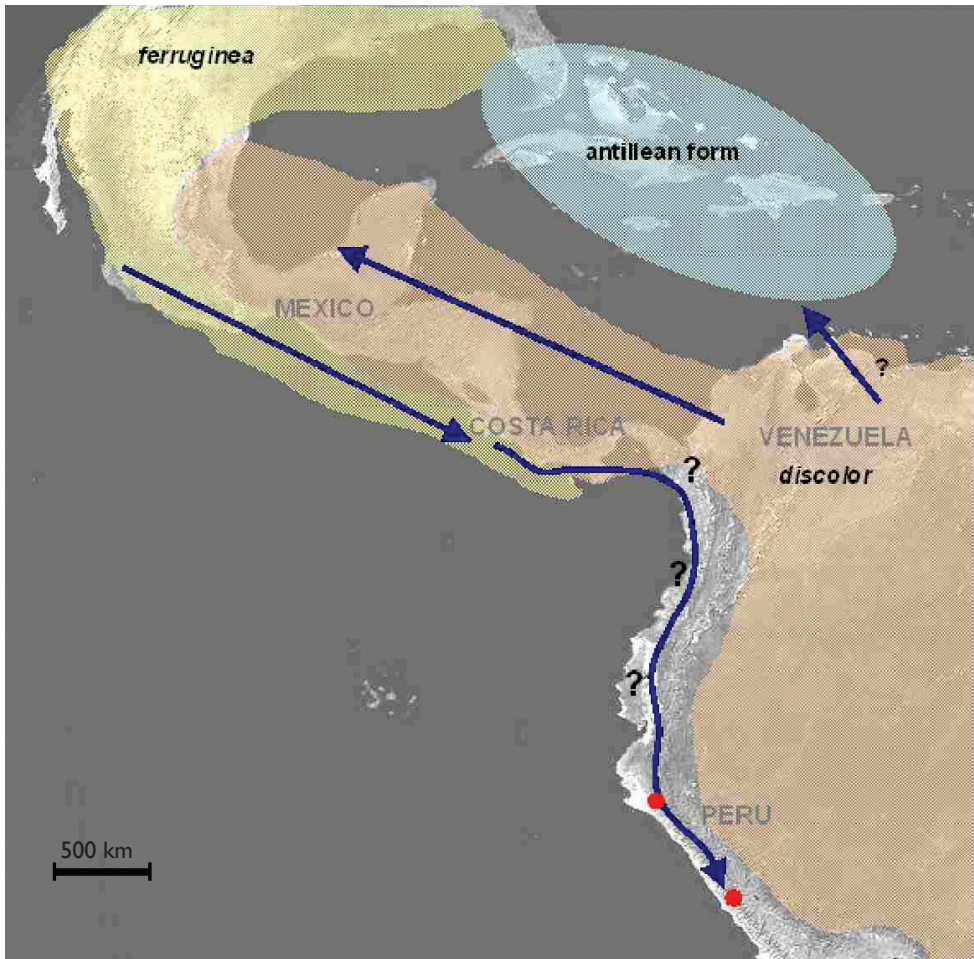
Figure 8. Distribution map of the Central American and Northwest South American regions of *Orthemis ferruginea*, *O. discolor* and the Antillean form. Arrows show the dispersion directions, question marks stand for open dispersal questions, the dots show the two places with records of *O. ferruginea* in the Peruvian Yunga.

at 2,800 m are from sheltered valleys (e.g. middle Santa and middle Pisco valley). The increase of the annual mean temperature, especially in higher altitudes was greater than the average for the whole country. Thus the annual mean for the temperature has increased in the Canyon del Pato from 18.6°C before 1980 to 19.7°C after 2000 (comm. of the data by Minera Huallanca S.A.C. 2006). Accordingly it must be supposed that the immigrations occur vertically. The species probably will be able to establish itself up within the next years up to the upper Quechua, particularly as it can reproduce successfully because it has a short larval development of three to five months (cf. Corbet 1999) and because of the formation and warming of some waters to more than 18°C (see above).

Conclusions and open questions

The present data provide merely indications for the influence of the change of climate on dispersion and ecological adaptation of dragonflies to changing environmental conditions in the western Peruvian Andes. In most cases these data do not suffice for a statistical verification of the hypotheses.

Furthermore there is knowledge of only some few Anisoptera and also only in an area between 8° and 14° southern latitude. For rare species (as for example almost all gomphids) also, it will not be possible in future to collect the required data because of the necessary high personal financial expenditure and because of the extensive, mostly inaccessible area of approx. 200,000 kms ² in the western Peruvian Andes. Therefore, suitable investigations should concentrate in future also on a few groups and species but of redundance without losing sight of the requirement to compile an inventory. Furthermore it is nessecary to collect the data on the ecology of each species, since this is incompletely, known.

Whether and how climate changes in the western Peruvian Andes have an effect on the Zygoptera fauna, cannot at present be answered, because there are too few data and many species have not been even described up to now. Similar effects as described above can be expect. For example this may be shown by *Protallagma titicacae* and *Ischnura capreola*. Within the last few years, both species could be collected in nature regions from where there were no previous records. Furthermore, for both species adaptations to higher respectively lower temperatures are noticeable. To what extent drift through altered wind directions and wind forces are responsible (possibly these do influence also the dispersal behaviour of different Anisoptera), remains unanswered.

Changes in the UV radiation regime as a possible factor effecting the dispersal and diversity of dragonflies (and certainly also of other groups) should be taken into account in future and examined more closely.

During the last two study campaigns in August / September 2006 an Frebruary / March 2007 extremely high UV levels (UV-A and UV-B) could be measured primarily in the Puna at levels of more than 4,000 m.

So the level was 15 UVI at the lagoon Ututo (4,464 m), 12 UVI at the lagoon Querococha (3,980 m) and 14 UVI at the lagoon Pumapashimin (4,242 m). These are extremely high values[5] which are accompanied by low atmospheric humidity (day averages 36% resp. 37% resp. 20%). Conspicuous was that no dragonfly larvae could be found in any of these lagoons, while only several adult *Rhionaeschna peralta* flew in the shadows of the *Polylepis* stands (rosacean trees) near the lagoon Querococha. Especially UV-B radiation (wavelength 280–320 nm) can also lead to considerable damage in insects - the smaller the wavelength the higher the energy and therefore the possibility of damage. Thus the genetic hereditary material is most sensitive to radiation of the above wavelengths (Tevini 1996). Studies on crustaceans which live just below the wa-

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[5]   For comparison purposes: in the equatorial sea highland in Kenya maximum levels of 13 UVI were measured

ter surface showed heavy damages and high rates of mortality at low-frequency UV-B radiation levels (Siebeck 1996).

Furthermore it cannot be excluded, that the imagines, which have a visual valence in the UV band, are impaired by changes of reflectivity. Thus may occur possible changes for the dragonflies originally visible species-specific colourings (Corbet in 1999) which could lead perhaps to irritations in the search for females and thus prevents matings. It is also conceivable that the colour of water surfaces and / or egg-laying habitats (e.g. plants and plant groups) are differently perceived[6].

Beside the inclusion of changed climate factors (wind and cloud cover included), it should be particularly important in future to examine the influence of UV radiation changes at high mountain levels.

The changed conditions considerably influence biotope and habitat structures and possibly also have an effect on the occurrence and the ecology of dragonflies in the western Peruvian Andes. Of the species discussed here, it can be suspected that the aeshnids react, with some few exceptions, predominantly to habitat losses, but probably are able to adapt flight times and reproduction times to the changed conditions. The libellulids seem to be much more flexible and appear to be able to conquer and colonize new areas and nature regions much more quickly, as well as to adapt flight times and reproductive times.

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[6] Insects can perceive UV; e.g. for humans equally blue tones are very well distinguished by bees if with one the UV proportion of the light is absorbed and with the other is reflected. The similar is valid with white and green tones (Dustmann and Geffcke 2000)

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RESEARCH ARTICLE

Impacts of extreme weather and climate change on South African dragonflies

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Abstract

The absence of ice sheets for many millions of years, yet variable topography and changing climate, has generated considerable biodiversity in South Africa. There is no evidence to date that anthropogenic climate change has affected odonate populations in the region. One reason is that the highly varying weather and climate constitutes considerable background noise against which any effects of modern climate change must be measured. Evidence is accumulating that the Holocene interglacial and gradual warming has left some species with isolated populations in montane areas among a matrix of arid land. Many South African odonate species are remarkably vagile and elevationally tolerant, readily immigrating into and emigrating from pools during wet and dry phases respectively. Some species take this movement to greater extremes by moving the southern margins of their geographical range back and forth with varying climate. After floods, populations of riverine odonates can recover within a year, although where the riparian corridor has been stripped of its trees, the recovery is very slow. Various synergistic impacts, particularly from invasive alien woody plants, are having a severe impact on many riverine species, and reducing their ability to respond positively to changing environmental conditions. Large-scale removal of these woody aliens is greatly benefiting the odonates' ability to survive in the short-term and to restore natural corridors for movement in the face of possible future climatic changes.

Keywords

Climate change, extreme weather, dragonflies, South Africa

Introduction

The last 130 000 years has seen three major events in the earth's climatic history. During the Eemian (130 000 – 110 000 years BP) the climate was a major driver of plant populations and their evolution. During the glacial period (110 000 – 10 000 years BP) there were alternating cold and temperate conditions with major shifts in insect assemblages at any one location (Elias 1994, Coope 1995, Ponel et al. 2003). In the current interglacial (10 000 years BP to Present) there has been a general warming of the earth's climate (with minor cool periods) when human pressure on the landscape increased considerably, especially in localized areas (Fagan 2004).

This natural background warming has accelerated in recent years through the impacts of the industrial age. The important point here is that in very recent years, it has been a combination of global climate change and anthropogenic landscape fragmentation that has caused considerable stress on insect populations (Warren et al. 2001, Travis 2003).

While the southern hemisphere has been subject to the various climatic changes as in the north, it has not had a major glaciation event for over 200 million years. This lack of cold sterilization, combined with milder climatic variations, various orographic conditions and much soil variation, has been the background for considerable speciation and the evolution of many localized endemics (Fjeldsa and Lovett 1997a,b; Goldblatt 1997; Jürgens 1997). Additionally, the historical human impact on the landscape has only been intensive over wide areas in the last 200 years, but still leaving today many areas that are only minimally disturbed. These various factors have all played a major role in determining the local distribution of the biota. Yet there is another factor that is part of this backdrop when assessing any contemporary climate change on dragonflies in the region. This is the 'El Niño Southern Oscillation' (ENSO), which produces alternately droughts and floods, often devastatingly so. ENSO, in addition to the overall warming during the current interglacial, constitutes the background noise against which we must measure the localized effects of anthropogenic climate change.

What the botanists have to say

Rutherford et al. (1999) undertook an interesting study on the effect that current anthropogenic climate change may have on floristic composition in reserve areas in South Africa. A climate change scenario of increased temperature but no change in precipitation would result in an increased growing season in some areas and a decrease in others. In this latter group is a reserve in the Northern Cape (Augrabies Falls National Park) which could lose a third of its plant species. However, such extinctions depend on the tolerances of the focal species, and their departure may be partly balanced by immigrating species more tolerant of altered conditions. Within the Cape Floristic Region, most species of Proteaceae are likely to experience geographic range contractions and even a shift to higher elevations (Midgley et al. 2003). The evidence clearly points to

the necessity of maintaining landscape linkages to ensure propagule migration. The challenge however, is that 30% of the currently remaining natural vegetation could be transformed within the next 20 years, with increased agriculture, urbanization and invasion by alien woody plants (Rouget et al. 2003). Midgley et al. (2002) go on to point out that the biome-level approach appears to underestimate the risk of species diversity loss from the impacts of climate change because many narrow range endemics will experience range dislocation throughout the biome and not necessarily just in areas identified as biome contractions. Midgley et al. (2002) recommend that targeted vulnerable plant species be monitored both for early warning signs of enhanced climate change and as empirical tests of predictions. Williams et al. (2005) then add that the sensitive and vulnerable species may not necessarily be able to make use of linkages unless particular and suitable habitat conditions are available for stepping stone events. Indeed, many Proteaceae species will not even disperse across gaps of unsuitable habitat of only 100 m.

Marginality and the South African odonate fauna

South Africa has a proportionately high number of endemic and globally threatened odonate taxa compared with neighbouring areas (Samways 1992). These globally threatened taxa have small and restricted geographical ranges mostly in ecosystems sensitive to human impact. In contrast, most of the nationally threatened taxa are marginal, and the threats are largely natural, driven by ENSO events (Samways 2006a). This has an important bearing on practical national Red Listing, because the issue is intrinsically bound to marginal rarity and associated risks of natural local extinction. Such local extinctions of even common insects are not unusual (Dempster 1989). Typically, marginal populations are small, sparse and isolated from each other (Lawton 1993) with considerable variation between the populations in genotype and phenotype (Shreeve et al. 1996). Little evidence is available on how these odonate species respond to climatic variations in the core of their geographical range. However, evidence from East Africa (Clausnitzer 2005) and Seychelles (Samways 2003b) suggests that in general the forest species are restricted to that particular habitat, and only following forest corridors, while many of the open habitat species are more vagile and opportunistic.

Evidence for loss of marginal South African odonate populations is strong. Besides the well-known migrants such as *Anax ephippiger*, *Pantala flavescens*, *Sympetrum fonscolombii* and *Tramea* spp. (the 'sweepstake' species), which readily colonize temporary pools, there are many species (the 'stepping stone' species) which rapidly locate and colonize newly-created artificial water bodies (Osborn and Samways 1996). Among this group of species is *Anax tristis*, with its remarkable flight ability. Most of the species in this last category are geographically widespread generalists, although not necessarily strong fliers (e.g. *Africallagma* spp. and *Agriocnemis* spp.), although *Agriocnemis falcifera* (Fig. 1) is a localized species and national endemic which readily colonizes artificial

Figure 1. *Agriocnemis falcifera*, a South African endemic, but nevertheless an opportunistic species which readily colonizes new pools.

water bodies so long as they have a constant water level and a wide and shallow margin with an abundance of grasses and sedges.

These 'stepping stone' species are highly elevationally tolerant and may move according to prevailing weather conditions (Samways 1989a; Niba and Samways 2006). Species such as *Diplacodes luminans* (Fig. 2), *Urothemis edwardsii* and *Rhyothemis semihyalina* occasionally colonize high-elevation pools when weather conditions are suitably warm. These 'stepping stone' species are highly vagile and habitat-tolerant, responding to ENSO events with remarkable speed. Even the localized *Orthetrum robustum* (Fig. 3) behaves in this way. In wet years, it is common in temporary pools in iSimangaliso Wetland Park, retreating to permanent lakes such as Lake Bhangazi North, during dry years.

Most of these 'stepping stone' species are inhabitants of still water, which includes pools ('kuile') left behind in dropping rivers as the dry season advances. In the Western Cape, species in this category include the very rare and threatened *Metacnemis angusta* (Fig. 4) and *Proischnura polychromatica*, which despite their extremely limited geographical distribution, are highly responsive and rapidly locate their preferred habitat (Samways et al. 2005). Furthermore, the riverine 'stepping stone' species recover within one year after an extreme flood event (Samways 1989b).

There is a further category, the 'range shifting' species, which change the southern limits of their geographical range margins in accordance with ENSO events. During the extreme floods in February 2000, two taxa *Pseudagrion coeleste coeleste* and *P. sjoestedti* became nationally extinct, as their habitat was changed from tree-lined river channels to early succession vegetation in the south-eastern corner of the

Figure 2. *Diplacodes luminans*, a 'stepping stone' species which moves to new pools up elevational gradients during warm years.

Figure 3. *Orthetrum robustum* populations expand to new pools in wet years, retreating to permanent ones in dry years.

Kruger National Park. While *P. coeleste* has recovered by colonizing another location, *P. sjoestedti* has not yet reappeared. These were not the only species that were affected. Others, such as *Lestinogomphus angustus* (Fig. 5) and *Pseudagrion sudanicum*, suffered severe population crashes but nevertheless survived on a reduced source population.

Figure 4. *Metacnemis angusta* is an extremely rare species which readily colonizes suitable habitat when, for example, it is restored by removing invasive alien woody plants.

Figure 5. *Lestinogomphus angustus* populations dropped substantially during the huge floods of February 2000.

In contrast, some others benefited from these weather-induced habitat changes. The locally rare *Trithemis werneri*, which prefers savanna rivers with wide riparian zones, responded by becoming abundant the following year. Similarly, *Crocothemis erythraea* readily colonizes quiet river zones where the natural tree canopy has been thinned or largely removed.

Figure 6. *Aciagrion dondoense* is a recent invader into South Africa, possibly driven south by extreme floods to the north, and seemingly partly responsible for the local demise of *Agriocnemis ruberrima ruberrima.*

The most extreme geographical range shift was by *Aciagrion dondoense* (Fig. 6), which prior to the floods of 2000, was not known in South Africa. By 2001, it was present in large numbers breeding in the iSimangaliso Wetland Park. It appears that the extensive flooding in southern Mozambique pushed it southwards where it then established, possibly with the benefit of warm conditions in recent years. This was not an isolated case, with other species, such as *Lestes dissimulans* and *L. uncifer* apparently also moving south. Both these species appear to oscillate their southern range margins, as indicated by records over the last few decades. In 1956, *L. uncifer* was even recorded as far south as Durban (Pinhey 1984).

Evidence (from the ongoing South African dragonfly database) is accumulating that these huge shifts in southern range margins may be a relatively common phenomenon in species with a wide African distribution. This cautions mapping exercises, and emphasizes that a distribution map for many of these species can be spurious depending on the timing of the original data records in the ENSO cycle.

The case for narrow-range endemics

All except two (*P. coeleste umsingaziense* and *Agriocnemis ruberrima ruberrima*) of the 14 globally Red Listed South African odonate taxa inhabit running water or pools in river systems. The two species which inhabit still water are subject to both anthropogenic pressure, such as overgrazing and loss of habitat to urbanization, and extreme natural events such as drought. This combination of anthropogenic impact and

adverse natural conditions appears to be particularly synergistic, causing permanent local extinction at many sites, without recolonization, as seen in *O. robustum*. There seems to be another twist in the case of *A. ruberrima*, which went rapidly extinct when *Aciagrion dondoense* invaded its stronghold, Mfabeni Swamp in the iSimangaliso Wetland Park. It appears that *A. dondoense* became an intense competitor and possibly predator, as it became very abundant in the same swamp microhabitats as *A. ruberrima* when it disappeared.

Impacts on all the remaining globally Red Listed South African odonates are distinctly anthropogenic, although of course, adverse weather cannot be ruled out as a future synergistic threat. The major impact for most of these taxa is from invasive alien trees (IATs) which shade out the microhabitats and stress the local populations (Samways and Taylor 2004; Samways 2006b). The reverse also occurs. When the IATs are removed there is remarkable recovery of populations, and for three species possibly even extinction reprieve (Samways et al. 2005; Samways and Sharratt 2010). The recovery effect is largely through re-establishment of suitable sunny habitats, although in some cases there is also recovery of populations through improvement in the water table when the IATs are removed.

Evidence points to many of the endemic species having climatic relictual distributions. Certain outlier populations show this very distinctly. There is an isolated population of *Chlorolestes tessellatus* in Sevenweekspoort, apparently at least a hundred kilometers from the nearest population, with arid and unsuitable habitat in between. It is a similar situation for *Chlorolestes fasciatus* (Fig. 7) which is represented by an isolated population in the mountains of the Mountain Zebra National Park, surrounded by a particularly arid and unsuitable matrix.

Synthesis of findings to date

Although there has been a claim that recent human-induced climate change has induced range shifts in certain herbivorous insect species in South Africa (Giliomee 1997), the range expansions can be more parsimoniously explained by a switch in host plant (Geertsema 2000). Nevertheless, there is the potential for major geographical range shifts, and even local extinctions of insects with climate elevation of only 2°C (Erasmus et al. 2002). However, empirical evidence from insects suggests that simple climate envelope models overlook the nuances of biology of a species, making future predictions of geographical range change extremely tenuous (Samways et al. 1999).

Evidence from dragonflies in the region clearly suggests that they have already been through substantial climatic bottlenecks, with vicariance being common among many of the narrow endemics, and great elevational tolerance and vagility being a feature of the more widespread species. This situation parallels that in plants, where certain species are at risk of extinction from lack of responsive mobility to climatic change (Williams et al. 2005), which could also be the case with dragonflies (Samways 2008). However, there are two mitigating factors. Firstly, evidence from highly threatened species' responsiveness to invasive alien plant removal shows that they are remarkably

Figure 7. *Chlorolestes fasciatus* is a South African endemic, with climatic relictual populations in isolated montane areas now in an arid matrix.

resilient, rapidly colonizing and populating re-instated habitats where the invasives have been removed. Secondly, many of the narrow-range endemic species still have the opportunity to shift elevation and move up the streams. This assumes of course that the streams still would have sufficient flow at the higher elevations. This is indeed a problem in Mayotte (Samways 2003a), while in the Seychelles, the high elevation endemic species are to some extent tolerant of droughting conditions and minimal flow in the upland streams (Samways 2003b). Behavioural flexibility to elevation is thus already built into the genotype of many dragonfly species in this ENSO-prone region.

Probably the greatest threat to South African dragonflies in the current changing climate scenario is from the synergistic effects of anthropogenic disturbance, particularly from alien plants. This sort of synergism between climate change and habitat disturbance has been described by Travis (2003) as "a deadly anthropogenic cocktail". For South African dragonflies, like British butterflies (Warren et al. 2001), this may well be the case, with the mountains possibly being their saviour, as has been the case during the Quaternary of Europe (Hewitt 2003). Clearing of the invasive alien woody plants not only improves the maintenance of biodiversity on site but also opens up riparian pathways along the elevational gradient. This has long-term evolutionary value as well as short-term ecological benefit. Bearing this in mind, there does appear to be something concrete that we can do to lessen the blow of further climate change. The first results on South African Odonata species suggest that rehabilitating riparian corridors might well benefit a whole range of aquatic species (Smith et al. 2007; Samways and Sharratt 2010; Magoba and Samways in press).

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RESEARCH ARTICLE

Climate and elevational range of a South African dragonfly assemblage

Contribution to EU/ALARM Project

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Abstract

Elevation and climate are interrelated variables which have a profound affect on biota. Flying insects such as dragonflies can rapidly disperse and select optimal habitat conditions at appropriate elevations. Such behaviour is likely to be especially important in geographical areas which are subject to major climatic events such as El Niño. Accordingly, we studied dragonflies and environmental variables in a series of reservoirs over an elevational range of 100–1350 m a.s.l. at the same latitude on the eastern seaboard of South Africa. The aim was to determine how elevation and climate (as regional processes), as well as local factors, influence species assemblage variability, habitat preference and phenology. Certain environmental variables strongly explained the main variation in species assemblage. These included local factors such as pH, marginal grasses, percentage shade, exposed rock, marginal forest and to a lesser extent, marshes and flow. Different species showed various tolerance levels to these variables. Elevation and climate as regional processes had very little influence on dragonfly assemblages in comparison with these environmental factors. These odonate species are essentially sub-tropical, and are similar to their tropical counterparts in that they have long flight periods with overlapping generations. Yet they also have temperate characteristics such as over-wintering mostly as larvae. These results indicate evolutionary adaptations from both temperate and tropical regions. Furthermore, most were also widespread and opportunistic habitat generalists. The national endemics *Pseudagrion citricola* and *Africallagma sapphirinum* only occurred at high elevations. However, the endemic *Agriocnemis falcifera* was throughout all elevations, suggesting regional endemism does not necessarily equate to elevational intolerance. Overall, the results suggest that many millennia of great climatic variation have led to a highly vagile and elevation-tolerant dragonfly assemblage which readily occupies new water bodies. Such an assemblage is likely to be highly tolerant of global climate change, so long as there is sufficient water to keep the reservoirs at a constant level.

Introduction

Insect phenology usually varies with topography and associated environmental factors (Wolda 1987). Interactions between temperature-dependent development and micro-climate are important features of insect life-history, leading to the maintenance of considerable genetic variation in populations (Bradshaw and Holzapfel 1990; Roff 1990). Studies in insects and other arthropods suggest that microclimatic gradients sometimes can have larger effects on emergence phenology than do annual fluctuations in weather conditions (e.g. Kingsolver 1979; Weiss et al. 1993). Moreover, field evidence (Thomas et al. 2001) supports theoretical predictions (Thomas et al. 1999) that certain types of thermophilous insects have expanded to occupy broader niches, and hence larger patch sizes near their northern range margins in the northern hemisphere during some warm summers in recent years (Ott, this volume).

Small reservoirs are a characteristic feature of the South African agricultural landscape, acting as important reserves for dragonflies (Samways 1989a). These reservoirs have been shown to be important in promoting the conservation of insect diversity, but mostly of generalist species (Samways and Steytler 1996). Such reservoirs increase the area of occupancy of the local species. Thus, they are present in the local area in natural water bodies and simply move across to the reservoirs.

The topography of KwaZulu-Natal, South Africa ranges in elevation from 0–3000 m a.s.l along a 200 km E-W transect at one latitude. This area is strongly modified by montane climate at higher elevations, and has a sub-tropical/tropical climate at sea level. The study area within KwaZulu-Natal is situated at the edge of a major escarpment comprising a highly heterogeneous landscape structure with a wide variety of aquatic habitats. This elevational transect supports a high diversity of dragonfly species making up close to three-quarters of the South African odonate fauna. This provides a basis for measuring how species phenologies and distribution respond to the seasonal (temporal) and elevational changes. This information can be useful for subsequent conservation action, and for providing baseline data for future studies on the impacts of global climate change.

Using a series of five moderately-sized artificial, but well-established reservoirs (which only reach about 1400 m a.s.l.), the aim here was to determine the extent to which elevation (as a regional process), alongside local factors, influence habitat preferences and species distribution. Furthermore, as there is no information on the effects of seasonal changes on southern African odonate species, the aim was also to determine how phenology might vary with elevation.

Materials and methods

Study area

The study area was in KwaZulu-Natal between the coast and the Drakensberg escarpment (<3000 m a.s.l.). Elevation exerts a major influence on climatic features at all spatial scales, being a barrier to rain-bearing air masses, and by altering temperature through lapse rates and aspect (Tyson 1986; Schulze 1997).

Reservoirs, all of which were over 30 years in age, were selected within this elevational gradient (Fig. 1) to be at the same latitude (with 26 minutes latitude) and to be relatively comparable (Table 1). The maximum elevation that could be entertained for these comparative studies was 1400 m a.s.l, even though the mountain peaks reached 3000 m a.s.l.

Methods

Each reservoir was about 1 ha, and stratified into six sub-sites, each measuring 20 m length (along a line transect on the reservoir edge) by 2 m width (1 m on land and 1 m into water). Data were collected on 42 sampling occasions, and covered various stages of dragonfly development (adults, tenerals and young adults (together here simply called 'tenerals'), larvae and exuviae). Mating or oviposition were also recorded (mostly tandem flights and occasional dipping of ovipositors). Environmental variables were recorded twice a month from January 2001 to December 2002, except for the winter months of June, July and August when data were collected once each month.

Adult males were recorded using close-focus binoculars, and walking along the 20 m sub-sites and counting within 6 min all individuals perching or flying. Counts of Anisoptera at sub-sites can be virtually 100% accurate and that of Zygoptera exceeds 80% (Moore 1991). Counts were between 10h00 and 14h00 during sunny, high activity periods of the day.

Exuviae and tenerals were recorded as an indication of successful breeding. In this study, population changes were indicated by comparing the maximum numbers of individuals (adults, tenerals and larvae) observed each month for the whole sampling period. Unidentified tenerals from the field were collected and reared in the laboratory until their body colour (with genitalia morphology) could be used for subsequent identification.

Larvae were sampled with a dip-net (41 cm diameter × 1 mm mesh sieve). Two dips per sub-site (12 dips/site) were done within 20 min. Each dip was followed by vigorously shoving the net back and forth in water once among water weeds, along rushes and besides banks. We fully accept that no single, quantitative collection method is equally efficient for all species of larvae, and even all ages. However, the comparative efficiency of the collection method, being standardized, will be the same at different sites. Individual larvae in the net were identified using a 9× hand lens, counted and

Figure 1. The mid-elevation site (790 m a.s.l.) with reedy margins typical of all the sites.

released back into water except where individuals could not be identified in the field, in which case, they were picked out with soft, flexible forceps and placed in aerated plastic cages containing reservoir water. Usually only last-instar larvae were collected for subsequent rearing and identification in the laboratory.

Marginal vegetation (both structural and compositional) was estimated using percentages of sub-sites they covered. At all sub-sites, aquatic plants were recorded as: marginal forest stands (Mfor), marginal grasses (Mgra), floating and submerged vegetation (Fsv), marginal herbs, sedges and reeds (Mhsr).

Meteorological data e.g. rainfall, ambient and water temperatures (At/Wt) collected at Goodhope Estate (GH), Cedara (CE) and the Botanical Gardens (BG) were compared with that collated by the weather bureau at Cedara Agricultural College. Also, rainfall and temperature data for Krantzkloof (KL) and Stainbank (SB) Nature Reserves were compared with that collated by the Durban Airport weather station.

Other measured environmental variables were percentage exposed rock in the sampling sub-site (Exrock %), percentage shade (% Sh), water depth (Wd), turbidity (Tur %), pH, flow (1 = running, 0 = still), reservoir circumference (Pcir (m)) and elevation (Elev (m)).

Data were analysed with univariate methods for species richness and abundance relationships using diversity indices, distributional models and graphical methods. Species spatial and temporal variability was analysed using Analysis of Variance (ANOVA). Spearman's rank correlation coefficients were used to measure the association between variables and species abundance and richness. These correlations were

Table 1. The five elevational sites used in this study

Site name/code	Grid reference and Elevation	Land use
Kenneth Stainbank Nature Reserve (SB) (Low elevation)	29°50'S; 30°55'E; 100 m a.s.l.	Nature reserve
Krantzkloof Nature Reserve (KL) (Mid-low elevation)	29°46'S, 30°5'E; 450 m a.s.l	Nature reserve
Botanical Gardens, Pietermaritzburg (BG) (Mid-elevation)	29°35'S; 30°25'E; 790 m a.s.l.	Botanical gardens
Cedara (CE) (Mid-high elevation)	29°61'S; 29°06'E; 1050 m a.s.l.	Low-intensity agricultural area
Mondi Goodhope Estate (GH) (High elevation)	29°40'S; 29°58'E; 1350 m a.s.l.	Extensive grassland corridors (natural state) among pine stands

calculated using the software SPSS version 6.1. MINITAB and SPSS software were used to run ANOVA, relating species to sites and site variables. In addition to ANOVA, Similarity coefficients calculated between every pair of samples helped facilitate a classification or clustering of samples into groups which are mutually similar or an ordination plot in which the samples are 'mapped' into multidimensional space in such a way that the distances between pairs of samples reflect their relative dissimilarity of species composition.

Hierarchical agglomerative clustering, using the program 'Cluster' in the computer software PRIMER (Clark and Warwick 1994) was used to compare sites. The species by sub-site (SS) data matrix was transformed using 4th root-transformation to balance rarer and commoner species. The Bray-Curtis similarity index was then used to produce a similarity matrix and then fused successively through hierarchical clustering using group-average linking, to produce a dendrogram with the x-axis defining a similarity level at which two samples or groups are considered to have fused, and the y-axis representing the full set of samples.

Correspondence analysis (CA), operates on a site and species data matrix and represents it on a two-dimensional plane (ter Braak and Smilauer 1998). It uses a site-by-species scores data matrix and summarises it such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. Conversely, from a species-by-site matrix, CA ordinates the data such that the closer two species are to one another on the same ordination plane, the greater the likelihood that they will occur at the same or similar sites and vice versa. Canonical Correspondence Analysis (CCA) was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the bi/triplot, and is therefore a measure of how much the species distribution differs along that environmental gradient. Important environmental gradients therefore tend to be represented by longer arrows than less important ones (ter Braak and Looman 1995). The software CANOCO version 4 and CANODRAW version 3.1 (ter Braak and Smilauer 1998) were used.

Results

Species phenology

A total of 47 species was recorded throughout the study (Table 2). Adults of only three species (*Ceriagrion glabrum, Lestes plagiatus* and *Crocothemis erythraea*) were recorded during winter, and then only at Mid (BG) elevation. Accumulation curves reached asymptotes for tenerals with 10–14 species, and for adults with 21–25 species, and varied with elevation (Fig. 2).

Relative proportions of adults, tenerals and larvae

Larvae stayed at about the same level all year round (Fig. 3). Tenerals and adults showed the same trends as in Fig. 2 i.e. none in July and August. However, there was trend for maximum numbers to be reached later at higher elevations, from October to December for tenerals and November to February for adults. Larval abundance varied from 20 individuals in January at Mid-low (KL) elevation to 138 in April at Mid-high (CE) elevation. Teneral counts also varied from two individuals in June at High (GH) elevation to 175 individuals in November at Mid-high (CE) elevation. Thereafter, larval abundance at all elevations was high in November for both years. No teneral individuals were recorded at any elevations during winter (July to August). Adult abundance was greatest in November for both years and at all sites except at High (GH) and Mid-low (KL) where it was in December.

Peak occurrence periods

There was continual emergence over the summer months, and there was continuous presence of two or three developmental stages between September and June. *Lestes plagiatus* and *L. tridens* probably over-wintered in the egg stage. Table 3 summarises the months for peaks in adult, teneral, larval stages, and mating/oviposition in Anisoptera and Zygoptera species. Anisoptera adults from High (GH), Mid-high (CE) and Low (SB) elevations had peak occurrences mostly from December to March, although most species peaked in November during the first sampling year at the High (GH) elevation. Species peaks in Mid (BG) and Mid-low (KL) elevation were also similar, occurring in November in both sampling years. Double peaks occurred at the Mid-high (CE) elevation for *C. erythraea,* occurring in March and November 2001, January and November 2002. *Trithemis stictica* peaked in March and November 2001, April and November 2002.

Zygoptera species had very similar peak adult occurrence periods at High (GH), Mid (BG) and Low (SB) elevations, from December to March in both years. At Mid-high (CE) and Mid-low (KL) elevations, peak adult appearance was April/May. Zygop-

Table 2. Odonata species sampled during this study with species code names

Species	Elevations					
	Code	SB	KL	BG	CE	GH
Anisoptera						
Aeshnidae						
Anax imperator Leach, 1815[3]	Aimp	AL*	AL	AL	AL	AL
A. speratus Hagen, 1867[3]	Aspe	A	A	A	A	A
A. tristis Hagen, 1867[1]	Atri	A	–	–	–	–
Gomphidae						
Ceratogomphus pictus Sélys, 1854[3]	Cpic	–	–	–	A	A
Ictinogomphus ferox (Rambur, 1842)[2]	Ifer	A	–	–	–	A
Notogomphus praetorius (Sélys, 1878)[2]	Noto	–	AT	–	–	AT
Paragomphus cognatus (Rambur, 1842)[3]	Pcog	–	–	A	–	–
Libellulidae						
Acisoma panorpoides Rambur, 1842[2]	Acis	ATL	–	–	ATL	ATL
Brachythemis leucosticta Burm., 1839[3]	Bleu	A	–	–	–	–
Chalcostephia flavifrons Kirby, 1889[1]	Chfl	A	–	–	–	–
Crocothemis erythraea (Brullé, 1832)[3]	Cery	ATL	ATL	ATL	ATL	ATL
Diplacodes lefebvrii (Rambur, 1842)[2]	Dlev	A	–	–	–	–
Hemistigma albipunctum Rambur 1842[2]	Halb	A	–	–	–	–
Nesciothemis farinosa (Förster, 1898)[3]	Nfar	AT	AT	AT	AT	AT
Notiothemis jonesi Ris, 1919[1]	Njon	–	A	–	–	–
Orthetrum caffrum (Burmeister, 1839)[3]	Ocaf	–	–	–	ATL	ATL
O. hintzi Schmidt, 1951[1]	Ohin	–	–	–	–	A
O. julia falsum Longfield, 1955[3]	Ojul	ATL	ATL	ATL	ATL	A
Pantala flavescens (Fabricius, 1798)[3]	Pfla	A	A	A	A	A
Palpoleura portia (Drury, 1773)[3]	Pluc	AT	AT	AT	–	–
P. jucunda jucunda Rambur, 1842[2]	Pjuc	–	–	–	–	AT
Diplacodes luminans (Karsch, 1893)[1]	Plum	AT	AT	AT	–	–
Sympetrum fonscolombii (Sélys, 1840)[2]	Sfon	A	A	A	A	A
Rhyothemis semihyalina Desjardins, 1832[2]	Rshy	AT	–	AT	AT	–
Tetrathemis polleni Sélys 1877[1]	Tpol	A	–	–	–	–
Tramea basilaris (Beauvois, 1817)[2]	Tbas	AL	AL	A	AL	AL
Trithemis arteriosa (Burmeister, 1839)[3]	Tart	A	A	A	AL	AL
T. dorsalis (Rambur, 1842)[3]	Tdor	–	ATL	ATL	ATL	ATL
T. stictica (Burmeister, 1839)[2]	Tsti	–	ATL	ATL	ATL	ATL
Urothemis assignata (Sélys, 1872)[2]	Uass	A	A	A	A	A
Zygonyx natalensis (Martin, 1900)[2]	Znat	–	A	A	–	–
Zygoptera						
Chlorocyphidae						
Platycypha caligata Sélys, 1853[3]	Pcal	–	–	AT	A	–
Coenagrionidae						
Africallagma elongatum (Martin, 1907)[1]	Aelo	–	–	A	–	–

Species	Elevations					
	Code	SB	KL	BG	CE	GH
A. glaucum (Burmeister, 1839) [3]	Aglm	ATL*	ATL	ATL	ATL	ATL
A. sapphirinum (Pinhey, 1950)[4]	Asap	–	–	–	–	A
Agriocnemis falcifera Pinhey, 1959[4]	Afal	ATL	ATL	ATL	ATL	ATL
Azuragrion nigridorsum (Sélys, 1876) [2]	Azn	AT	–	–	–	–
Ceriagrion glabrum (Burmeister, 1839) [3]	Cglm	ATL	ATL	ATL	ATL	–
Ischnura senegalensis (Rambur, 1842) [3]	Isen	ATL	ATL	ATL	ATL	ATL
Pseudagrion citricola Barnard, 1937[4]	Pcit	–	–	–	–	A
P. hageni Karsch 1893[2]	Phag	AT	AT	AT	–	–
P. kersteni (Gerstäcker, 1869) [3]	Pker	ATL	ATL	ATL	ATL	ATL
P. massaicum Sjöstedt, 1909[3]	Pmas	ATL	–	ATL	ATL	–
P. salisburyense, Ris, 1921[3]	Psal	ATL	ATL	ATL	ATL	A
Lestidae						
Lestes plagiatus (Burmeister, 1839) [3]	Lplg	–	ATL	ATL	ATL	ATL
L. tridens McLachlan, 1895[1]	Ltri	AT	–	–	–	–
Platycnemididae						
Allocnemis leucosticta Sélys, 1863[2]	Aleu	–	–	A	–	–

* Record of adult, teneral and/or larval stage of the corresponding species. [1] Common African species whose range extends south just over the border into South Africa, but are local or rare in the country, [2] African species that are widespread and/or locally common in South Africa, [3] African species that are regularly seen in the right habitats, some of these are very common throughout South Africa, [4] Species endemic to South Africa (i.e. South of the Limpopo River).

tera species with two peaks per year were *Ischnura senegalensis* and *C. glabrum*, each occurring at various elevations (*C. glabrum* was absent at High (GH) elevation). Also, *Africallagma glaucum* and *Pseudagrion massaicum* had two peak appearances in Mid-high (CE) elevation. *L. plagiatus* had two peaks per year at Mid (BG) and Mid-low (KL) elevation, while *L. tridens* and *P. massaicum* had two peak abundances per year in Low (SB) elevation during both years. *L. tridens* from Low (SB) elevation had four peaks at different times during the two sampling years: April and December 2001, March and November 2002, indicating more than one generation per year. The number of species per family was very similar from one elevation to the next.

Fifteen species occurred at all five elevations, while 17 species were restricted to only one elevation: eight in Low (SB); four each at High (GH) and Mid (BG) and one only occurred at Mid-low (KL). 15 species occurred over at least two elevations at all five elevations (Table 4).

The dominant species at the Low (SB) elevation site was *L. tridens* (22%), while *T. stictica* dominated in Mid-high (CE) elevation. Both elevations had relatively high percentage levels of species dominance patterns compared to the other elevations. Mid-low (KL) elevation and High (GH) elevation showed some similarity in patterns of species dominance, with *T. arteriosa* (17%) and *T. stictica* (18%) being the dominant species.
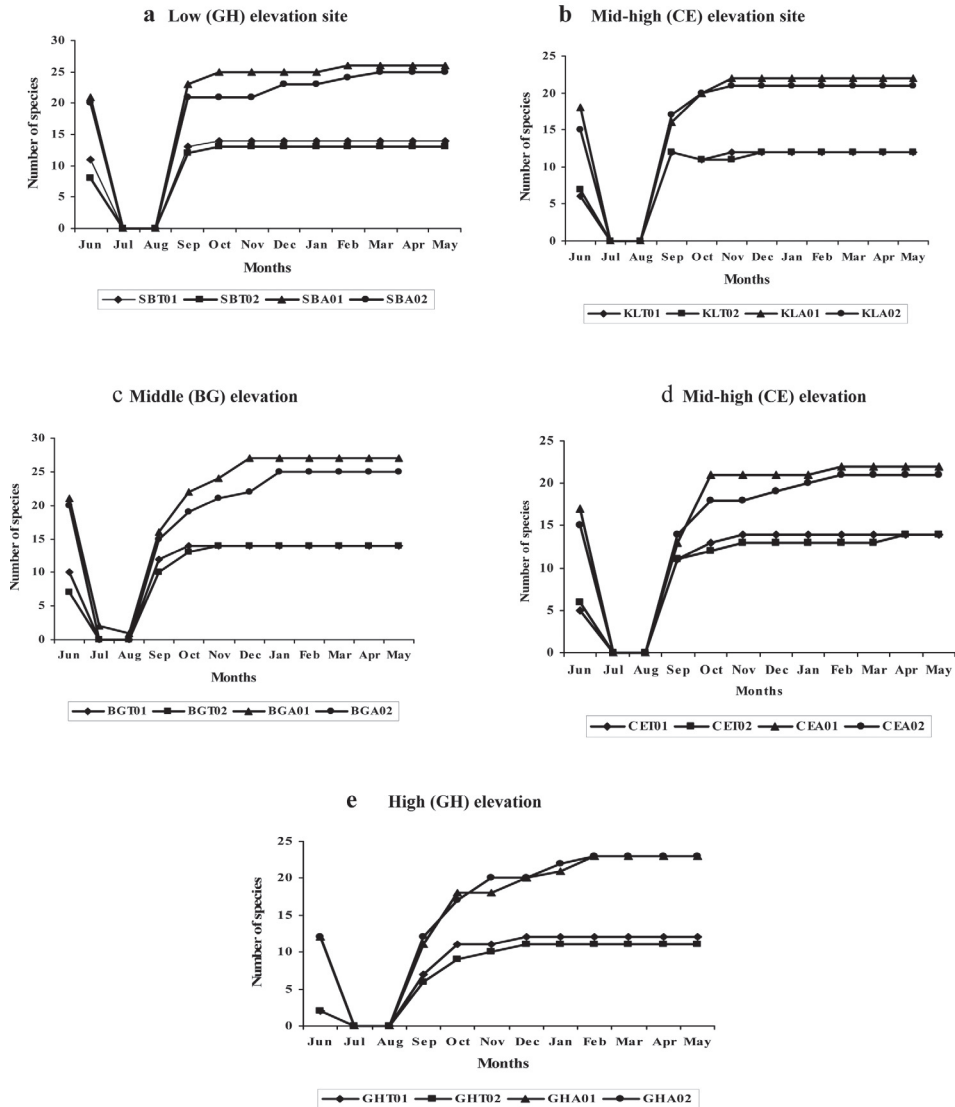
Figure 2. Accumulative dragonfly tenerals (T) and adults (A) species recorded at **a** Low (SB), **b** Mid-low (KL), **c** Mid (BG), **d** Mid-high (CE) and **e** High (GH) elevations during the first (01) and second (02) year of the study.

Spatial variations in adults, tenerals and larvae with elevation

Larval species richness and abundance was highest at Mid-high (CE) elevation. Patterns of teneral species richness across elevations ranged between 14 and 16 species per elevation during the study, with Mid-low (KL) recording lowest individual counts. Overall number of adults species varied slightly across elevations, with Low (SB) eleva-
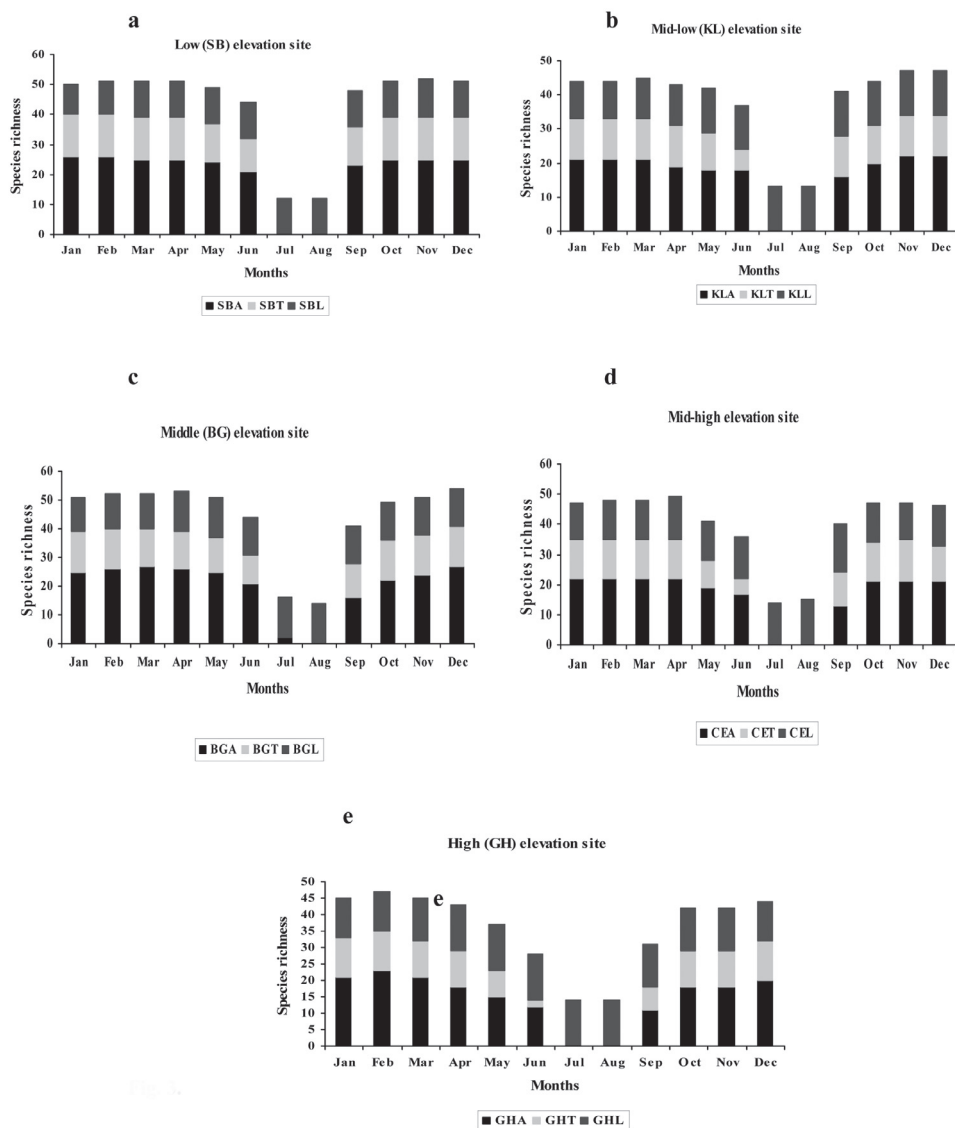
Figure 3. Dragonfly species recorded at **a** Low (SB), **b** Mid-low (KL), **c** Mid (BG), **d** Mid-high (CE) and **e** High (GH) in terms of adults (A), tenerals (T) and larvae (L), and during the two-year sampling period.

tion supporting the most species. Adult abundance was highly variable across elevations, with Mid-low elevation (KL) recording lowest abundance. Larval species richness was significantly positively correlated with elevation ($F = 19.25$; $P = 0.002$), as was abundance ($F = 7.69$; $P = 0.024$). Teneral species richness was negatively correlated with elevation but not statistically significantly. There was weak, non-significant positive correlation for teneral individuals with elevation ($F = 4.73$; $P = 0.056$). Regressions of adult dragonfly species richness ($P = 0.27$) and abundance ($P = 0.32$) on elevation were

Table 3. Summary of species phenologies recorded during this study.

Site Elevation (m a.s.l.)	Adults		Mating/ oviposition		Larvae	
	Zygoptera	Anisoptera	Zygoptera	Anisoptera	Zygoptera	Anisoptera
Low (SB) 100 m	Dec–Mar 2002 Dec–Mar 2001	Dec–Mar 2002 Dec–Mar 2001	Feb–Jun	Jan–Apr	Apr–May Dec	Apr–May Dec
Mid-low (KL) 450 m	Nov 2002 Nov 2001	Apr 2002 Apr 2001	Feb–Mar	Feb–Mar Oct–Nov	Apr–Jun Dec	Apr–May Dec
Middle (BG) 790 m	Nov 2002 Nov 2001	Jan–Mar 2002	Feb–Mar Sep–Nov	Feb–Mar	Mar–Apr, Jul, Nov–Dec	May, Sep– Oct
Mid-High (CE) 1050 m	Dec–Mar 2002 Dec–Mar 2001	Apr–May 2002 Apr–May 2002	Jan–May Oct–Nov	Feb–May	Mar–May Sep–Dec	Apr, Jul–Aug
High (GH) 1350 m	Dec–Mar 2002 Nov 2001	Dec–Mar 2002 Feb–Apr 2001	Jan–May	Feb–Jun	Feb–Sep	Feb–Sep

not statistically significant even though there was a generally decreasing trend in species as elevation increased.

Two-way ANOVA of the response of adults, tenerals and larvae to elevation across seasons showed no statistically significant effect on adult species (F = 1.2, P = 0.31) or teneral individuals (F = 1.6; P = 0.41). However, there were statistically significant responses for adult individuals (F = 2.9; P = 0.01), teneral species (F = 2.1; P = 0.05), larval species (F = 4.2; P = 0.002) and larval individuals (F = 10.0; P = 0.001) (Table 5).

Relationship between species and environmental conditions

Species associations with elevation were strongest on ordination plots when all Odonata were separated into their component sub-orders (Anisoptera and Zygoptera). CA results for Anisoptera (Fig. 4a) showed most open water species clumped at the centre of the ordination. Zygoptera species showed various trends as species were more dispersed from the centre of the ordination (Fig. 4b). They were more tolerant of diverse conditions of shade as well as of open water. Separate CCA ordinations were also run for species belonging to Anisoptera and Zygoptera again for better interpretation of the effects of measured variables and elevation on patterns of dragonfly assemblage composition and distribution. Species-site-variable triplots for Anisoptera (Fig. 5a) and Zygoptera (Fig. 5b) showed that most assemblages were related to a number of environmental variables, and indicated how species responded or not to gradients of these variables in space.

Accordingly, elevation, marginal grasses, pH, reservoir circumference, atmospheric temperature and percentage shade appeared on the first (horizontal ordination axis) as the most important variables, while water depth, floating /submerged vegetation and marginal forest occurred on the second axis (vertical) and were less important in determining Anisoptera species assemblage distribution patterns. Marginal forest, percentage shade, water depth and floating/submerged vegetation were the most important

**Table 4.** Odonata species and elevational distributiona

Elevations	Species
One elevation 100 m (SB)	Azn, Ltri, Atri, Bleu, Chfl, Halb, Dlev, Tpol
450 m (KL)	Njon
790 m (BG)	Pcal, Aleu, Aelo, Pcog
1050 m (CE)	None
1350 m (GH)	Asap, Pcit, Ohin, Pjuc
Two elevations CE, GH	Cpic, Ocaf
KL, BG	Znat
KL, GH SB, GH	Noto Ifer
Three elevations SB, CE, GH	Acis
SB, BG, CE	Pmas, Rshy
SB, KL, BG	Phag, Pluc, Plum
Four elevations KL, BG, CE, GH	Lplg, Tdor, Tsti
SB, KL, BG, CE	Cglm
All five elevations 100–1350 m	Uass, Tart, Sfon, Pfla, Ojul, Nfar, Cery, Aspe, Pker, Psal, Isen, Afal, Aglm, Tbas, Aimp

SB (Low) = (100 m), **KL** (Mid-low) = (450 m), **BG** (Mid) = (790 m), **CE** (Mid-high) = (1050 m) and **GH** (High) = (1350 m). Species codes are as in Table 2.

variables, while marginal grasses, elevation and pH were important for Zygoptera. The following Anisoptera species were also associated with marginal grasses of reservoirs at High (GH) and Mid-high (CE) elevations: *T. stictica, Palpopleura jucunda, Acisoma panorpoides, Orthetrum caffrum. N. jonesi* was associated with highly shaded conditions of sub-site three at Mid-low (KL) elevation.

Low (SB) elevation species (when the elevation gradient is projected backwards on the ordination triplot) had the typical species *Hemistigma albipunctum, Chalcostephia flavifrons, Tetrathemis polleni, Diplacodes lefebvrii, Rhyothemis semihyalina* and *Tramea basilaris,* even though the last three species were also present at higher elevations. Open reservoirs at all elevations had the following species in common, located mostly at the centre of the ordination for Anisoptera: *O. julia, C. erythraea, T. arteriosa, P. lucia, A. speratus, A. imperator, T. dorsalis, N. farinosa* and *P. flavescens.*

High (GH) elevation zygopterans like *Pseudagrion citricola* and *Africallagma saphirinum* were strongly associated with sunny conditions, high pH and marginal grasses. Low (SB) elevation species were *L. tridens* and *A. nigridorsum* while *P. hageni* was associated with Middle (BG) to Low (SB) elevation shade conditions. *A. elongatum, P. kersteni* and *P. salisburyense* were associated with minimal flow, exposed rock and marshy conditions.
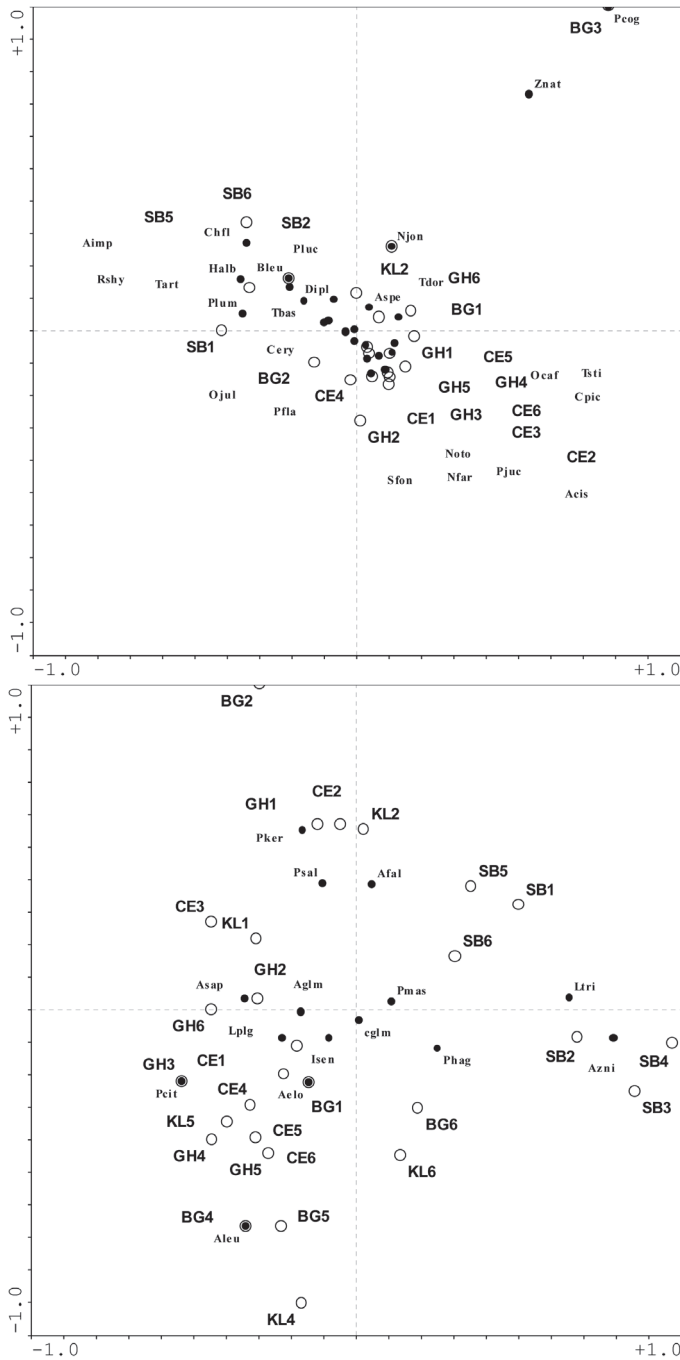
Figure 4. a CA biplot of Anisoptera species (closed circles) and sampling sites (open circles), and **b** CA biplot of Zygoptera species (closed circles) and sampling sites (open circles) for pooled 2001 and 2002 data. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Species codes are as in Table 2.
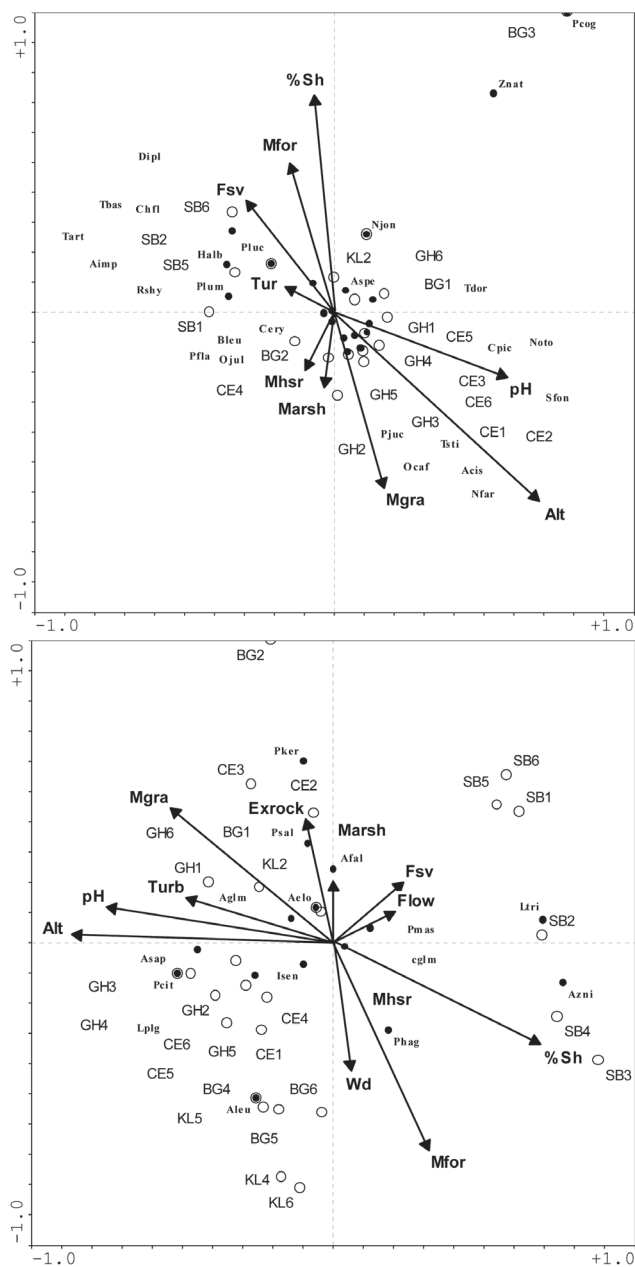
Figure 5. a CCA triplot of Anisoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) and **b** CCA triplot of Zygoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) for pooled 2001/2002 data. Axis 1 is horizontal and axis 2 vertical. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Site variables are: Alt= elevation, Mgra= marginal grasses, Mhsr= marginal herbs, sedges and reeds, Mfor= marginal forest, Tur= water turbidity, Fsv= floating and submerged vegetation, %Sh= percentage shade. Species codes are as in Table 2.

Table 5. Two-way-ANOVA results of elevation and seasonality interaction for mean dragonfly adults, tenerals and larvae richness and abundance, and measured site variables during the whole sampling period.

Site variable	Summer					Autumn					Winter					Spring					F	P
	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH	SB	KL	BG	CE	GH		
Asp	25	21.5	24	21	21	25.5	21	26	21.5	23	20	16	20	16	12	23	21	22.5	20	19	1.2	0.31 ns
Aind	700	351	418	296	790	572	374	480	567	648	130	62	98	112	75	600	404	552	554	534	2.9	0.01
Tsp	13.5	12	14	13	11	13.5	11	13	14	11.5	9.5	6.5	8.5	6.5	2	13.5	12	14	13	11	2.1	0.05
Tind	172	94	132	230	215	122	125	137	223	200	25	15	20	19	5	216	162	190	243	200	1.6	0.14 ns
Lsp	12.5	13	13	13	13	12	12.5	14	14.5	14	12	13	14	15	13.5	13	12.5	13	16	13	4.2	0.002
Lind	124	141	84	93	77	145	120	146	193	83	83	70	89	131	135	121	75	147	134	151	10	0.001
% Sh	19	12.4	16.5	0	0	12	15.8	11	0	0	11	16	10	0	0	17	11	14.6	0	0	1.3	0.26 ns
At	24.5	30	30	29	30.4	28	29.3	29	30.5	30	17	17	18	20	21.9	26	28	26.3	28	25.5	0.8	0.59 ns
Fsv	30.8	17	24	21	11.3	30	2	28	20.5	6	18	0.6	15	14	3.7	24	1.9	21.8	16	6.8	0.7	0.6 ns
Mfor	30	40	25	0	0	30	50	25	0	0	30	50	25	0	0	30	50	25	0	0	1	0.44 ns
Mgra	27.5	16	12.5	22	21	25	4.8	12	23.4	22	11	2.2	5.5	10	8.3	22	6.2	11.7	22	26.2	1	0.46 ns
Marsh	27	27	23	12	7.5	29	29	24	14.8	7.3	12	5.5	12	6.6	4.2	26	28	15.6	11	8.2	7.4	0.001
pH	7.2	6.9	6.9	7.2	7	7	7	7.3	7.1	7.1	6	7.2	7.1	7	6.8	6	7.1	7.1	6.9	7.2	0.8	0.58 ns
Tur	18	25	20.5	23	20	15	26	24	17	25	22	28	20	19	28.8	20	21	20	19	17.4	0.5	0.86 ns
Wd	25	28	29.3	26	24	24	25	22.8	25	20	15	15	16	16	18.9	24	24	24	23.4	20.2	1.4	0.24 ns

Asp = Adult species, **Aind** = adult individuals, **Tsp** = teneral species, **Tind** = teneral individuals, **Lsp** = larval species, **Lind** = larval individual. **SB** (Low) = (100 m), **KL** (Mid-low) = (450 m), **BG** (Mid) = (790 m), **CE** (Mid-high) = (1050 m) and **GH** (High) = (1350 m). **% Sh** = percentage shade, **At** = atmospheric temperature, **Fsv** = floating and submerged vegetation, **Mfor** = marginal forest, **Mgra** = marginal grass, **Tur** = turbidity, **Wd** = water depth. (ns = non-statistically significant at the 5% level of probability)

Table 6. Intra-set correlations between each of the site variables and Canonical Correspondence Analysis axes 1 and 2 for adult Anisoptera and Zygoptera species and site variables sampled over two years across all five elevations.

Odonata/ Environmental Variables[a]	Anisoptera		Zygoptera	
	CCA axis 1	CCA axis 2	CCA axis 1	CCA axis 2
Eigenvalues	–	0.319	0.318	0.127
Mfor	-0.1912	0.3923	-0.5049	0.3524
Fsv	-0.279	0.3370	0.2001	0.0900
Mgra	-0.6625	0.1082	-0.5586	0.2150
Erock	0.1777	-0.0413	-0.0947	0.5153
Marsh	-0.2967	-0.1065	0.0274	0.2826
%Sh	-0.5394	-0.3895	0.5454	-0.2373
Wd	0.1248	-0.1075	0.0642	-0.2924
Tur	0.0261	-0.2375	-0.5051	-0.0390
pH	-0.5495	0.2382	-0.7604	-0.0177
At	-0.1793	-0.0333	0.0526	-0.0476
Mhsr	0.1714	0.0286	0.0490	-0.1449
Flow	0.0776	0.1496	0.2145	-0.2579
Alt (Elev (m))	0.7523	-0.3495	-0.8522	0.0251
Pcir (m)	-0.2418	-0.3889	-0.29990	0.0141

SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = Cedara (1050 m) and GH (High) = (1350 m). [a]Variable abbreviations as in Methods.

Intra-set correlations of environmental gradients with axes (Table 6) showed that elevation, pH, percentage shade and marginal grasses were highly correlated with axis one for both odonate sub-orders, with marginal forest being an additional correlate to this axis for Zygoptera. Reservoir circumference for Anisoptera and exposed rock for Zygoptera were the only important correlates with axis two in both ordinations. Axes three and four were not important. A summary of weightings attributed to the first two axes of ordinations for Anisoptera and Zygoptera showed that species-environment correlations using CANOCO were strong. The respective eigenvalues, cumulative species variances and Monte-Carlo tests for CCA are given in Table 7. With a cumulative percentage variance for species data and for species-environment relations of 89%, it meant that measured site variables were probably responsible for the main variation in species patterns for Anisoptera. A Monte Carlo permutation test of probability further strengthened this inference as the first axis (Ax1: $F = 5.98$; $P < 0.005$) and all four axes (global: $F = 3.140$; $P < 0.005$) were highly significant. A cumulative species variance for species data and for species-environment relations of 39.9% for Zygoptera suggests that measured site variables accounted for little variation in species assemblage distribution patterns for this taxon. Although a Monte Carlo permutation test of probability showed that the first axis (Ax1: $F = 1.99$; $P < 0.01$) was significant, the overall test using all four ordination axes (global: $F = 1.75$; $P < 0.4$) was not significant.

Table 7. Summary of weightings of the first two axes of CA and CCA for both Anisoptera and Zygoptera adults sampled during the study in terms of variances accounted for by the two axes. Monte Carlo probability tests of significance are given for the first canonical axis (AX1) and all four axes.

Axes weightings	Anisoptera					Zygoptera				
	CA		CCA		All 4 axes	CA		CCA		All 4 axes
AXES	AX1	AX2	AX1	AX2		AX1	AX2	AX1	AX2	
Eigenvalues	0.457	0.343	0.358	0.319		0.352	0.186	0.318	0.127	
SP-ENC[1]			0.949	0.905				0.954	0.897	
CPVS[2]	28.9	50.6	22.7	42.9		31.7	48.3	28.5	39.9	
CPVS-EN[3]			27.5	52.1				39.9	55.8	
F-Ratio			5.989		3.140			1.992		1.759
P-value			0.005		0.005			0.01		0.4 ns

[1] Species-environment correlations; [2] Cumulative species variance of species data; [3] Cumulative species variance of species-environment relationship. (ns= statistically non-significant at the 5% level).

Discussion

Phenology

Seasonal rhythms with dormant (over-wintering) periods during winter are an integral part of the life history of temperate dragonflies (Corbet 1999). A similar trend was observed in this study, larvae generally being the only developmental stage sampled in winter (June and July). There were no adult and/or teneral species at any elevation except at Mid (BG), where adults of three species (*Ceriagrion glabrum*, *Lestes plagiatus* and *Crocothemis erythraea*) overwintered. Larvae of the dragonfly species sampled throughout this study, occurred (at various stadia) throughout the year at all elevations, but varied in diversity, richness and abundance. This was also the case for temperate regions where the larval stage is the most common over-wintering stage in Odonata (Norling 1984a; Corbet 1999).

Some species e.g. *I. senegalensis, L. plagiatus, C. erythraea*, and *T. stictica* appeared to have several distinct generations per year. This may be the case when the larval population is provided for by the synchronised return of adult residents, and oviposition occurring early enough to allow more than one generation in a year (Corbet 1999). Other species appeared to have a general overlap of larval cohorts. Nevertheless, there were still noticeable peaks in adult emergence for some species, with three distinct seasonal categories of species peaks appearing at all five elevations: 1) Spring peak (September–November), 2) Summer peak (early: December-March), and 3) Autumn peak (April-May).

Species with adult occurrence peaking in spring and/or summer probably overwintered between June and August as final-instar larvae or intermediate stadia, resuming growth to subsequent higher-instar larvae as favourable climatic conditions

and food became available from September. Autumn species perhaps over-wintered as eggs e.g. members of the family Lestidae (Corbet 1999; Norling 1984a), or as early-instar larvae. The subtropical Anisoptera species studied here were generally elevation-tolerant, univoltine, yet had prolonged emergence. In contrast, most Zygoptera were multivoltine, although also highly elevation tolerant.

Since climatic changes associated with seasons act locally and its effects are most apparent on the level of populations and metapopulations (McCarty 2001), many factors may have accounted for species temporal variations e.g. 1) mean annual precipitation as it affects the long-term quality and quantity of water available (Dent et al. 1989; Pinhey 1978) with rain in this study falling in summer, 2) as there are temperature irregularities usually attributed to topographical variation (Schultze 1997) in this study area, this may have resulted in warm coastal climate with high precipitation levels versus the cooler climates at higher elevations, or, 3) simple chance migrations could also have caused variation.

Aspects of dragonfly species adaptations in the sub-tropics

The centre of biogeographical distribution of a dragonfly species is very important in determining the number of generations the species can go through in a year (Corbet 1999). Most dragonflies colonising the temperate zone for example, have evolved a life cycle where winter is spent in the larval stage.

Usually a large number of stadia is a means of resisting cold (e.g. Paulson and Jenner 1972; Norling 1984b). It is possible that the first step in the colonisation of the temperate zone has been to evolve a mechanism where the larval stage coincides with the adverse season. According to Corbet (1957a,b; 1964) and Norling (1984a), two important ecological demands are imposed upon aquatic insects like dragonflies in temperate climates. These include the need for all members of a population to pass the winter in a stage resistant to cold, and the need for the adult, reproductive stage to be restricted to the warm season. Also, there is the subsidiary need for the adult stage to be restricted to a certain period in the warm season so that competition with sympatric species may be reduced. All these demands involve conspecific synchronisation and the reduction of temporal variation at certain stages of development. Larval photoperiodic responses, interacting with temperature, also provide the framework for seasonal regulation (Norling 1984b; Suri Babu and Srivastava 1990).

Although this study was carried out in a sub-tropical region, relatively close to the tropical centre of species distribution, species temporal trends reflected some aspects of synchronisation, as with their temperate counterparts. Both the temperate and sub-tropical regions are characterised by four seasons with cold or cool winters. In contrast, the larval lifespan is very short in the tropics, where growth is usually rapid and the adult life often fairly long, bridging the dry season (Happold 1968; Gambles 1960; Corbet 1999; Hassan 1981; Van Huyssteen and Samways 2009). This is perhaps because of reduced fluctuations in environmental conditions (especially temperature)

leading to unsynchronised odonate emergence, and the fact that long-lived dispersal stages are probably a prerequisite for species which inhabit temporary pools in the tropics.

Most odonate species sampled here were on the wing for about nine months of the year, from September to May/June, and showed marked monthly variations in richness and abundance during this flight period. Thus in these sub-tropical species, the over-lapping generations show similarity to their tropical counterparts by long adult flight periods (Parr 1984), yet like the temperate species in overwintering as larvae.

Furthermore, species that regularly move between habitats may need to adjust to climate changes that are occurring at different rates in different areas, such as between high, medium and low elevations (Inouye et al. 2000). Overall, the subtropical species studied here are characterised by wide elevational tolerance, as well as long flight period with overlapping generations. However, this does not mean that these species are toler-ant of the full 3000 m elevational range, with the Alpine zone being very species poor (Samways 1989a, 1992).

Biogeographical implication of elevational tolerance

Overall, odonate species richness ranged from 24 to 27 species between 301 and 1350 m a.s.l. However, below this (<300 m (SB)), richness increased to 31 spe-cies. Factors that may account for the high numbers of species at low elevations include high primary productivity (Connell and Orias 1964), increasingly benign, less variable and predictable environments (MacArthur 1975; Thiery 1982) and in-creased resource diversity (Gilbert 1984). Other processes (competition, predation and evolutionary time) may have also influenced species richness. Also, besides the advantages of a warm climate promoting larval development, the Low (SB) eleva-tion site also, predictably, had a wide range of habitat types. Additionally, there are no mountain chains that might otherwise prevent either temporary or permanent movement south from the species-rich northern areas, thus maximising regional recruitment.

The influence of elevation on distribution patterns can also be highly dependent on latitude (Corbet 1999; MacDonald 2003; Koleff et al. 2003). This is illustrated by species which are found at progressively narrower elevations farther south. For in-stance, the intolerance of low temperatures by tropical species (e.g. *Tetrathemis polleni* in southern Africa) causes them to contract their southern range into a narrow lowland strip, extending down the eastern seaboard of southern Africa which is warmed by the south-moving Agulhas current.

Most species sampled were widespread and common African species. However, three (6.4%) of species sampled were national endemics, accounting for just 13.6% of the total South African odonate endemics. *Pseudagrion citricola* and *Africallagma sapphirinum* occurred only at the High (GH) elevation, while *Agriocnemis falcifera* was across all elevations, suggesting that regional endemism does not necessarily equate to

elevational intolerance (Fig. 7). Interestingly, like the non-endemics, two of these are relatively common, with only *A. sapphirinum* being rare.

Although climate is important to odonate development, assemblage variation and geographical distribution, local factors (e.g. vegetation structure and composition) are also significant in this geographical area as well as elsewhere (Steytler and Samways 1995; Samways and Steytler 1996; Osborn and Samways 1996; Niba and Samways 2001). Furthermore, water depth is also important for larval stages (Samways et al. 1996). Most adult species here responded to sub-sites reflecting pH, open sunny versus shady and waterfall (flow) versus still water conditions. Influence of regional and local conditions were seen for example in *Notiothemis jonesi* which occurs only at the shady lower elevation gradient of Mid-low (KL).

Zygoptera species were more strongly elevation dependent than Anisoptera species. *A. sapphirinum, A. elongatum, P. citricola, L. tridens* and *Azuragrion nigridosum* were highly elevation-sensitive species. Elevation-tolerant species were *L. plagiatus, I. senegalensis, C. glabrum, A. falcifera, Pseudagrion massaicum, P. salisburyense* and *P. kersteni*. As well as this regional response, there was also a local response. Zygoptera species mostly showed a higher degree of habitat specificity than the Anisopteran species. *Allocnemis leucosticta,* a South African endemic, for example, was restricted only to SS4 and 5 at the Botanical Gardens. One reason for this appears to be that Zygoptera are generally less vagile than Anisoptera.

Implications of results for dragonfly response to global climate change

South African dragonflies are extremely sensitive to fluctuations in water levels, with great fluctuations being impoverishing to the odonate assemblage (Osborn and Samways 1996). Furthermore, the geographical area where this study was undertaken is subject to great variations in rainfall from one year to the next. Floods can be severe, yet the odonate assemblage can recover within a year (Samways 1989c), indicating its great resilience in this El Niño-prone area. This means that the effects of global climate change will possibly be two-fold. Firstly, changes in temperature per se would appear, from these preliminary findings, not likely to have a great affect upon the assemblage. This is because the species involved, even the endemics, are vagile and opportunistic, and will simply colonize the habitats at the appropriate elevations. Secondly, but in contrast, the colonization process will depend greatly on the constancy of the water levels in the water bodies. While increased rainfall and flooding are likely not to be detrimental, any prolonged dry period is likely to be harmful. However, unless there is a prolonged and extreme drought, coupled loss of all local water bodies, there will almost certainly be remnant pools. Such pools would act as source habitats from which these resourceful species will disperse to new pools once the rains have returned (see Samways, this volume).

Acknowledgements

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RESEARCH ARTICLE

Southern dragonflies expanding in Wallonia (south Belgium): a consequence of global warming?

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Abstract

The occurrence of seven southern Odonata species has been watched in Wallonia over the last two decades (from 1981 to 2000). They have clearly expanded in the meantime and this pattern is still highly significant when the data are corrected for the increase of sampling efforts. Moreover, reproduction evidences have been collected recently (from 1993 onwards) for all these species and several settled and have now resident populations in Wallonia. In a second step, all present regular and irregular resident species of Wallonia were looked for change in range size and observation rate per visit between two six years periods of a survey and monitoring scheme, from 1989 to 2000. Analysis was achieved on grid cells visited at the right time at both periods, a procedure designed to neutralize the spatio-temporal heterogeneity of sampling. The comparison of results in relation to the distribution types of species and their habitat preferences show a significant global trend toward an increase for southern species during the investigated time interval, contrasting with other groups of species. If there is a tendency to rise for species preferring eutrophic still waters, this proves to be clearly due to the southern species sub-group, the other dragonflies of this habitat type showing a stable or even decreasing trend. Three distinct hypotheses are examined and discussed as possible explanations of the expansion pattern of southern species: (1) global warming, (2) change in aquatic habitats, especially eutrophication, and (3) intrinsic population dynamics. The rise of temperatures appears to be the main factor explaining the observed expansions.

Keywords

Odonata, range shift, climate change, aquatic habitat change, eutrophication, Belgium

Introduction

Climate has proved to change rapidly during the last century, with the rising of global temperatures, and this warming has proved already to bring about significant impacts on earth's life (Hughes 2000; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003).

One of the main expected responses of organisms to changing climate is to shift their geographical range poleward. Insects are likely to be particularly sensible to climate change and there have been actually many publications showing evidences of poleward range shifts in insects, especially butterflies (Parmesan et al. 1999; Hill et al. 1999, 2001, 2002; Warren et al. 2001; Ryrholm 2003), but also other groups like syrphids (Reemer et al. 2003). For dragonflies, reports of range shifts are plentiful in Europe as well as in America (Ott 2000 and 2001; Parr 2003) or Japan (Aoki 1997) but quantitative studies are still rare (De Knijf et al. 2003; Hickling et al. 2005).

To be properly appreciated, range shifts have to be looked at large scale, a continent scale ideally, in order to monitor as well southern as northern boundaries of species geographical distributions (Parmesan et al. 1999; Parmesan and Galbraith 2004). This can be watched also in latitudinaly extended countries like in Great Britain (Hill 1999, 2002; Warren et al. 2001) or Sweden (Ryrholm 2003). However, range shifts have been also inferred from abundance changes of warm- vs cold-adapted species within local communities which have proved to contribute also to a 'coherent fingerprint' of climate change impacts if examining overall patterns (Parmesan and Yohe 2003). The present study takes place between these two extremes, as it refers to a rather small region (Wallonia area = 16844 km^2) extending over about 180 km (1°20') in latitudinal height, lying around the middle of western Europe. I used the data gathered during two decades about Odonata by the *Gomphus* Working Group in the perspective of distribution atlases and population monitoring.

A range/abundance shift observed for a single species in the direction predicted by climate change may suggest its influence but, alone, doesn't demonstrate it. Indeed, other causes can lead to the same result and several species may potentially move in diverse, even opposite, directions, in a particular region of the world. Therefore, it is needed to search for overall trends deducted from many species and address different alternative hypotheses and their predictions, before to conclude that climate change is the main driving force (Parmesan and Yohe 2003; Parmesan and Galbraith 2004). Apart from climate change, two other main causes can be *a priori* put forward to explain range or abundance shifts in Odonata, as those in most organisms (Warren et al. 2001; Parmesan and Yohe 2003): (1) habitat or land-use change and (2) intrinsic population dynamics, driven by (eventually unknown) species-specific factors. Eutrophication appears to be an important process which induced profound and widespread modifications in aquatic habitats. It is particularly the case in industrialised regions during the XXth century due to discharge of domestic sewage and excessive use of manure in modern agriculture (Jefferies and Maron 1997). It is regarded also as one of the main threat for many Odonata species in north-western Europe (Corbet 1999; Kalkman et al. 2002). This phenomenon could have favoured southern dragonflies, as

it is known that southern species are more linked to eutrophic waters while northern ones thrive preferably in oligotrophic ones (Corbet 1999).

In this paper, I firstly gave a synthetic view of the apparent status change of seven southern species during the last two decades in Wallonia, addressing the question of the confounding effect of recording increase. Then, I measured trends in occurrence for 59 regular and occasional breeding species between two periods from 1989 to 2000, with a method minimizing the impact of spatio-temporal variation of sampling efforts. Finally, I compared these trends in relation to the distribution types of species and their habitat preferences, in order to evaluate the potential roles of global warming, water habitat modification (eutrophication) and intrinsic population dynamics on the observed frequency changes.

Material and methods

Dragonfly data

Biogeographical information about Odonata has been regularly recorded since at least the beginning of the eighties in Belgium, thanks to the *Gomphus* Working Group, formed in 1982. Volunteers have been stimulated to collect field observation data with the aim to produce comprehensive atlases (Michiels et al. 1986; Goffart et al. 2006). As a matter of fact, there has been a clear increase of dragonfly watching during the next two decades. In Wallonia, an important step has been the start, in 1989, of the so called «monitoring scheme », which is more a continued survey (Goffart 2006): on average, around 1700 individual records (unique combination of one species - place - date) were gathered every year from 1989 to 2000, against around 400 between 1981 and 1988 (Fig. 1). The records of rare and difficult species were submitted to a ratification process, based on field descriptions, photographs or voucher specimens. Since all the species identified on a particular place were generally mentioned on the data sheets, the relative frequency of the species in the data set are thought to be close to that in the field.

Conversely, the data available for the period before 1981 are more scattered and originated mainly from insect collections or literature, sources generating biased frequencies, with typically, an overestimation of rare species. Therefore, they were not considered here for comparison and quantitative analysis with subsequent data.

In all, since the beginning of the search for dragonflies, during the XIXth Century, 66 species have been listed in Wallonia, from which 61 have been recorded from 1981 to 2000.

Trend analysis

Variations of recording efforts over time and space are a general problem with biological atlas data (Dennis et al. 1999). So, there is a need to counter theses sampling biases when
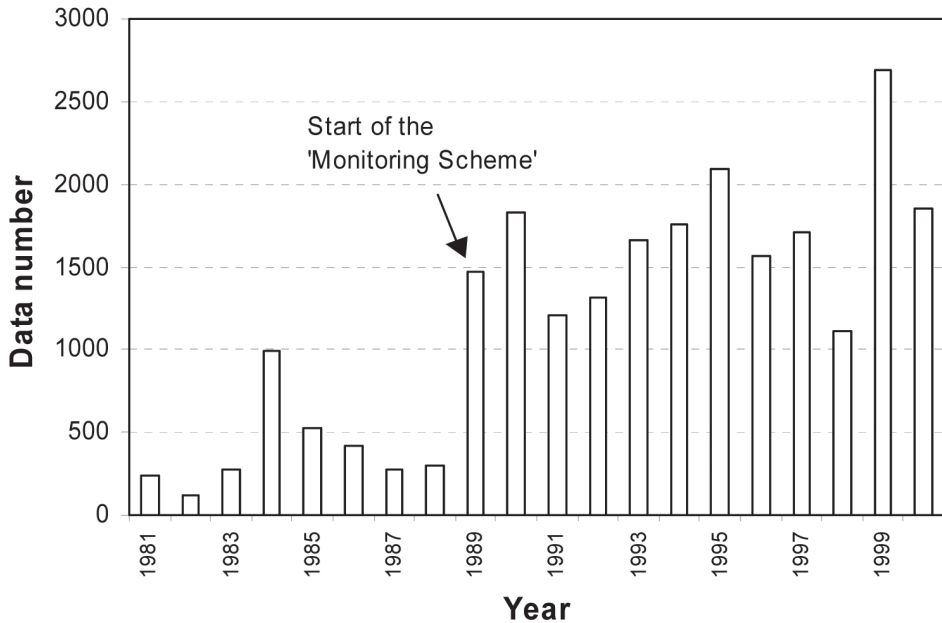
Figure 1. Temporal pattern of data gathered by the Gomphus Working Group during the last two decades.

quantifying change in range size, spatial frequency or abundance (Telfer et al. 2002). Here, an adapted procedure was developed, combining elements from earlier methods (Stroot and Depierreux 1986; Telfer et al. 2002; Warren et al. 2001; Thomas et al. 2004) and new ones.

First, only the more numerous data collected since the start of the Monitoring Scheme were used for the analysis (from 1989 to 2000). Second, I divided this period into two periods of six years (called p1 & p2) for subsequent comparisons. Then, I selected the grid cells (of 1 km square) which were sampled at both periods during the main flight period of each species. On that selection, i.e. a sub-sample of the original data, I calculated the differences in (1) the number of grid cells of 1 km square with observation (UTM1) and (2) the observation rate per visit (OBS), which were converted in percentage change (from the first period). The variable UTM1 evaluate the range size and spatial occupancy, when the parameter OBS add to these a component dealing with species persistence and abundance within individual grid cells. Finally I applied goodness of fit tests (G-test with William's correction – Sokal and Rohlf 1995; H0: ratio of 1:1 between p1 and p2) comparing both different variables for each species. These data selection and analysis processes have been conducted with SAS System (SAS Institute Inc. 1999).

Comparisons among species

Groups of species were distinguished according to (1) their general distribution in Europe and (2) their main habitat type preference, with the aim to compare their global

trends and to separate the potential influence of climate versus habitat changes on the changing frequency of our dragonfly fauna.

For these purposes, species were classified into five "distribution type" categories, according to the relative position of the centroïd of their european distribution area (as given by d'Aguilar and Dommanget 1998 and Bos and Wasscher 1998) towards Wallonia: southern species (n = 15), mid-european spp. (n = 34), northern spp. (n = 7), eastern spp. (n = 2), montane spp. (n = 1) (see appendix for individual species' attributions). Similarly, they were classified into five "main habitat type" categories: eutrophic still waters species (n = 18), mesotrophic still waters spp. (n = 17), oligotrophic still waters spp. (n = 5), rheophilic spp. (n = 9), ubiquist spp. (still and running waters) (n = 10) (see appendix).

Because of being widely skewed, distribution of trends (as measured by percentage of change) were submitted to non-parametrical tests (with SAS System), to test hypotheses of (1) median diverging from zero (sign test) and of (2) medians differing between groups of species (median test).

Results

Southern species with changing status

For seven southern species which were former rare, there has been an increasing number of observations during the last two decades (Fig. 2a). The data were still very restricted during the eighties, and very much more numerous during the second half of the nineties, from 1994 onwards, years which experienced summer heat records. The number of species concerned has clearly increased too. The pattern is globally similar when using relative frequency rate of observation (Fig. 2b), behalf of the first bars which are higher than before the correction due to low sampling efforts before 1989. The observations of these seven 'new colonists' species are still, proportionally, more than four times higher in the nineties than in the eighties (G-test of independence, with William's correction: Gadj = 60.3, 1 df, P < 0.001).

Table 1 gives a synthetic view of the observations done about these seven rare southern species, by decreasing order of frequency. Six of these species had been already noted before 1981: some individuals were already catched during the XIXth century, during hot summers and at least two of them reproduced sometimes, as reported by de Selys-Longchamps, namely C. scitulum and S. meridionale. Evidences of successful reproduction exist now for all these species, even if casual for some. *Crocothemis erythraea* is one of the first and most numerous of these new colonists noted in Belgium and is now a regular breeder on still waters in Wallonia (Fig. 3a). *Lestes barbarus* has appeared later but also in great numbers; its establishment seems less stable however than *C. erythraea*, and a decrease is worth to notice in the last years (Fig. 3b). Like as for other species, true waves of migrants have been noticed some years in Wallonia, as in other countries of north-western Europe, generally
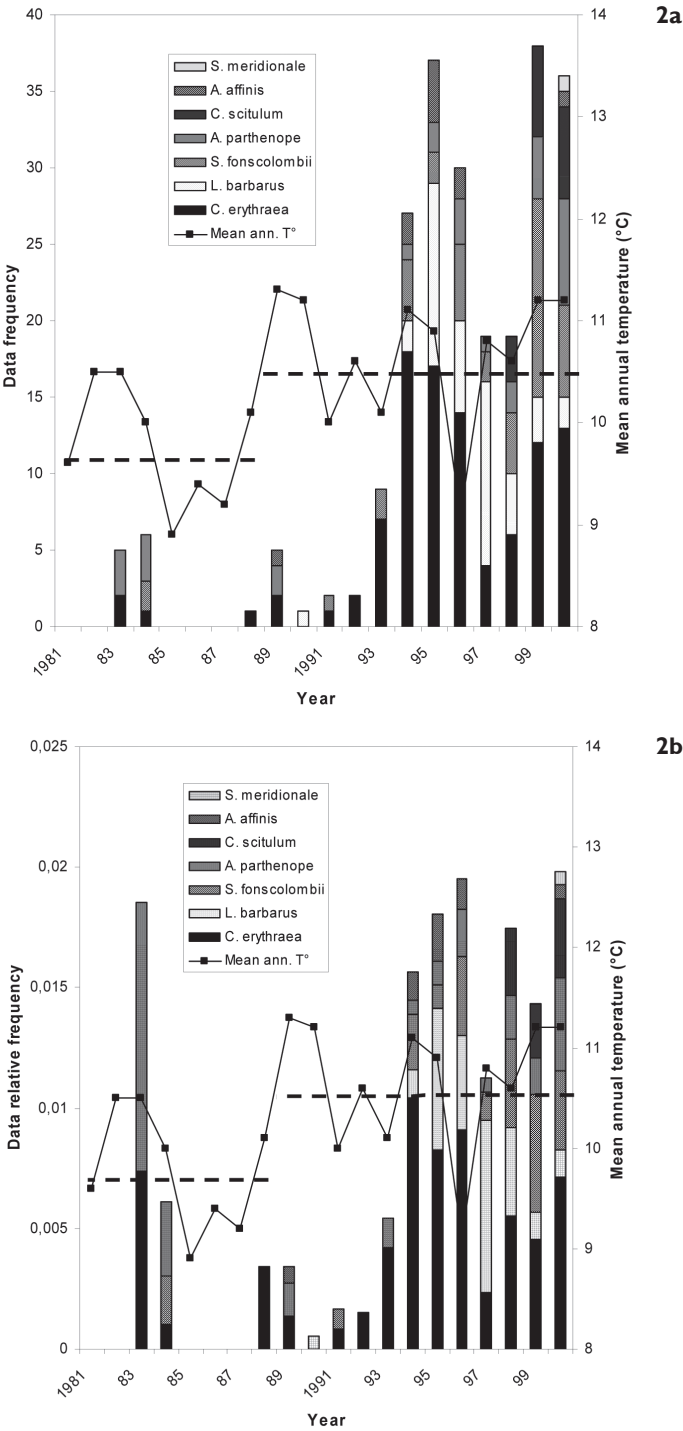
Figure 2. Temporal pattern of observations of seven southern species in Wallonia during the last two decades (period 1981 – 2000). **2a** Observation number **2b** Relative frequency.

Table 1. Data frequency of seven Southern Odonata species in Wallonia during the last two decades. First date and type of reproduction evidences are indicated for each species.

Species	Data				First reproduction reported
	before 1980	1981–1990	1990–2000	Total	
Crocothemis erythraea	yes	6	94	109	1993 (egg-laying, emergences)
Lestes barbarus	yes	1	41	48	1996 (egg-laying, emergences)
Sympetrum fonscolombii	yes	2	39	51	1998 (egg-laying, emergences)
Anax parthenope	no	8	20	28	2000 (egg-laying, >1 year population)
Coenagrion scitulum	yes	0	15	23	1999 (egg-laying, >1 year population)
Aeshna affinis	yes	1	9	13	1995 (>1 year population)
Sympetrum meridionale	yes	0	1	9	2000 (emergence)
Total (southern spp.)	6 spp.	18	219	237	
Total (all spp.)	3345	6436	16956	23392	

during periods of hot and humid winds from the south (sirroco) (Ott 2000, 2001; Parr et al. 2004).

The data about these species are distributed all over the territory of Wallonia, but more species have been observed in the hottest regions like Lorraine, Fagne-Famenne and the Hainaut and Brabant provinces (Fig. 4). Appearances were in general very sudden and wide over the territory for most species, and a slow geographic progression taking several years has been noticed for only one species, *Coenagrion scitulum* (Vanderhaeghe 1999; Goffart 1999, 2000, 2001).

Trends of the southern species

The results of the analysis made on all the southern species known in Wallonia are summarised in Table 2. Eleven species, out of 14, show a positive trend in terms of the number of grid cells occupied between both periods, against one with negative trend and two with a stable situation. The global median of their trends (+81%) differs thus significantly from zero (sign test: P = 0.0063). The same is true when looking at their observation rate per visit with twelve positive trends and two negative ones (median = + 82%; sign test: P = 0.0129). However, only six species show a significant increase of at least one of both variables, probably because of too low absolute numbers of grid cells or observations. Only one species seems to decline, *Orthetrum brunneum*, a pioneer species, but the figure is not significant for the change in UTM1 and significant only at the level 0.1 for the change in OBS. *Coenagrion mercuriale* is also unique by the fact that it presents a positive change for one variable (UTM1) and a negative one for the other (OBS), both insignificant.

When pooling all 14 southern species together, there were 62% more grid cells occupied during the second period to compare to the first one (146 in p2 vs 90 in p1; G-test for goodness of fit, with William's correction: Gadj = 13.4, 1 df, P < 0.001) and
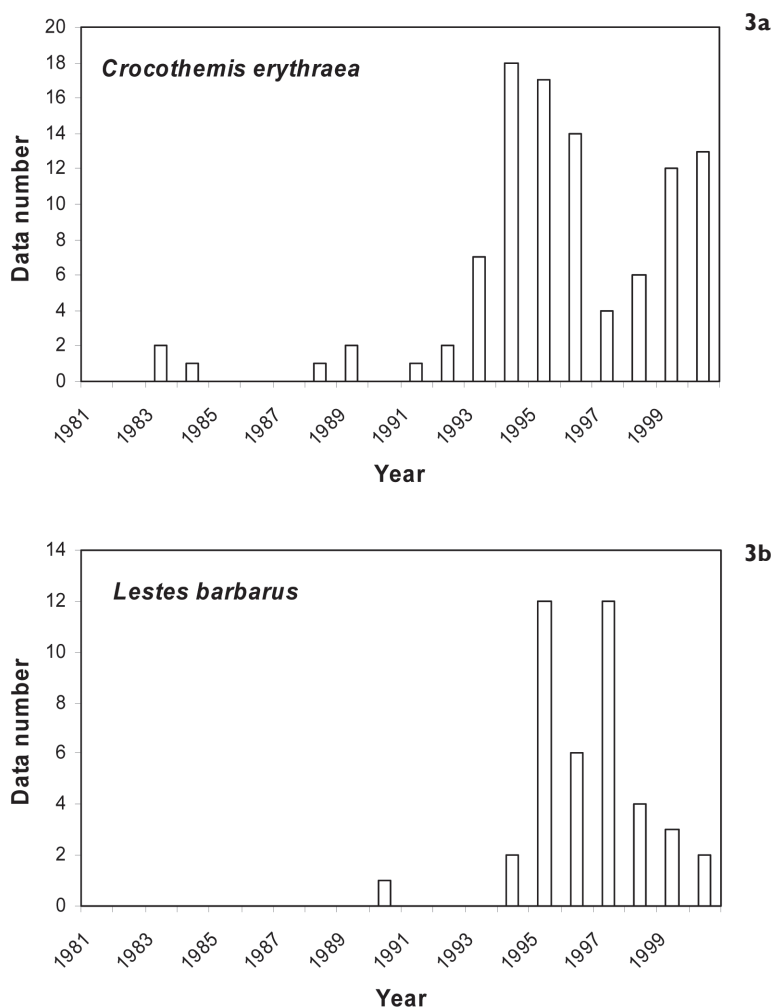
Figure 3. Temporal pattern of records of the two most frequent southern species. **3a** *Crocothemis erythraea* **3b** *Lestes barbarus.*

65% more observations per visit (321/1398 in p2 vs 203/1457 in p1; G-test for goodness of fit: Gadj = 31.9, 1 df, P < 0.001).

Trends comparisons of the whole regional fauna

The comparison of species grouped by distribution type shows that the global trend of the southern species presence differ significantly from that of the other groups, namely the mid-european species and the northern spp., whatever the variable considered, UTM1 (median test: X2 = 7.9, 2 df, P = 0.019) or OBS (median test: X2 = 11.22,
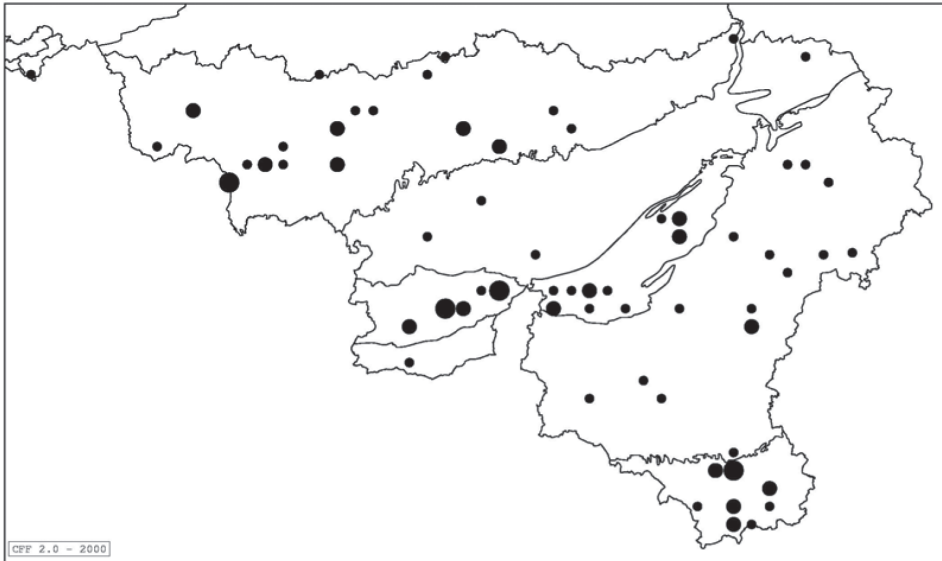
Southern species (total: 7 spp.)

● > 3 spp.
● 2 - 3 spp.
• 1 sp.

Figure 4. Distribution of seven new colonising southern species (same as on Fig. 2) during the period 1990–2000. Natural regions are (from north to south): **1** Loess region north of Meuse and Sambre, **2** Condroz **3** Fagne-Famenne, Calestienne **4** Ardenne **5** Lorraine.

2 df, P = 0.0037) (Fig. 5): the first ones are globally expanding when the others are more or less stable or in decline. Note this last trend, although not significant (median UTM1 = -33%, sign test: P = 0.453; median OBS = -31%, sign test: P = 0.125), for the northern species, in particular.

When comparing species groups classified by main habitat type (Fig. 6), the differences are weaker and not significant, probably due to the great variances of species trends in each group. But a tendency is worth to notice: species characteristic of eutrophic still waters show more positive trends, than ones from mesotrophic and oligotrophic waters (the species from the last habitat having a negative median, which do not differ significantly from zero with the variable UTM1 (sign test: P = 1.0) but well with the variable OBS at the level of 0.01 (sign test: P = 0.063)). However, this tendency is not significant, even when pooling mesotrophic and oligotrophic dragonflies together against eutrophic species. Interestingly, the positive trend of the eutrophic species (at least with the variable UTM1 : median = 16%) appears clearly to stem from the southern components of this group (Fig. 7), which is much increasing (median UTM1 = 150 %, sign test: P = 0.0156; median OBS = 307 %, sign test: P = 0.0156) and show highly significant differences with the non-southern subgroup (median test UTM1: X2

Table 2. Change in frequency of 14 southern species in Belgium between the periods 1989–1994 (p1) and 1995–2000 (p2). Comparison of the number of grid cells with observation (UTM1) and of the observation rate per visit (OBS). Statistical significance level (G-test of independence, adjusted): + P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001; ns = non-significant P > 0.10).

NB: three other southern species were not included in this table because of (1) impossibility of evaluation due to insufficient occurences (*Sympetrum meridionale)* or (2) their status of scarce vagrants *(Gomphus simillimus* and *Onychogomphus uncatus).*

| Species	Grid cell nb > 1989	Grid cell nb sampled p1 & p2	Percent change (UTM1)	Sign. Level	Percent change (OBS)	Sign. Level	Trend synthesis
Gomphus pulchellus	142	51	0%	ns	22%	ns	Unchanged
Erythromma viridulum	90	36	61%	ns	70%	**	Expansion
Erythromma lindenii	54	21	900%	***	872%	***	Expansion
Crocothemis erythraea	40	21	45%	ns	85%	*	Expansion
Lestes barbarus	23	11	350%	*	861%	***	Expansion
Orthetrum brunneum	23	11	-22%	ns	-50%	+	Unchanged ?
Sympetrum fonscolombii	20	9	350%	*	466%	***	Expansion
Oxygastra curtisii	16	4	100%	ns	125%	ns	Expansion?
Sympecma fusca	16	7	33%	ns	9%	ns	Expansion?
Anax parthenope	11	6	150%	ns	307%	*	Expansion
Coenagrion mercuriale	10	3	50%	ns	-32%	ns	Unchanged?
Coenagrion scitulum	8	1	1000%	ns	1000%	-	Expansion?
Aeshna affinis	4	5	100%	ns	80%	ns	Expansion?
Ceriagrion tenellum	1	1	0%	ns	10%	ns	Unchanged?

= 11.37, P = 0.0007; median test OBS, X2 = 10.81, P = 0.001). Moreover, the non-southern sub-group is maybe experiencing a decline, as appears from the significant decrease of the observation rate per visit (median OBS = -16.5%, sign test: P = 0.0117).

The whole fauna (all 59 species) appears to be globally stable, as the median trend equal zero with the variable 'number of grid cells of 1 km square with observation' (UTM1)(sign test: P = 0.576) and -2.7% with the 'observation rate per visit' (OBS) (sign test: P = 0.603). There is a good correlation between the changes measured with the variables UTM1 and OBS (Spearman corr. coeff. = 0.677, P < 0.0001).

Discussion

Expansion or sampling increase?

Although there has been a sensible increase of recording effort about dragonflies over the years in Wallonia, especially since the start of the survey and monitoring scheme in 1989, we obtained convincing evidences of a global expansion of southern species during the eighties and the nineties. Indeed, the use of a method of trend analysis coping with the variation of sampling in space as in time and applied on the more
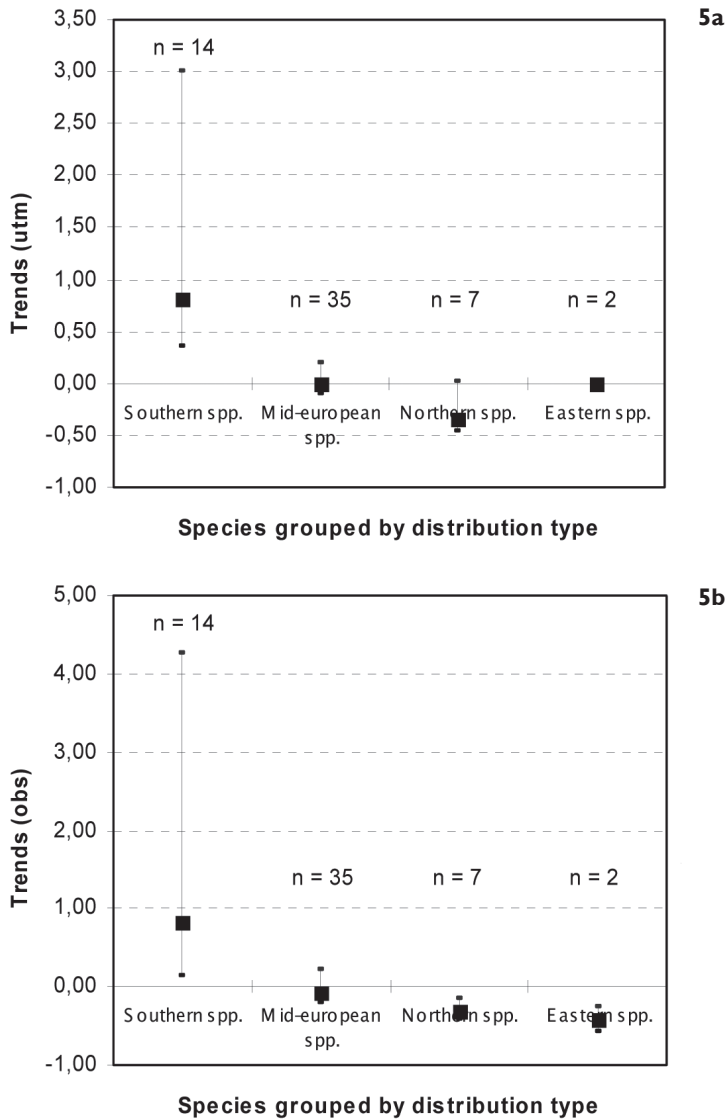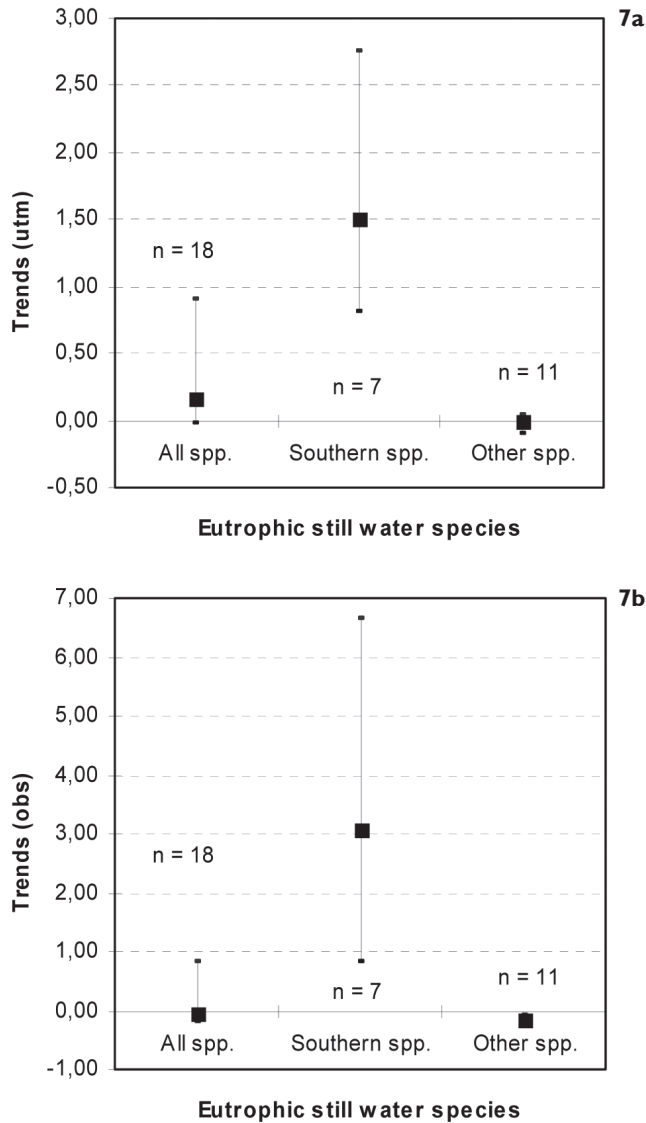
Figure 5. Median trends and interquartile range of 58 species (from 61) grouped by distribution type. The only montane species (*C. bidentata*) is not shown. **5a** Percentage of change in UTM1 **5b** Percentage of change in OBS.

comprehensive data from 1989 to 2000, gave still significant increases for the group of 14 southern species pooled together, from which 13 showed a positive change of at least one of both variables selected, significant for six of them (Table 2). These analyses should be viewed as rather conservative as only the presence of species were considered in grid cells or per visit and not their abundance. For many of these species, numbers on sites rose also, as their frequency over the territory.
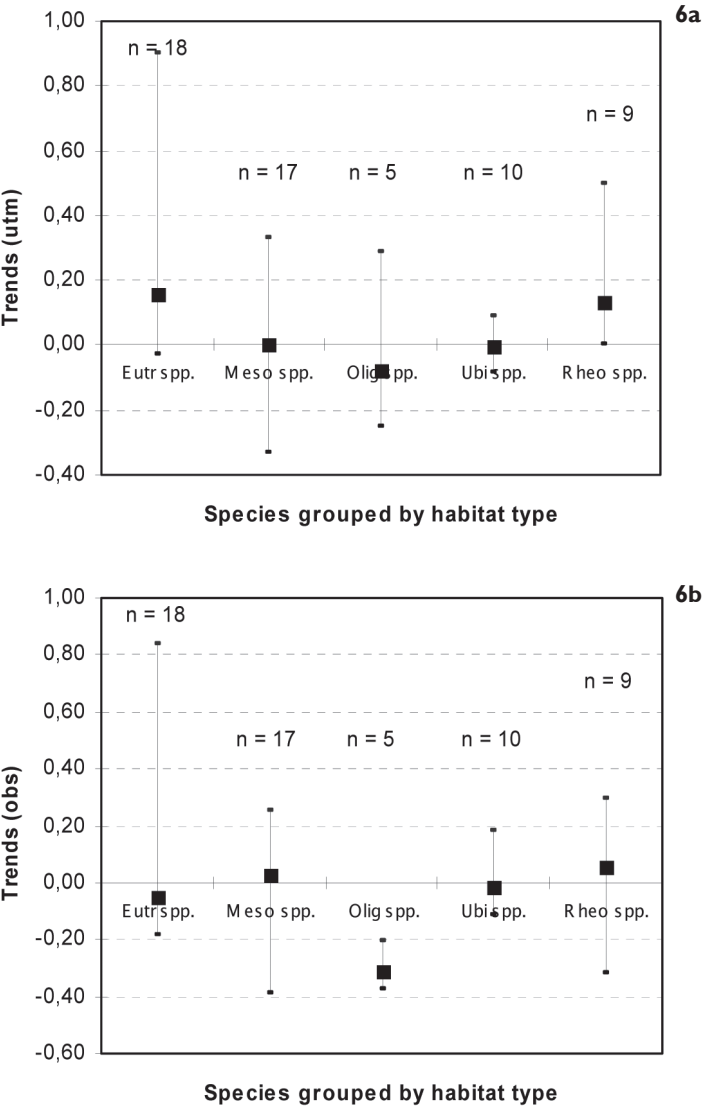
Figure 6. Median trends and interquartile range of 59 species (from 61) in relation to their habitat preferences. **6a** Percentage of change in UTM1 **6b** Percentage of change in OBS.

Incidentally, there is a more obvious indication of the reality of expansions, which is the enrichment in species on particular sites, which have been regularly sampled. For instance, at the lake of Virelles, there were around 23 species observed per year in the early nineties (p1), and about 29 species per year at the end of the same decade (p2). The difference is due to the arrival and establishment of diverse southern species, like *Erythromma lindenii*, *Anax parthenope*, *Crocothemis erythraea* and *Sympetrum fonscolombii*.

Figure 7. Median trends and interquartile range of eutrophic species (n = 18) dissociated in southern ones (n = 7) and non-southern ones (n = 11). **7a** Percentage of change in UTM1 **7b** Percentage of change in OBS.

Patterns of change in southern species

In which concern the seven new colonists (Fig. 2), two of them (*A. parthenope* and *S. fonscolombii*) are well known as migratory species: they can take advantage of rising air currents to ascend to higher altitudes and then be carried by winds for long distances, probably about several hundred kilometres (Corbet 1999). They were often noticed together on the same sites, the same day, in southern Belgium as in the neighbouring regions, often after events of warm humid southerly winds (Parr

et al. 2004). Along with *C. erythraea*, these species were the first to arrive in Wallonia during the hot summers of 1983 and 1984. But it seems that, in the eighties, these waves of immigrants were not followed by establishment of the species. Similar scenarii probably happened already in the past, as suggested by old records of these species, as early as in the XIXth century. The very quick pattern of colonisation on a wide front of some other species, like *L. barbarus, C. erythraea* and to a lesser extent *A. affinis,* suggest that these southern dragonflies can also travel with winds on rather long distances. However that may be, the new thing of the last decade is that all these species were observed on several consecutive years (except *S. meridionale*) and were able to reproduce, or even establish populations in our region. These changes are paralleled by the evolution of mean annual temperatures which showed also a significant rise during the nineties in Belgium. Similar events have been reported for the same dragonfly species in all adjacent countries of Western Europe (Ott 2000, 2001; Parr et al. 2004). This change of status, from migratory behaviour to residency, has also been picked out recently for several migratory Lepidoptera in Britain, whose arrivals as migrants in the past proved to be strongly associated with temperatures in France (Sparks et al. 2005).

The eight other southern species mentioned in Table 2 were already present before the eighties in Wallonia and all of them had probably resident populations. For six of them, their range size and/or their frequency on the territory increased during the nineties. The only species which apparently decreased during the time interval, *Orthetrum brunneum*, is actually a pioneer species mainly thriving in recently created biotopes in Wallonia: the observed pattern could result from the method used to measure trends, which can record the disappearance of the species on older places but has fewer chances to detect colonisation events on newly created sites (evicted from the analysis if they were not surveyed during the first six years' period). The case of *Coenagrion mercuriale*, with opposite changes of both variables, can be explained maybe by the apparently rather dynamic colonising success of the species during the nineties, but its unstable situation (low persistence or decline) on many new (or old) sites in Wallonia (Goffart et al. 2001).

Table 3. Synthesis of the predictions following from the three explaining hypotheses for changes of species occurrence.

Hypotheses Predictions	Habitat change (eutrophication)	Intrinsic population dynamics	Climate change
Expanding species	Eutrophic spp	No particular group	Southern spp
Decreasing species	Oligo- & meso-trophic spp	No particular group	Northern spp
Temporal synchronisation	Yes, moderately	No	Yes, highly
Habitat selected by expanding species	Eutrophic waters	Diverse waters	Hot waters

Explaining hypotheses

The main predictions that can be formulated from the three potential causes considered *a priori* to explain expansions or contractions of geographical ranges (and increase or decrease of populations) are synthesised in Table 3.

The first one, dealing with the groups of species expected to extend, points obviously in favour of the climate change hypothesis. Indeed, the group of the southern species is the only one presenting a consistent positive trend, which has been observed on most of its species (Figure 5). The group of eutrophic species, even if it shows a slight tendency to rise, has proved to be highly heterogeneous in this matter. Moreover, its trend was clearly brought over by the southern species included in this group (Figure 7). If eutrophication had significantly spread during the twelve years interval and had represented a main driving force for southern species, it should have favoured also the non-southern species eutrophic thriving in this kind of habitat. This was not the case and even some species showed maybe signs of declining numbers in this latter sub-group.

The second line of predictions, related to the declining species, cannot help to discern between hypotheses of climate change and habitat change, but it add to the first ones to disqualify the hypothesis of 'intrinsic population dynamics'. Indeed, there is a tendency for northern species and oligotrophic species to decline, but the trends are not sufficiently consistent: these two groups include few species from which most are in common. Hickling et al. (2005) have found already that dragonfly species were shifting faster at their northern range margin than at their southern margin in Britain, as did also Parmesan et al. (1999) for butterflies at the European scale.

The prediction about temporal synchronisation seems again to point out to the climate change hypothesis, as several southern species have colonised the region in a very short period (a decade) and immigration events sometimes occurred simultaneously during warm summer periods.

Concerning habitats predictions, these have not been yet strictly tested in Wallonia, but it is worth to notice that new southern colonists were found (1) on many kinds of waters, including oligotrophic ones, where breeding has been often noticed, like in sand pools and, most of the time, (2) on thermally favourable regions (Fig. 4) and habitats (sunny and shallow waters that can warm up more quickly during the good season), supporting again the climate change hypothesis.

In conclusion, global warming appears to be the main explaining cause to the observed pattern of expansion of southern species, even if other factors could also have played a role.

Perspectives

From this and previous studies, it appears that dragonflies can be viewed as useful indicator for climatic change effects. This can be assigned to their generally high capacities

of dispersal and movement (Corbet 1999) which make them not too sensitive to the available habitat network (Travis 2003). In contrast, many butterflies will have little opportunity to expand northwards in fragmented landscapes, due to their low mobility and highly specialised requirements, as already shown in Great Britain (Warren et al. 2001; Hill et al. 2002). For the most mobile Odonata, namely the 'migrant' species like *A. parthenope* or *S. fonscolombii*, their movement propensity even give them the ability to track yearly climatic fluctuations and to change their range annually, with quick advance or retreat phases, but with the inconvenience that longer time series are needed in order to distinguish year-to-year variation from the long-term trends.

Further studies will be needed to better investigate the precise link between climate parameters and dragonfly range shifts, population trends, larval development, reproductive success, migration movements or impacts on aquatic communities.

Acknowledgments

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RESEARCH ARTICLE

BioRisk

Monitoring of Odonata in Britain and possible insights into climate change

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Abstract

The history of recording and monitoring of Odonata in Britain is briefly described. Results are then presented which suggest that the country's Odonata fauna is currently in a period of flux, in a manner consistent with the actions of a high-level regulatory factor such as climate change. The ranges of many resident species are shifting. *Leucorrhinia dubia* has recently been lost from southern England, but many species are presently expanding their ranges to the north and west, some (such as *Aeshna mixta* and *Anax imperator*) with considerable speed. In addition to these changes, a number of 'southern' species have started to appear in Britain for the very first time. These include *Lestes barbarus*, *Erythromma viridulum* (which has now become a locally-common resident in southeast England), *Anax parthenope* and *Crocothemis erythraea*. In addition to these distributional changes, some recent trends in flight times are also discussed. Evidence indicates that many species are now emerging significantly earlier than in the past, though trends relating to the end of the flight period are less clear cut.

Keywords

Introduction

The study of Odonata in the British Isles goes back a considerable time; several publications devoted at least in part to dragonflies appeared as early as the end of the 18th century. These included "An exposition of English insects" (Harris 1782) and "The natural history of British insects" (Donovan 1792–1813). Interest in Odonata was

however never as great as that for groups such as birds, flowers or Lepidoptera, and it was not until the time of W.J. Lucas that much in the way of centralised distributional data became available. In his key book (Lucas 1900), Lucas listed the then known localities for each species on a county basis. Cynthia Longfield (Longfield 1937, 1949), later assisted by Norman Moore and Philip Corbet (Corbet et al. 1960) continued to update the available distributional data. Structured monitoring of dragonflies within the UK was finally formalised in 1967, with the establishment of the Odonata Recording Scheme under the auspices of the national Biological Records Centre at Monks Wood, and the first high-detail distribution maps started to become available (e.g. Hammond 1977, 1983). These events partly reflected, but to an even greater extent induced, a substantial increase in the popular observation of dragonflies - a trend that still continues today. In 1983 the British Dragonfly Society (BDS) was formed, and after a period of intense field observations a national Atlas (Merritt et al. 1996) was produced, dealing with observations up to, and a little beyond, 1990. At about this time administration of the Odonata Recording Scheme was formally devolved to the BDS, but the last year or two has then seen something of an extension into a more centralised organisation with the development of the National Biodiversity Network (NBN). This aims to facilitate the exchange of biological information of many sorts by making a wide range of biological records readily available to all over the internet (see the NBN Gateway at http://www.searchnbn.net/). The BDS has been closely involved with this scheme from the start.

Clearly there is a long history of recording Odonata in the British Isles, and although the volume of the older data is perhaps not as great as that for some other biological groups it still provides much useful background information. Coupled to the well-developed modern recording and monitoring scheme, sufficient data is now available to make it relatively easy to detect changes to the region's dragonfly fauna and allow some investigation of the underlying causes. Indeed, with the current BDS membership standing at roughly 1500 (although admittedly not all will be highly active in the field), Britain must be one of the most intensively-recorded countries in Europe, if not the world, as far as Odonata are concerned. In this article many recent developments are described and the possible role of climate change is discussed. In Britain, climate change, whatever its underlying cause, would appear to be very much a reality, with the standardized annual mean Central England Temperature (Manley 1974) having exceeded the 1961–1990 average during nineteen of the last twenty years (Hadley Centre 2008). In England, six of the seven warmest years on record (going back as far as 1659) have also occurred since 1995 (Hadley Centre 2008). Currently, the averaged CET anomaly stands at very nearly +1.0°C (Hadley Centre 2008).

Species recorded from the British Isles

One of the most obvious ways in which a country's Odonata fauna can be affected by climatic conditions is by the direct influence on what species can maintain a presence.

Three species have become extinct in Britain during the last 60 years, *viz. Coenagrion armatum* (last seen 1958; Brownett 2005), *C. scitulum* (last seen 1952, Merritt et al. 1996), and *Oxygastra curtisii* (last seen 1963, Merritt et al. 1996). All three were at the then limit of their European range, and had extremely localised distributions even at their peak, so that they all eventually succumbed to habitat degradation of one form or another. These were thus probably 'chance' events. It is however worth noting that *C. scitulum* was only ever recorded during the period 1946–1952, and it seems possible that it was only a transient resident, initially colonising during the good migrant years of the 1940s (Longfield 1949; Parr 1996) that also saw a number of unusual records from the Channel Isles (Silsby and Silsby 1988).

With the exception of the extinctions listed above, the British Odonata fauna remained relatively stable for an extended period of time. As with many other countries in northern Europe, the last few years have however seen the arrival of a substantial number of new species, many of them having their strongholds in the Mediterranean region. *Erythromma viridulum* was first observed in 1999 and colonised rapidly, with it now being a locally-common resident in SE England (Parr 2004, 2005). *Lestes barbarus* was first observed at a single site in Norfolk during 2002, with records from there and at another site in coastal SE England during 2003 and 2004. Despite thorough searches, the species was not however noted at these sites in subsequent years, although a single individual was found at a third, inland, site in 2006 (Parr 2007). As far as Anisoptera are concerned, there was an unconfirmed report of *Anax parthenope* in the mid 1980s, though it had to wait until 1996 for a substantiated record to be forthcoming. Since then the species has been seen annually, with several hundreds of individuals now having been recorded; during 2000 one even reached as far north as 59°17'N (Parr et al. 2004). Most sightings of *A. parthenope* currently seem to refer to migrants, but successful breeding has been proven at two sites in the southwest (Jones 2000), and has been strongly suspected from several further areas. Confirming that the situation is still evolving, during 2006 record numbers were seen, with ovipositing being reported from at least 5 sites (Parr 2007). Other dragonflies added to the British List in recent years include *Sympetrum pedemontanum* - with one record in 1995 and another 'possible' seen by a member of the public in 2003 (Parr 2004) - and *Anax junius*, where the first European records of this Nearctic species were made in southwest England during autumn 1998 (Pellow 1999). In addition, *Crocothemis erythraea* has also started appearing in Britain in recent years, with 6 records in England since the first sighting in 1995. These records principally refer to single males seen near the south coast (no females have as yet been definitely observed), though there was an unexpected sighting of a sub-mature male in Cumbria, at very nearly 55°N, during 2004 (Parr 2005). Finally, although not strictly directly related to the British mainland, it is worth noting that *Orthetrum brunneum* was recorded for the first time ever from the Channel Isles (on Guernsey) during 2001 (Parr 2002).

In addition to the occurrence of new species, the frequency of appearance of certain more 'normal' migrant species also appears to be changing. *Sympetrum fonsco-*

lombii was for many years regarded as only an erratic visitor to British shores, often apparently being absent for several years in a row (Longfield 1949). In the late 1980s and early 1990s fairly regular records started to come from southwest England, and the species is currently regarded as an expected and often not-uncommon migrant to Britain, with major influxes having been noted in 1996, 1998, 2000, 2002 and particularly 2006 (Parr 2003, 2007). Successful breeding is now also regularly reported (e.g. Parr 2002, 2004, 2007). Although the recent increase in numbers of active recorders must complicate interpretation, observed changes do seem to be real. Thus the related *S. flaveolum*, a migrant of more easterly rather than southerly origin, shows a very different trend to its pattern of records (Parr 1996, 2003).

Range expansions and contractions for resident species

One of the advantages of the relatively long history of dragonfly monitoring in Britain, and its focus on distributional aspects, is that it is now feasible to sensibly analyse range changes of the resident species. As with other countries in northern Europe, it is clear that many species are currently undergoing significant changes to their range. These are mostly expansions, typically to the north and west, but a few species do seem to be contracting their range. Hickling et al. (2005) have provided an overview of changes seen over the period 1960–1995, but there are problems in interpreting some of the data and events have also progressed since the time period they cover. It may thus be worthwhile describing further certain species for which range changes are being seen:

Calopteryx splendens. There is evidence for a recent strengthening and range expansion of the more northerly sub-populations in Britain (Clarke 1999; Ward and Mill 2004), especially since 1990. The role of possible improvements in water quality however remains to be evaluated.

Brachytron pratense. This species declined or disappeared in several areas during the post-World War II period, perhaps in part due to pollution and changes in land use associated with an intensification of agricultural practices. A recovery described by Merritt et al. (1996) and Perrin (1999) has continued, and there have been records from many new areas in recent years. To some extent there has simply been an infilling of range, but in addition there seems to have been an extension into western parts of Wales. The species has also been recorded from a few southern and western areas of Scotland since 1984 (Smith and Smith 1984; Merritt et al. 1996), though may perhaps have been overlooked there previously, since Sélys (1846) reported being shown a specimen from the region.

Aeshna mixta. In older times this species was essentially a scarce immigrant to Britain, though there is circumstantial evidence that it may have been temporarily established in East Anglia at the end of the 19th century (Mendel 1992). A large invasion during 1935 saw records from several areas of southeastern England, and somewhere around this time it apparently started to become increasingly established as a resident

(Mendel 1992). Merritt et al. (1996) describe the gradual expansion of the species throughout southeast and central England up until 1990. Since then range expansion has continued, and seems to be increasing in rate. The species reached Ireland in small numbers during 2000 (Nelson and Thompson 2004), and is now established there, while the first confirmed records for Scotland were in 2004, with reports from at least three sites, one of which was well to the north (Parr 2005).

Aeshna isoceles. In the 19th century this species was found in a few widely-scattered fenland localities throughout East Anglia, but became restricted to the Broadland area of Norfolk and the immediately adjacent part of Suffolk as a result of habitat loss (Merritt et al. 1996). This highly localised distribution warranted the species being afforded legal protection under the Wildlife and Countryside Act 1981. In the 1990s, individuals began to be seen on the Suffolk coastal strip, and ovipositing has been observed here in the last few years. Although these sites are not a great distance from prior strongholds (up to 30 km), the move into a new habitat is of some significance for such a rare and localised species in Britain. Interestingly, while at most of its Norfolk sites the species is apparently associated with the presence of Water Soldier *Stratiodes aloides*, this is not the case in coastal Suffolk. The relationship between this range expansion and the occasional record on the east coast of what might be immigrants of Continental origin (Parr 2004) remains to be established.

Anax imperator. As with *Aeshna mixta*, this is another common species that is now rapidly expanding its range (see Fig. 1A). Before 1982 there were very few records north of 52°55'N, and those mostly referred just to isolated individuals. By the early 1990s the species had however been found in Cheshire and Lancashire, north to about 53°45'N (Merritt et al. 1996), and good populations now exist in these areas. By 1995 it had reached Cumbria (Clarke 2004), and by 2003 records for Scotland (at *ca*. 55°00'N) were forthcoming (Parr 2004). It was first seen in Ireland during 2000 (Nelson and Thompson 2004), and now appears to be established there.

Libellula depressa. Long established in southern Britain, this species has been increasingly noted further north in recent years. The northern limit of its range was at roughly 53°30'N in 1990 (Merritt et al. 1996), but a wanderer or migrant reached very nearly 56°N in Scotland during 2003 (Parr 2004).

Libellula fulva. This species has always been very local in Britain, where it has the vernacular name of Scarce Chaser. Merritt et al. (1996) describe a distribution centred on roughly six scattered river systems and nearby still-water sites in southern and southeast England. The last few years have however seen a number of new areas being discovered (Parr 2005, 2006), including records from an additional four counties. Some of these new sites are up to 100 km away from previously known sites, and extend the overall range to the west and northwest.

Orthetrum cancellatum. This was once at best a rare and localised species in southern England, but in the 20th century *O. cancellatum* became increasingly more widespread and common, perhaps in part due to the spread of flooded gravel workings, which provide excellent habitat (Merritt et al. 1996). Range expansion in both Britain and Ireland has since continued, and a hot weather-related movement during late July/
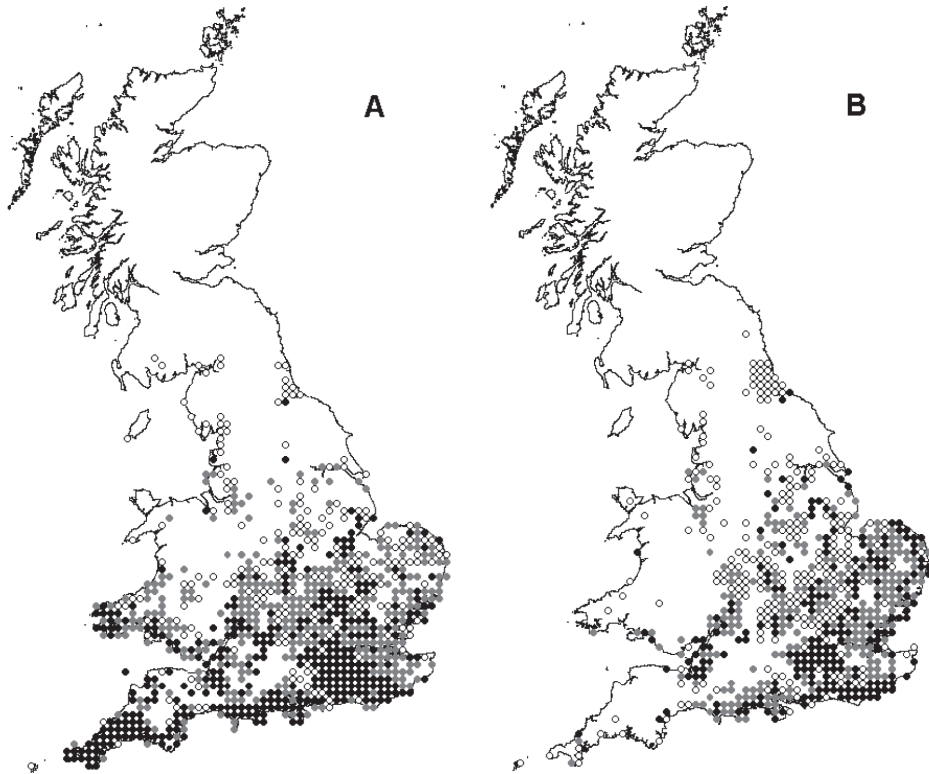
Figure 1. Distribution maps for **A** *Anax imperator* and **B** *Sympetrum sanguineum*. ● First recorded before 1980, ● First recorded 1981–1990, ○ First recorded 1991–2004.

early August 2006 saw the most northerly British records to date, including one from ca. 56°15'N in south-central Scotland (Parr 2007).

Sympetrum sanguineum. Speculation during the 1970s that this species might have been in decline in eastern England was probably exaggerated, earlier records having been biased somewhat by a period of good immigration in the 1930s and 1940s (Merritt et al. 1996). By the late 1980s it was clear that the species was in fact doing well in several areas, and recently the species has been expanding its range rapidly to the north (Fig. 1B). From a northern limit of *ca.* 53° 30'N in 1982, the species has now been recorded right up to the Scottish border, beyond 55° 30'N. Curiously, it still remains rather rare in the far southwest of Britain.

Leucorrhinia dubia. Although the British stronghold of this species has always been in Scotland, there are (or, in some cases, were) outposts in the north of England, the northwest Midlands and the Surrey heaths of southern England. In Surrey the species had been recorded over the years from at least three 10 × 10 km grid squares (Merritt et al. 1996). This southern population is however now extinct, the last individual having been noted at Thursley Common during 1999 (Perrin 2000). Certain other sub-populations have also experienced a decline, in part due to habitat loss (Merritt et al. 1996), though fortunately in places the species continues to do satisfactorily.

Phenology

The British Odonata database now contains nearly 500,000 records, which in addition to allowing the monitoring of distribution, will also contain extensive phenological information. Basic summary data and a preliminary analysis of the effects of latitude and year-to-year variation on phenology have been available for some while (Merritt et al. 1996). More recently, the appointment of a salaried BDS staff-member to work with the database (to ensure that its structure is compatible with the evolving National Biodiversity Network and to extract key data) has facilitated a more extensive analysis of phenological data. It is clear that since 1960 there has been a significant shift in the phenology of the British Odonata as a whole, with species experiencing a continuing advance in the leading edge of the flight period - i.e. they are starting to emerge earlier (Hassall et al. 2007). This correlates strongly with changes in British climate during the same period. On average the forward shift amounts to 1.5 days per decade, though there are indications that spring-emerging species are more strongly affected than those that emerge in summer (Hassall et al. 2007). No general trends relating to the end of the flight period were apparent, perhaps because different species respond differently (Hassall et al. 2007).

In addition to the detailed statistical analysis of the British Odonata database, other approaches to monitoring phenology are also available. For over 15 years, many BDS members have been routinely recording the dates of the first and last sightings of different species in their area, and a database of national 'first' and 'lasts' has been established. Such data has its limitations, but it does have an immediacy that has proved attractive, both for encouraging recorders and for attracting public attention. *Calopteryx splendens* is a useful species to examine in detail. Figure 2 illustrates changes in the dates of reported first and last sightings in Britain over recent years. Although there are a few historic records that are similar to recent extremes, there is a clear trend for the species to now be seen earlier in spring and later into the autumn than before. Indeed in 2005 individuals were recorded between 28 March and 10 October, which is unprecedented for Britain. Detailed analysis of the data is difficult as extreme dates are by definition somewhat atypical, and they are also sensitive to recording effort, with the increasing number of recorders in recent years being more likely to pick up individual rare events. *C. splendens* is however common and relatively large and showy, and is thus readily spotted. It is also easy to identify from a distance. First and last records are therefore less likely to be influenced by observer effects than those for many other species, and it would seem likely that there is indeed an increasing disturbance to what was considered the normal phenology, with both unusually early emergences and either increased adult survival or unusually late emergences now taking place.

Although the analysis of trends in first dates can be problematic, there is one situation where interpretation is easier, namely when one is comparing observations at a single site that has been regularly monitored over many years. Chartley Moss National Nature Reserve, Staffordshire, is one of the major sites for *Leucorrhinia dubia* in England, and the flight period and numbers of individuals seen each year has been closely
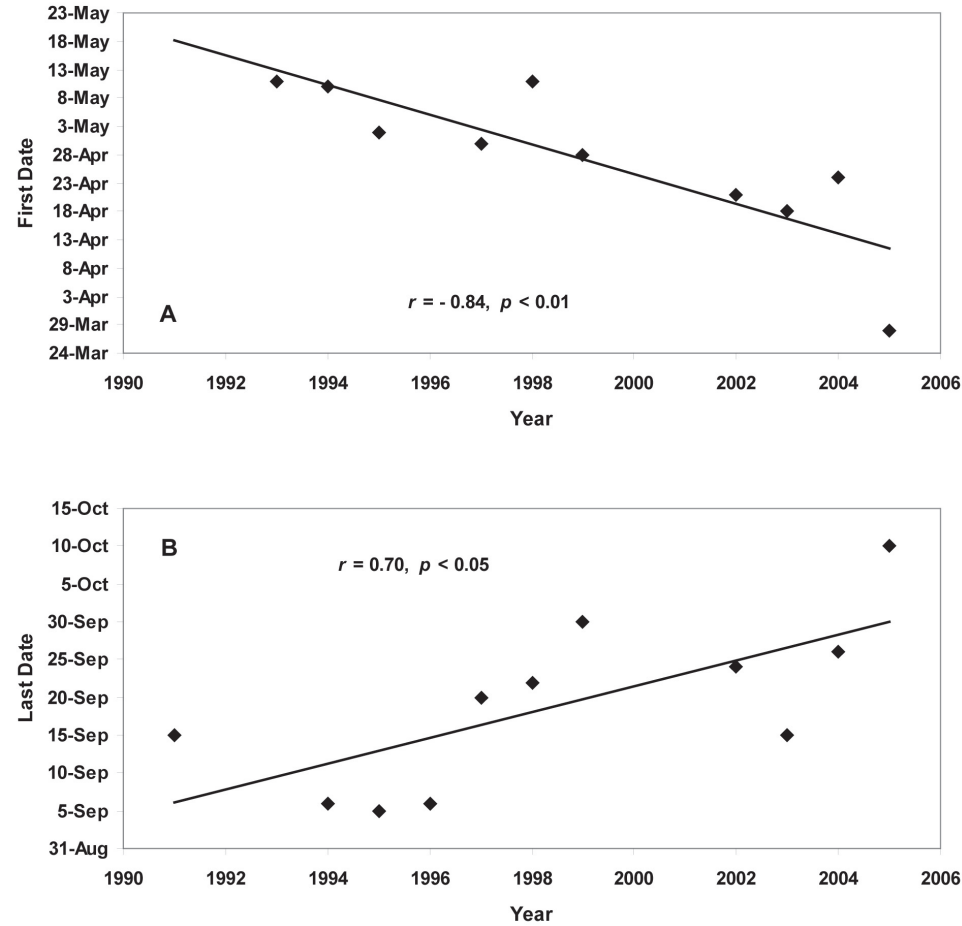
Figure 2. Yearly **A** 'first' and **B** 'last' dates for *Calopteryx splendens* in Britain during 1991–2005.

monitored for two decades. Figure 3A plots the recorded 'first dates' for *L. dubia* during this period; there is a statistically significant ($p<0.05$) trend towards earlier emergences in recent years. Although meteorological data for Chartley Moss itself is not readily available, it lies almost midway between the weather stations of Shawbury and Sutton Bonnington, for which extensive historical data sets exist (Met Office 2006). Analysis shows that over the period of observations at Chartley, both weather stations showed a slight trend towards increases in spring temperature, but this was small in comparison to yearly variation, and was not statistically significant. In itself, such a trend cannot therefore account for the phenological changes. More obvious was an increase in mean annual temperature, with both the mean annual maximum temperature (Tmax) and the mean annual minimum temperature (Tmin) increasing with time. Over the period in question, Tmax showed a mean linear increase of *ca.* +0.06°C per year ($p<0.05$ at Sutton Bonnington, $p<0.01$ at Shawbury - see Fig. 3B), while Tmin showed a mean linear in-
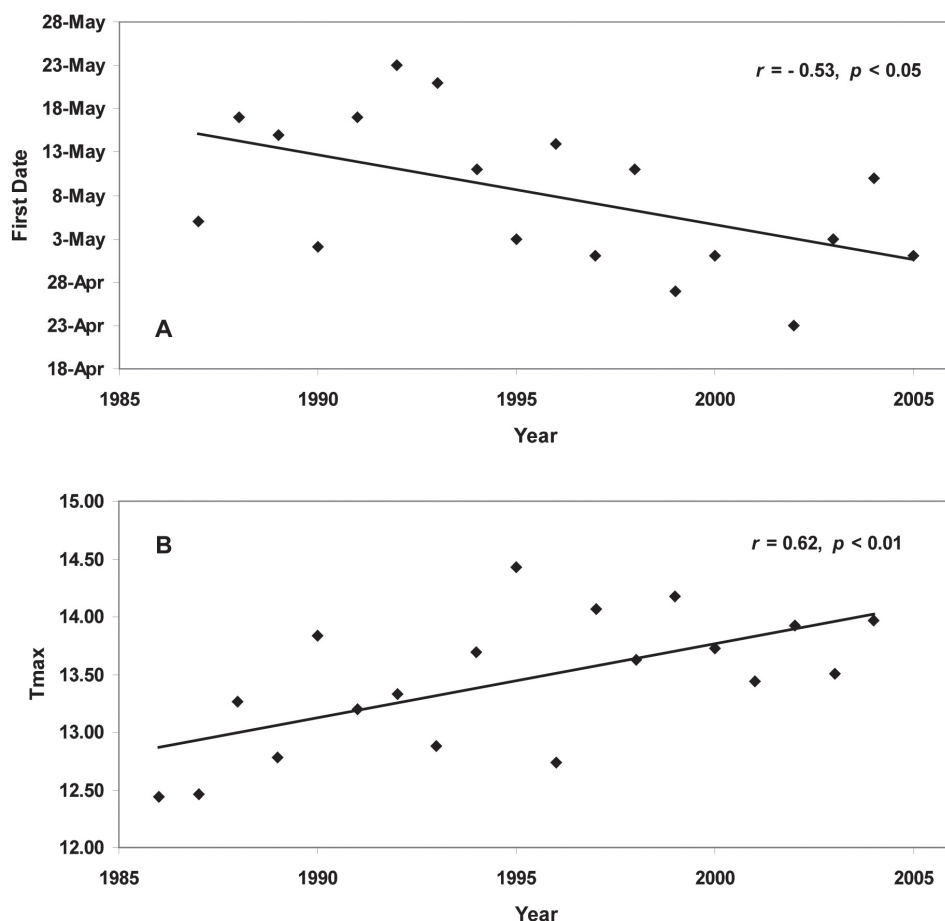
Figure 3. Phenological trends and climate: **A** 'First dates' for *Leucorrhinia dubia* at Chartley Moss NNR, Staffordshire, England, during the period 1987–2005. In most years the site was visited at 2–3 day intervals during the appropriate time period. In 1991–1994 it was only possible to visit weekly, and to avoid bias towards later dates, 'first dates' are here taken as midway between the visit on which *L. dubia* was first recorded and the preceding visit. **B** Mean annual maximum temperatures at Shawbury Weather Station.

crease of *ca.* +0.05°C per year (*p*<0.05). These trends may well account for the observed shifts in spring emergences. In contrast to the results for first dates, the data for late dates was more scattered, principally due to sporadic very late sightings (the latest being 12 October) apparently resulting from unexpectedly late emergences in certain seasons. This could sometimes be linked to poor weather in the early part of the season, but this was not always the case, and perhaps these observations are also of some significance.

In addition to the situation with *L. dubia* alluded to above, other instances of autumn emergences that seem at odds with accepted life-cycle strategies in northern Europe have been documented in recent years. These include September emergences of *Anax imperator* (Parr 1999), the larvae of which are normally considered to have an

autumn diapause to ensure synchronous emergence the following spring (Corbet et al. 1960). In this particular instance the presence of an immigrant population with a different phenology might be one explanation, but further investigation of unexpected autumn emergences might help throw light on changing phenologies in the region. Although such emergences are still rare events, it is, for example, not inconceivable that certain species are starting to show partial changes in voltinism.

Conclusions

It is clear that the British Odonata fauna is currently going through a period of considerable flux:

– Several resident species are currently expanding their ranges, though a few are in regression. Those expanding their range are often species of 'southern' affinity, and are expanding to the north and west, some with considerable speed. The 'northern' *Leucorrhinia dubia* is however contracting its range, having recently become extinct in its southern English outpost.

– Species never before observed in the British Isles are now starting to turn up in the region as they expand their ranges. Again, it is principally those somewhat thermophilic species with a 'southern' distribution in Europe that are involved, although there are exceptions (e.g. the more eastern *Sympetrum pedemontanum* and the American *Anax junius*).

– There is evidence for shifts in phenology, with earlier emergences in spring and at least for some species the suggestion of unusual late season records as well.

In addition to the Odonata, changes are also being observed in the UK for a very wide range of other taxa. Particularly in the case of birds, changes in range and phenology have already been extensively documented (e.g. Thomas and Lennon 1999; Musgrove 2002; Cotton 2003; Eaton et al. 2005). Within the Insect order, it is clear that in addition to dragonflies, several butterflies with a southerly distribution in the UK are also expanding their ranges, though there are signs that habitat limitation may be restricting the number of species involved (Warren et al. 2001). The spread of the warmth-loving sphecid wasp *Philanthus triangulum* has similarly attracted attention (Edwards 2000), as has the spread of the Orthopterans *Metrioptera roeselii* and *Conocephalus discolor* (Thomas et al. 2001). This latter situation is particularly interesting, with the dramatic north-westerly range expansions seen in the last 20 years being facilitated by the increased occurrence of long-winged forms with enhanced dispersive capabilities (Thomas et al. 2001). In addition to these range changes, a wide variety of insect species have recently been recorded in Britain for the very first time. These are too numerous to list fully, but include various moths such as *Thaumetopoea processionea*, *Ochropleura leucogaster*, *Dryobota labecula*, *Spodoptera cilium*, *Platyperigea kadenii* and *Pechipogo plumigeralis* (Waring and Townsend 2003; Clancy 2006), the bee *Bombus hypnorum* (Goulson and Williams 2001), the social wasps *Dolichovespula saxonica* and *D. media* (Edwards 2000), a good variety of Coleoptera including the coccinellids

Rhyzobius chrysomeloides, *Epilachna argus* and *Harmonia axyridis* (Biological Records Centre 2008), and also the hemipteran *Nezara viridula* (Shardlow and Taylor 2004). Although some of these records may represent accidental introductions, many species appear to have reached Britain unaided, in an extension of wider trends.

Since changes being seen in the UK are qualitative as well as quantitative, they cannot simply be artifacts of the increased interest in Odonata and many other areas of wildlife that has taken place in recent years. Rather, the types of change, and their widespread and consistent nature, seem to imply that some high-level controlling variable such as climate is involved, though of course this might operate in a variety of way (e.g. either directly or via effects on things such as habitat quality). Although it is difficult to be precise, recent changes seem to have started in earnest during the 1980s. The early 1980s roughly coincide with the onset (or, more strictly, intensification) of a significant and continuing increase in British, Northern Hemisphere and Global mean temperature (Jones & Moberg 2003; Climate Research Unit, UEA 2008; Hadley Centre 2008). Indeed, for Odonata, the closest historical situation in Britain to that which is currently taking place appears to be the good migrant years of the 1930s and particularly the 1940s (Longfield 1949; Parr 1996). This period was also associated with a phase of steeply rising temperature, though in this case it was not sustained (Jones and Moberg 2003; Hadley Centre 2008). Many current trends would thus appear likely to be linked to climate change.

It will be of considerable interest to continue monitoring changes to the British Odonata in years to come, and the BDS intends to strengthen its resident and migrant recording schemes, develop more detailed studies of dragonfly abundance, and also consolidate its studies on phenology.

Acknowledgements

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RESEARCH ARTICLE

When south goes north: Mediterranean dragonflies (Odonata) conquer Flanders (North-Belgium)

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Abstract

Since 1980, eight southern dragonfly species have been regularly recorded in Flanders. They show a significant increase in relative abundance, relative area as well as indications of reproduction since the beginning of the nineties, with peak occurrence mainly in the 1995–1999 period. Since 2000, numbers are lower but more species were simultaneously present. Three species, *Lestes barbarus*, *Crocothemis erythraea* and *Sympetrum fonscolombii*, show a combination of earlier arrival, earlier reproduction with a higher frequency and higher maximum ranges and can be considered as having stable populations in Flanders. All other southern species show in general a later arrival, only one confirmed or probable reproduction and have much lower maximum ranges. Two other species, reaching their northern limit of distribution in Flanders, *Erythromma viridulum* and *E. lindenii* have clearly expanded their relative area since the eighties. Their relative abundance also increased although this shows more fluctuations.

Keywords

Odonata, dragonflies, range extension, Belgium, climate change, relative abundance

Introduction

Climate change on Earth is causing a growing concern. It is still not fully understood whether this is part of normal global climate fluctuations or mainly the result of human activities. Whatever the cause, it is clear that the rate of warming during the last 30 years has been greater than at any other time during the last 1000 years and atmos-

pheric CO2 concentrations have never been so high (IPCC 2001). Increasing concern over the implications of this "global warming" for biodiversity have resulted in a large amount of studies on a wide array of taxa, communities and ecosystems (Parmesan and Yohe 2003). Ecological responses are already clearly visible on different levels, although in many regions there is an asymmetry in the warming and in the precipitation regimes that undoubtedly will contribute to heterogeneity in ecological dynamics across the system (Hughes 2000; Peňuelas et al. 2002; Walther et al. 2002). As a result of the predicted future increase in global temperatures, between 1.4 and 5.8°C (IPCC 2001; Stainforth et al. 2005), a number of species are expected to shift their ranges in response, rather than adapt to warmer temperatures *in situ* (Huntley 1991).

Among insects, some European butterflies have shifted or expanded their ranges northwards (Parmesan et al. 1999). It is expected that other winged insect species will show similar responses to climate change. However, few studies have focussed on other groups of insects. In particular, there is not much information available on taxa with aquatic larval stages such as dragonflies, and data are often lacking or conflicting (Hickling et al. 2005).

In Flanders (Northern Belgium) the distribution and abundance of dragonflies is well known over a long time (De Knijf et al. 2006). Flanders is situated in Northwest-Europe, somewhat halfway between the Mediterranean region and Fennoscandia. Moreover, it lays in the smallest part of the (Central) transition zone between the so-called Northern and Southern climatic zones, determined by the 18°C mean July temperature and the 2500 degree day (www.worldclimate.com). Therefore, it seems an interesting region to check for changes in fauna composition which could be due to increasing temperatures. Like most insects, dragonflies have short life cycles and often a high reproduction rate and dispersal capacity. They have the ability to react relatively quickly to changes in climate.

The aim of this contribution is to analyse in general to what extend southern dragonfly species have expanded their range into Flanders. In another paper (in preparation) we will threat in more detail the relations between these distribution patterns and climatic and other environmental variables. This will allow us comparisons with the recent analysis of Goffart (2006) for the adjacent Walloon region.

Material and methods

Data sources

Data are derived from the *Gomphus* Dragonflies Working Group's distribution database of Flanders. At the end of 2005 it contained about 55.000 records on 66 species, including historical data going back to the 19th century (Selys 1888). All records up to 2004 were used for the analysis. The Odonata were mapped using Universal Transverse Mercator (UTM) 5×5 km grid squares as units. Special efforts have been made to achieve a good coverage of the territory during the last 15 years. For the more

recent records the database includes information on precise locality, date and number of observed individuals and life-cycle stage (larva, exuvium, teneral, male, female, adult-copulation, egg-laying) thus providing indications of reproduction and/or permanent populations. For reproduction, three categories were considered: confirmed (exuvium, larva or tenerals), probable (tandem or egg-laying) and possible (population with high number of individuals). For historical records however, population and life-cycle information is often lacking or difficult to interpret, in particular from literature sources.

Selection of species

For our analysis we selected 10 species which have their main distribution area in the Mediterranean part of Europe (Askew 1988; d'Aguilar and Dommanget 1998) but are actually present in Flanders (De Knijf et al. 2006). We distinguished two groups:

– group A: 8 species for which Flanders is no part of their historical distribution area (< 1980): *Lestes barbarus* (Lb), *Aeshna affinis* (Aa), *Anax parthenope* (Ap), *Orthetrum brunneum* (Ob), *Crocothemis erythraea* (Ce), *Sympetrum fonscolombii* (Sf) and *S. meridionale* (Sm), and *Coenagrion scitulum* (Cs) although the status of the latter is less clear-cut than for the other 7 species due to its much more fragmented southern distribution range and the probability of its historical distribution area having reached Flanders.

– group B: 2 species that reach in Flanders the northern limit of their distribution range: *Erythromma lindenii* (El) and *E. viridulum* (Ev).

Analysis

To detect general changes in range and numbers, we used Relative Area and Relative Abundance in time per Group (combined), and per species. We define Relative Area in a period as the percentage of different 5×5 km UTM squares occupied by the selected species (or by a group) compared to the total number of different squares occupied by all dragonfly species in that period. A higher percentage does not *a priori* mean a greater "range" (enlargement of occupied territory) as squares can be clustered without really "enlarging" the range. However, an analysis of the distribution maps per species for the different periods (years) showed that higher relative percentages resulted in a real increase of occupied territory. Therefore, we decided to use this as a measure for broad changes in range. Relative Abundance is the percentage of the combined record numbers of a group or species compared to the total number of records. We compared first the data for 8 time periods. To obtain sufficient records, we used two broader categories <1900 and 1900–1949 for the "historical data". From 1950 on, data were grouped in five decades (and one pentade 2000–2004). To better visualize the recent evolution in the last 25 years (1980–2004), figures are given per year. To determine permanent and

non-permanent populations, we used reproduction frequencies and categories as well as presence patterns of distribution and abundance during the last 25 years.

Results

Relative area, relative abundance and reproduction per time period (Table 1)

For each species group, relative area and abundance are highly correlated (Spearman-Rank A:0.88, B:0.89, p < 0.05). Before 1900 species of Group A were found in 13.8% of the investigated squares. From 1900 onwards the proportion is much lower but in the 1990ties we see a remarkable increase (27%). In the pentad 2000–2004 the proportion reaches even 34.6%. For the species of Group B, proportions increase from the 1980ties but vary in the earlier periods. The relative abundance of Group A and B show a similar pattern as the relative area. Both species of Group B have been present in all but one time period. Group A species have been recorded in each time period but numbers are higher before 1900 and since 1990. Indications of reproduction are also higher since that decade. For Group B, reproduction can not always be confirmed in the older data.

Relative area and abundance by groups per year in the recent period (1980–2004)

For each species group, relative area and abundance are again highly correlated (Spearman-Rank A:0.97, B:0.87, p < 0.05). The cumulative relative area for both groups during the last 25 years (Fig. 1) gives for almost all years a higher percentage for Group B than for Group A, except in 1996 and 2003. Compared to the first 15 years, Group A shows a clear increase in relative distribution during the last decade. There is a prominent peak in 1996.

Table 1. Relative area, relative abundance, number of species and reproduction confirmation for Group A (8 spec.) and Group B (2 spec.) in the 8 time periods (****** = confirmed reproduction, ***** = probable reproduction, see also Material & Methods).

time period		Relative area		Relative abundance		Number of species	
		Group A	**Group B**	**Group A**	**Group B**	**Group A**	**Group B**
1	<1900	13,8	17,2	4,4	2,7	6 (2*?)	2**
2	1900–1949	1,8	8,0	0,4	1,4	2	2 (1*?)
3	1950–1959	2,5	2,5	0,5	0,5	1	1*?
4	1960–1969	3,1	14,4	1,3	2,8	3	2(1*+1*?)
5	1970–1979	1,6	1,6	0,2	0,2	2	2 (1**)
6	1980–1989	2,4	18,2	0,2	1,5	4 (1*)	2**
7	1990–1999	27,1	39,9	2,1	3,8	7 (4**)	2**
8	2000–2004	34,6	41,1	2,1	2,9	8 (4**, 3*)	2**

The cumulative relative abundance for both groups (Fig. 2) gives a very similar pattern to the cumulative relative area (see Fig. 1).

Relative area and distribution by species per year in the recent period (1980–2004)

The relative area and abundance per year for each species of Group A separately shows again a clear increase in presence and number of occupied squares in the last 10 years (Fig. 3, 4). Four species (*Coenagrion scitulum*, *Anax parthenope*, *Orthetrum brunneum* and *Sympetrum meridionale*) remain at a very low percentage and have an irregular presence pattern. *Aeshna affinis* has slightly higher numbers but is also frequently absent. *Lestes barbarus*, *Crocothemis erythraea* and *Sympetrum fonscolombii* show a rather stable presence although numbers fluctuate. In *Lestes barbarus* the area is smaller during the last five years. All three species have a greater or maximum range in 1996, with *Sympetrum fonscolombii* showing an extreme peak.

In Fig. 4 the recent cumulative distribution of *Crocothemis erythraea* for four consecutive time periods (a = < 1990, b = 1990–1994, c = 1995–1999 and d = 2000–2004) is given. We also indicate the investigated squares (dotted) for each time period. The species shows since 1990 a real increase in distribution area in Flanders.
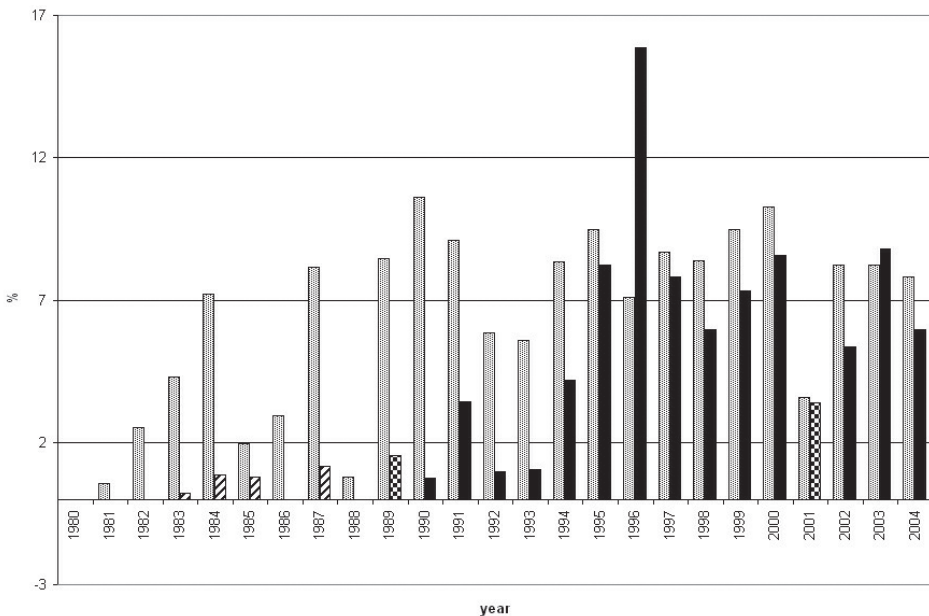
Figure 1. Cumulative relative area per year from 1981–2004 for the 2 species of Group B (left: dotted bars) and the 8 species of Group A (right: barred, checkered and black bars indicating respectively no reproduction, probable and confirmed reproduction of at least one species of the group).
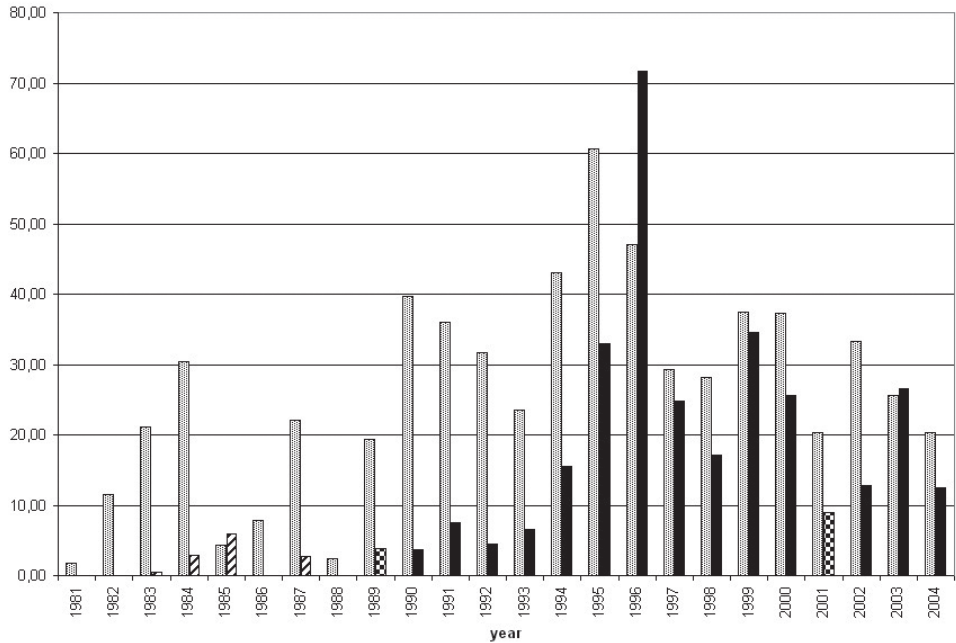
Figure 2. Cumulative relative abundance (%) per year from 1981–2004 for the 2 species of Group B (left: dotted bars) and the 8 species of Group A (right: barred, checkered and black bars indicating respectively no reproduction, probable and confirmed reproduction of at least one species of the group).
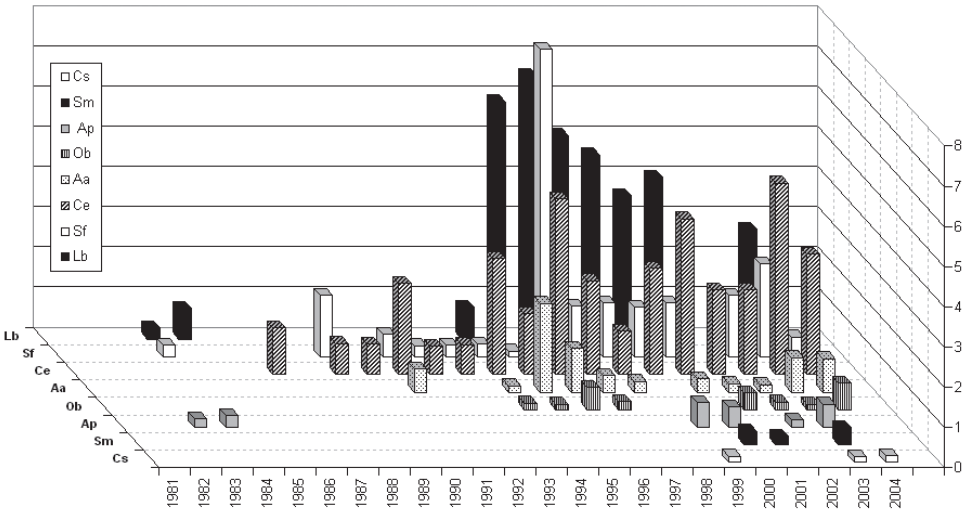
Figure 3. Relative area for the 8 species of Group A in Flanders during the period from 1980–2004. **Lb** = *Lestes barbarus* **Cs** = *Coenagrion scitulum* **Ap** = *Anax parthenope* **Af** = *Aeshna affinis* **Ob** = *Orthetrum brunneum* **Ce** = *Crocothemis erythraea* **Sf** = *Sympetrum fonscolombii* and **Sm** = *Sympetrum meridionale*.

First presence, confirmed reproduction and maximum range

Table 2 summarises a number of presence and reproduction data. Three species (*Lestes barbarus, Crocothemis erythraea* and *Sympetrum fonscolombii*) show a combination of earlier arrival, earlier confirmed reproduction with a higher frequency and higher maximum ranges. All others (*Coenagrion scitulum*, *Aeshna affinis*, *Anax parthenope, Orthetrum brunneum* and *Sympetrum meridionale*) show only one (more recent) confirmed (or probable) reproduction and have much lower maximum ranges.

Discussion

In the 19th century, six southern species have been observed in Flanders. However, little is known about their distribution area and population abundance. In historical references like Selys (1859, 1888) and Bamps and Claes (1893), comprehensive descriptions often lack and there is certainly a bias resulting from heterogeneous sampling, low visiting effort and 'collectioning'. In the following periods, southern species were very rarely observed. Towards the last decades of the 20th century, this changed. Since 1980, eight southern dragonfly species have been recorded in Flanders. The first in row were *Anax parthenope* (1983), *Lestes barbarus* and *Sympetrum fonscolombii* (1984) and *Crocothemis erythraea* (1987). They were followed by *Aeshna affinis* (1991), *Orthetrum brunneum* (1994), *Coenagrion scitulum* (1999) and finally *S. meridionale* (2000). In general the present data of this group shows a clear increase in relative abundance as well as relative area since the beginning of the 1990ties, with "peak" occurrence mainly in the 1995–1999 period. Since 2000, numbers are lower but more species were simultaneously present. However, not all the members of the group have achieved a similar level of 'expansion' succes and permanence. Only three of them can actually be considered as having a "permanent" population: *Lestes barbarus*, *Crocothemis erythraea* and *Sympetrum fonscolombii*. Until 1980, only 6 records of *Lestes barbarus* are known from Flanders, three of them dating from the hot summer of 1976, without proof of permanent populations. In 1984 and 1985, the species was seen in several locations, and at one site there was a very small "population" present but reproduction could not be confirmed. In 1994 and in particular in 1995 there was an invasion of the species in North West Europe (Monnerat 2002; Parr 2003). Since then, the species maintains permanent populations in Flanders (De Knijf 1994; Stoks 1994; Stoks and De Block 1997). *Sympetrum fonscolombii* has been recorded 10 times before 1980, and although only isolated or very few individuals have been seen, the species might have reproduced in the past (Selys 1859). In the eighties the species had been observed in two sites, but since the nineties it occurs yearly and has been reproducing. Populations of more then 50 individuals have been sighted. Since a peak in 1996 during an invasion in North Western Europe (Dijkstra and van der Weide 1997; Lempert 1997), *S. fonscolombii* now is present in several tens of squares and maintains populations on several sites, also in the southern part of Belgium (Goffart 1999; Paternoster 2000). *Crocothemis eryth-*
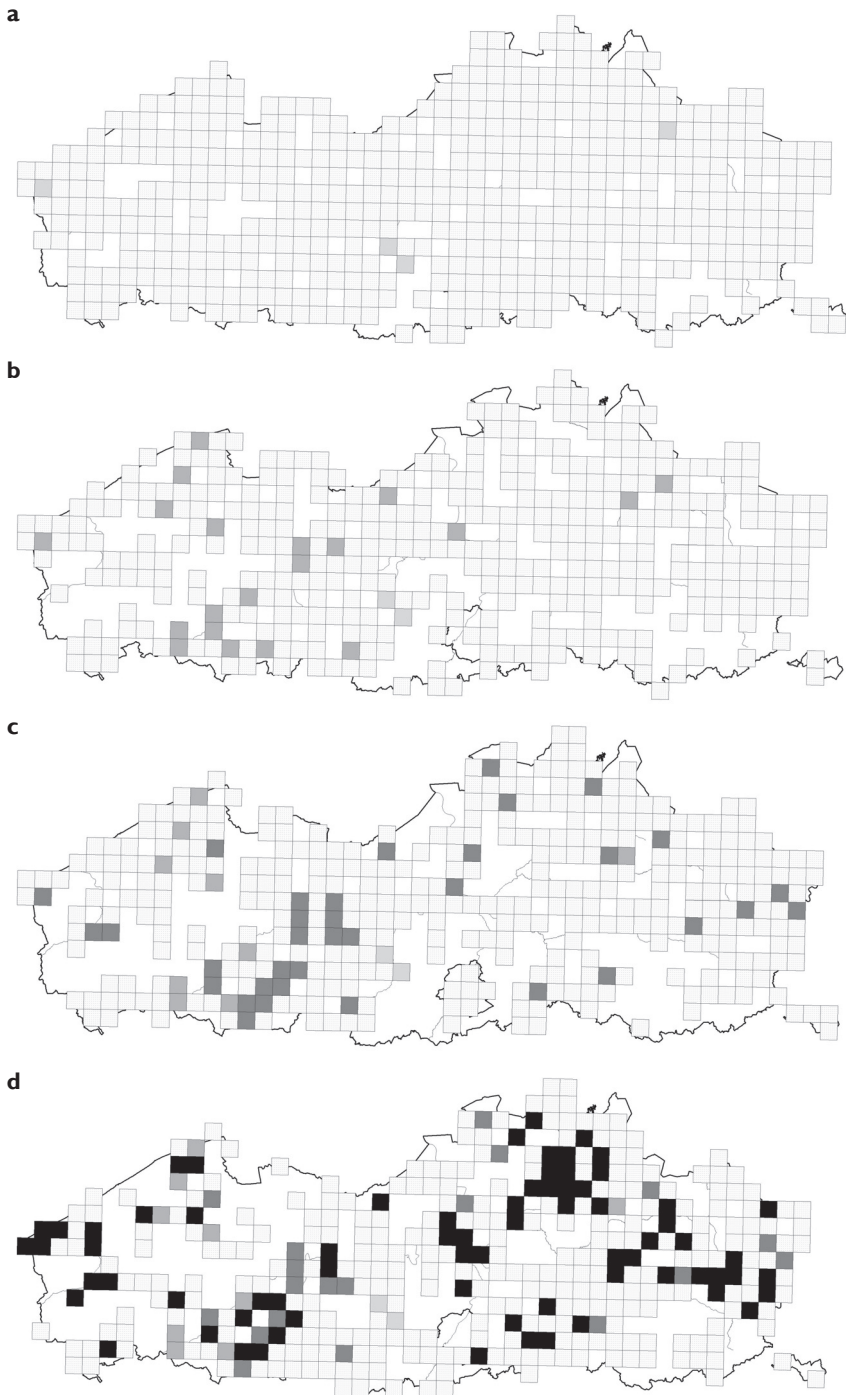
Figure 4. Cumulative distribution of *Crocothemis erythraea* in four consecutive time periods (**a** =< 1990, **b** = 1990–1994, **c** = 1995–1999 and **d** = 2000–2004) in Flanders, based on 5 × 5 km squares. For each time period the investigated squares are given as dotted squares in the background.

Table 2. Presence during the first five time periods (1–5) (see also Tab. 1) and year of first and last record in the period 1980–2004; Recent reproduction: first (Y1) and last year (Y2), time interval between Y1 and Y2 and frequency of reproduction in that period for confirmed** and probable* together; Maximum "range" recent: cumulative number of occupied 5×5 km squares in the period 1980–2004. Lb = *Lestes barbarus*, Cs = *Coenagrion scitulum*, Ap = *Anax parthenope*, Af = *Aeshna affinis*, Ob = *Orthetrum brunneum*, Ce = *Crocothemis erythraea*, Sf = *Sympetrum fonscolombii* and Sm = *Sympetrum meridionale*.

	Lb	Sf	Ce	Ap	Aa	Ob	Cs	Sm
Records								
Non-recent time (period 1–5)	1, 2, 5	1, 3, 4	4	1	4	1	1, 2, 5	1
Recent time (period 6–8) first	1984	1984	1987	1983	1991	1994	1999	2000
Recent time (period 6–8) last	2004	2004	2004	2003	2004	2004	2004	2003
Reproduction recent								
First: Y1	1994* 1995**	1989* 1992**	1990**	2003*	1996**	-	2003*	2003**
Latest: Y2	2004*	2004**	2004*	2003*	1996**	-	2003*	2003**
Y1 - Y2	11	16	15	1	1	-	1	1
Frequency in Y1 - Y2	11	9	13	1	1	-	1	1
Max. "range" recent	115	63	100	15	33	9	2	6

reae is without doubt the most successful of all southern species. The species has been observed in the past (Selys 1878), but permanent populations or reproduction have never been recorded. Apart from observations in 1963 (Cammaerts 1967; Dumont 1967), the species was only seen more regularly since the eighties when first reproduction was proved but is now present in more then 20% of all squares (De Knijf 1989, 1995; Tailly 1991). *Anax parthenope* has only once been observed in the surroundings of Brussels in 1884 but after this, the species was not recorded anymore until the eighties when there are several observations (all males) (Lerner 1984, Michiels 1984). In the nineties however, *Anax parthenope* has been recorded in 6 localities in Flanders, mostly individual males, with a small invasion in 1999 (De Knijf 1999). Probable reproduction was only recorded in 2003. It is clear that the species has still no permanent populations in Flanders. *Aeshna affinis* has never been observed in Flanders before 1900 and there is only one record (1969) before 1980. The species was again observed in 1991 and present in almost every year since 1994. An invasion in 1995 with higher numbers probably resulted in the first proof of reproduction in 1996 (Van de Meutter 1995; Andries 1997; Van den Berghe 1999). At several localities the species has been seen in consecutive years, but it cannot yet be considered as having permanent populations in Flanders. From *Orthetrum brunneum* there exist only a very few historical records although it might have reproduced in the past (Bamps and Claes 1893). Since 1980, the species was first recorded in 1994 (Verstraeten 1996) and has been present regularly but in very small numbers (Van de Meutter 2004). Reproduction occurred probably in 2005. *Orthetrum brunneum* has to be considered as an irregular and very rare species in Flanders. *Coenagrion scitulum* has been mentioned a few times by Selys (1868) but in contrary with the Walloon region without proof of reproduction in Flanders.
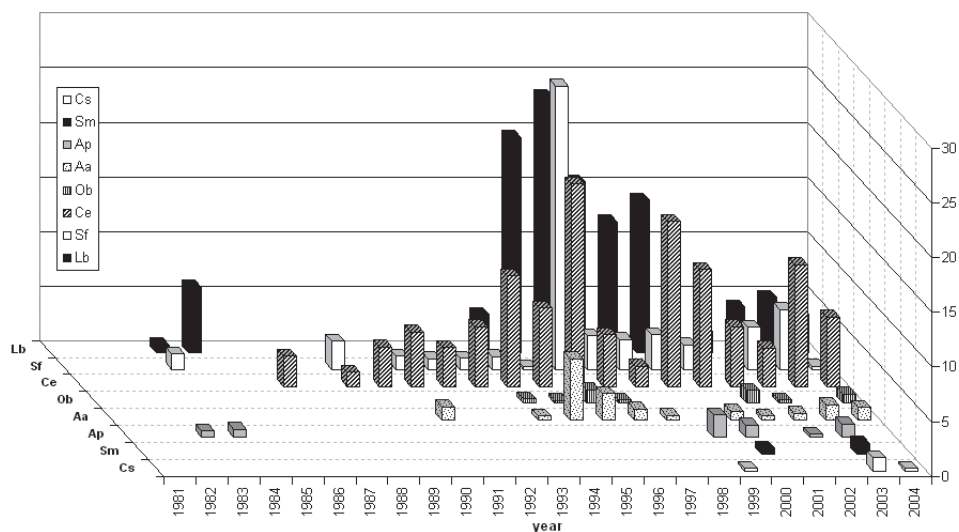
Figure 5. Relative abundance for the 8 species of Group A in Flanders in the period 1980–2004.
Lb = *Lestes barbarus* **Cs** = *Coenagrion scitulum* **Ap** = *Anax parthenope* **Af** = *Aeshna affinis* **Ob** = *Orthetrum brunneum* **Ce** = *Crocothemis erythraea* **Sf** = *Sympetrum fonscolombii* and **Sm** = *Sympetrum meridionale*.

Later only a few records are known from 1949 and 1973. Since 1980, the species has only been observed in 1998, in 2003 and in 2004, and although most probably there are now some small local populations present where reproduction may occur, the species can not be considered as permanently established yet (De Knijf 2004). The only known record of *Sympetrum meridionale* from the past dates from 1886 (Bamps and Claes 1893). In 2000 the species was seen again at two different localities, with even a young male at one site (Versonnen et al. 2002). In 2001 only one female was seen (Versonnen et al. 2002) and in 2002 no records are know. In 2003 reproduction took place at least at one site, with the observation of several tenerals. Since then, the species has not been observed again. Two species reaching their northern distribution range in the region, *Erythromma viridulum* and *E. lindenii* have permanently maintained it and even expanded their area (see also De Knijf 1995), although there are fluctuations in distribution and abundance.

The presented patterns of range extension of the southern species in Flanders are a part of a more general long-term expansion of these species into Northwest Europe (Reder 1993, Drees et al. 1996, Ott 1996, 2000, 2001, Dijkstra and van der Weide 1997; Lempert 1997; Vanderhaeghe 1999; Gonseth and Monnerat 2001; Guerold et al. 2001; Ketelaar 2002; Mauersberger 2003; Parr et al. 2004). However, whether in our region the observed patterns are only (or mostly) a result of increasing temperatures as is the case in Wallonia (Goffart 2006), or whether other environmental variables play also an important role, has still to be confirmed. This will be investigated in the next future.

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RESEARCH ARTICLE

Changes in the range of dragonflies in the Netherlands and the possible role of temperature change

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Abstract

The trends of 60 Dutch dragonfly species were calculated for three different periods (1980–1993, 1994–1998 and 1999–2003). Comparing period 1 and period 3 shows that 39 of these species have increased, 16 have remained stable and 5 have decreased. These results show a revival of the Dutch dragonfly fauna, after decades of ongoing decline. The species were categorized in different species groups: species with a southern distribution range, species with a northern distribution range, species of running waters, species of fenlands and species of mesotrophic lakes and bogs. The trends of these different species groups were compared with the all-species control group. As expected, a significantly higher proportion of the southern species show a positive trend than the all-species group. In the northern species group on the contrary, a significantly higher proportion of the species show a negative trend than the all-species group. Different explanations for these results are discussed, such as climate change, improved quality of certain habitats and degradation of other habitats. It is likely that the observed increase of southern species is at least partly caused by the increasing temperatures. The less positive picture of the northern species group is probably more influenced by other environmental factor than directly by climate change.

Three out of six southern species which have become established since 1990 have done so during the aftermath of large invasions. It is concluded that dragonflies are well capable of using changing climate circumstances to colonise new habitats.

Keywords

dragonflies, Odonata, climate change, invasion, trends, conservation, Netherlands

Introduction

During the last century, the Dutch dragonfly fauna has shown large changes. De-struction of habitats, canalisation of streams and rivers, desiccation, eutrophication, acidification and pollution led to an often strong decline of many species. This started in the first half of the 20th century, but was especially severe in the sixties and seventies of that century (Kalkman et al. 2002). Most affected were species of running waters and species of mesotrophic lakes and bogs (Wasscher 1994, 1999), some of which even disappeared from the Netherlands (*Coenagrion mercuriale*, *Nehalennia speciosa*, *Gomphus flavipes*, *Ophiogomphus cecilia*, *Oxygastra curtisii*, *Leucorrhinia caudalis*). The degradation of the Dutch dragonfly fauna reached a maximum in the 1980's. Since the start of the 1990's, many species have increased. This is very obvious for some species of running water and ubiquistic species for which the Netherlands lie on the northern limit of their distribution range. These species seem to have profited from the improving water quality (RIVM 2003) and the recent warm summer seasons (KNMI 2006). However, a number of species of other habitats, such as mesotrophic lakes and bogs, have also increased during last decade.

In this article we describe the revival of the Dutch dragonfly fauna, which seems to be happening. Special attention is given to the role of temperature change.

Methods

Database

The database used for this article is build and maintained by the Dutch Society for Dragonflies, Butterfly Conservation and the European Invertebrate Survey – the Netherlands. It contains over 307,000 records of 71 dragonfly species up to and in-cluding 2003, mainly submitted by volunteers. Each record constitutes a species on a date on a locality. The records are checked for mistakes by a committee of experts, based on the known distribution and flight period of the species. For records of rare species further documentation like a picture or a description is required.

More than 279,000 records are available from the period 1980–2003. By far the largest number of these records was collected from 1994 onwards, but the number of records prior to this period is large enough to give a good impression of the distribu-tion of the species in that period.

The database gives good information on the distribution of species. However it is subject to influences of the differences between fieldwork done by the volunteers and large-scale professional projects. Therefore, results based on the database can only be interpreted correctly with a good knowledge of the database itself.

Calculation of trends

The data set was divided in three periods: 1980–1993 (period 1), 1994–1998 (period 2) and 1999–2003 (period 3). Relatively few records are available from each year in period 1. Therefore, this period includes fourteen years while periods 2 and 3 only include five years. The 5×5 kilometre squares which had been visited at least in three different months in the period May till August were selected for each year (table 1). Only records from these squares were used for the analysis. For eleven of the 71 Dutch species this resulted in usable records for only one or none of the three periods. Therefore these species, all extinct or very rare, were not included in the trend calculation.

Presence or absence of dragonfly species in the selected 5×5 kilometre squares was used, instead of the recorded number of individuals, as the latter is more prone to differences in recording behaviour. The consequence of this method is that a decrease or increase in observed numbers or in localities within a 5×5 kilometre square will go unnoticed.

For each species and period the relative abundance (RA) was calculated as follows:

RA= (Number of squares in which a species is recorded)/(number of investigated squares) × 100%.

The RA's for each year were summed for each period and divided by the number of years. The relative change of a species was calculated as follows:

Trend= (RA in recent period – RA in historical period)/(RA historical period × 100%

The trends were divided in five trend categories (table 2).

Southern and northern species group

The Dutch dragonfly species were categorized as southern species, northern species or species without a typical southern or northern distribution pattern. This categorization was based on distribution maps of Northwest Europe (NVL, 2002). A southern species was defined as a species of which the northern limit of its range runs through the southern tip of Sweden or more southwards. A northern species was defined as a species of which the southern border of its range runs through the Netherlands or Belgium and which is further south only found at higher elevations or in small, scattered populations.

Habitat groups

Next to the southern and northern species groups, three ecological species groups were selected: species of running water habitats (rheophilic species), species of mesotrophic lakes

Table 1. The number of well investigated 5×5 kilometre squares

Period 1		Period 2		Period 3	
Year	Well investigated squares	Year	Well investigated squares	Year	Well investigated squares
1980	5	1994	151	1999	235
1981	9	1995	260	2000	235
1982	16	1996	242	2001	241
1983	12	1997	205	2002	260
1984	11	1998	180	2003	372
1985	14	**Total**	**1038**	**Total**	**1343**
1986	19				
1987	20				
1988	14				
1989	20				
1990	28				
1991	23				
1992	45				
1993	68				
1994	151				
1995	260				
1996	242				
1997	205				
1998	180				
Total	**1342**				

and bogs and species of fenlands. For this categorization the habitat preference of Dutch dragonflies was used, as given in NVL (2002). Table 3 lists the species of the four selected species groups. Note that some species are appointed to more than one species group.

Statistics

χ^2-tests were conducted to test the differences between the all-species group and the selected distribution and habitat species groups. This was done by using Microsoft Excel 2000 software. Species with increasing (>20 %) and strong increasing trends (>100 %) were lumped together and tested as increasing species.

Results

The relative abundance for each period and the trend between the periods is given for each species in table 4. Table 2 gives the number of species showing a certain trend between the different periods.

Table 2. Categories of trend and the number of species showing this trend between periods

Trend		In table 4 as	period 1 to 2	period 2 to 3	period 1 to 3
Strong increase	>100%	++	19 (32%)	6 (10%)	13 (25%)
Increase	>20% and <100%	+	9 (15%)	19 (32%)	14 (25%)
Stable	-20% to 20%	0	19 (32%)	28 (47%)	16 (31%)
Decrease	<-20%	-	13 (22%)	7 (12%)	9 (17%)

Trends between the first and the third period could be calculated for 60 species. 39 species (65%) show a positive trend, 16 species (27%) remained stable and 5 species (8%) show a negative trend. Most increasing species show the strongest positive trend between the first and second period (see figure 1).

The results of the χ^2-tests are given in table 5.

Species with a southern distribution pattern

Within the southern species group, significantly more species show a positive trend than the all-species group, when period 1 is compared to period 2 and when period 1 is compared to period 3. Furthermore, a significantly lower proportion of the southern species remained stable, when period 1 is compared to period 3 (figure 2).

Species with a northern distribution

Within the northern species group, significantly more species show a negative trend than the all-species group, when period 1 is compared to period 2. Furthermore, a significantly lower proportion of the northern species remained stable, when period 2 is compared tot period 3 (figure 3).

Differences in trends between habitats

Within the species group of mesotrophic lakes and bogs, significantly less species show a positive trend than the all species group and significantly more species show a stable trend, when period 1 is compared to period 3 (figure 4).

Within the ecological species groups of running waters and fenlands, no significant differences are found for the three trend categories.

Discussion

The results show that the Dutch dragonfly fauna has recovered since the start of the 1990's, which is in sharp contrast with some other groups of invertebrates as but-

Table 3. Categorisation of the species in five different species groups.

Species	Southern	Northern	Running waters	Lakes and bogs	Fenlands
Aeshna affinis	x				
Aeshna grandis				x	x
Aeshna isoceles	x				x
Aeshna juncea				x	
Aeshna mixta	x				
Aeshna subarctica		x		x	
Aeshna viridis		x			x
Anax imperator	x				
Anax parthenope	x				
Brachytron pratense					x
Calopteryx splendens			x		
Calopteryx virgo			x		
Ceriagrion tenellum	x			x	
Coenagrion hastulatum		x		x	
Coenagrion lunulatum		x		x	
Coenagrion puella				x	
Coenagrion pulchellum					x
Cordulegaster boltonii			x		
Cordulia aenea				x	x
Crocothemis erythraea	x				
Enallagma cyathigerum				x	
Erythromma lindenii	x				
Erythromma najas					x
Erythromma viridulum	x				x
Gomphus flavipes			x		
Gomphus pulchellus	x				
Gomphus vulgatissimus			x		
Ischnura elegans					x
Ischnura pumilio	x				
Lestes barbarus	x			x	
Lestes dryas				x	
Lestes sponsa				x	x
Lestes virens	x				
Lestes viridis	x				x
Leucorrhinia dubia				x	
Leucorrhinia pectoralis					x
Leucorrhinia rubicunda		x		x	
Libellula fulva	x				x
Libellula quadrimaculata				x	x
Ophiogomphus cecilia			x		
Orthetrum brunneum	x		x		
Orthetrum cancellatum	x			x	x
Orthetrum coerulescens			x		

Species	Southern	Northern	Running waters	Lakes and bogs	Fenlands
Platycnemis pennipes			x		
Pyrrhosoma nymphula				x	
Somatochlora arctica		x		x	
Somatochlora flavomaculata				x	
Sympecma fusca	x			x	
Sympecma paedisca		x			x
Sympetrum danae				x	
Sympetrum flaveolum				x	
Sympetrum fonscolombii	x				
Sympetrum pedemontanum			x		
Sympetrum sanguineum					x
Sympetrum vulgatum				x	x

terflies and bees (Peeters and Reemer 2003; Swaay and Groenendijk 2005). Only 5 dragonfly species have declined, while a majority of 39 species has increased and 16 species remained stable. Out of the 27 species placed on the red list in 1999 (Wasscher 1999) 17 show an increase, 4 a decrease, 1 remained stable and 3 are still extinct. For the remaining 2 red-listed species (*Coenagrion armatum* and *Leucorrhinia albifrons*) no trend was calculated, as they were only recorded in one period. Populations of both species have recently been rediscovered (Van der Heijden 2001; De Boer and Wasscher 2006) in the Netherlands and although they are extremely rare, there is no evidence for an actual decline.

Two different causes can be pointed out for the increase or decrease of the different species. The first is climate change, the second is changes in the quality of habitats.

Climate change

The average temperature in the Netherlands in the last twenty years of the 20th century was 0,7 degree higher than the average temperature of the first twenty years of the 20th century (KNMI 2006). Especially the spring temperature has shown a strong increase. This increase in temperature caused several southern species to expand their range northwards, becoming more common in the Netherlands. This is at least the case for *Lestes barbarus*, *Aeshna affinis*, *Anax parthenope*, *Crocothemis erytraea*, *Orthetrum brunneum* and *Sympetrum fonscolombii*. *Coenagrion scitulum* expanded its range in northern France and Belgium and was first found in the Netherlands in 2003 (Goudsmits 2003). Also for more common southern species like *Lestes virens* and *Ceriagrion tenellum* a positive effect of increasing temperatures is expected.

Whether or not higher temperatures also play a role in the negative trend shown by some northern species is difficult to say, because the habitats of northern species are

Table 4. Relative abundance (RA) and trends for each species.

Species	RA period 1	RA period 2	RA period 3	trend 1st to 2nd period	trend 2nd to 3rd period	trend 1st to 3rd period
Aeshna affinis Vander Linden, 1820		1	0,6	++	-	++
Aeshna cyanea (O.F. Müller, 1764)	33,6	47,1	53,6	0	0	+
Aeshna grandis (Linnaeus, 1758)	36,3	36,3	40,9	0	0	0
Aeshna isoceles (O.F. Müller, 1767)	7,5	12,3	17,2	+	+	++
Aeshna juncea (Linnaeus, 1758)	18,1	13,5	13,4	0	0	0
Aeshna mixta Latreille, 1805	21,9	54,9	61,9	+	0	++
Aeshna subarctica Walker, 1908	0,4	0,9	0,5	++	-	+
Aeshna viridis (Eversmann, 1836)	1	4,2	6,4	++	0	++
Anax imperator Leach, 1815	23,5	59,5	73,2	+	0	++
Anax parthenope (Selys, 1839)		0,3	0,4	++	+	++
Brachytron pratense (O.F. Müller, 1764)	17,8	20,3	30,3	0	+	+
Calopteryx splendens (Harris, 1782)	33	32	32,4	0	0	0
Calopteryx virgo (Linnaeus, 1758)	5,2	3,2	3,1	-	0	-
Ceriagrion tenellum (de Villers, 1789)	11,9	8	13,8	-	+	+
Coenagrion armatum (Charpentier, 1840)			0,3			
Coenagrion hastulatum (Charpentier, 1825)	4,3	1,9	2,4	-	+	-
Coenagrion lunulatum (Charpentier, 1840)	19,3	8,3	9,5	-	+	-
Coenagrion puella (Linnaeus, 1758)	54,9	57,7	62,2	0	0	0
Coenagrion pulchellum (Vander Linden, 1825)	50,8	48,5	49,8	0	0	0
Coenagrion scitulum (Rambur, 1842)			0,1			
Cordulegaster boltonii (Donovan, 1807)	2	1,1	0,9	-	-	-
Cordulia aenea (Linnaeus, 1758)	28,8	22,7	24,7	0	0	0
Crocothemis erythraea (Brullé, 1832)		1,7	3,6	++	++	++
Enallagma cyathigerum (Charpentier, 1840)	63,7	59,6	64,1	0	0	0
Erythromma lindenii (Selys, 1840)	2,8	2,7	4,6	+	+	++
Erythromma najas (Hansemann, 1823)	28,3	44,3	42	+	0	+
Erythromma viridulum (Charpentier, 1840)	7,1	42,3	36,5	++	0	++
Gomphus flavipes (Charpentier, 1825)			2,8	++	++	++
Gomphus pulchellus Selys, 1840	10	8,7	8,2	0	0	+
Gomphus vulgatissimus (Linnaeus, 1758)	2	2,1	3,9	++	+	++
Hemianax ephippiger (Burmeister, 1839)		0,2				
Ischnura elegans (Vander Linden, 1820)	79,3	93	90,5	0	0	0
Ischnura pumilio (Charpentier, 1825)	6,2	4,9	9,1	0	++	++
Lestes barbarus (Fabricius, 1798)	2,2	16,9	15,7	++	0	++
Lestes dryas Kirby, 1890	14,7	14	11,7	0	0	0
Lestes sponsa (Hansemann, 1823)	62,9	50,9	48,2	0	0	0
Lestes virens (Charpentier, 1825)	5,1	7,1	12,3	+	+	++
Lestes viridis (Vander Linden, 1825)	32,7	51,4	54,2	0	0	+
Leucorrhinia dubia (Vander Linden, 1825)	18,6	11,2	12,3	-	+	0
Leucorrhinia pectoralis (Charpentier, 1825)	1,2	1,2	3,1	0	+	++
Leucorrhinia rubicunda (Linnaeus, 1758)	20,4	13,5	22,9	-	+	0

Species	RA period 1	RA period 2	RA period 3	trend 1st to 2nd period	trend 2nd to 3rd period	trend 1st to 3rd period
Libellula depressa Linnaeus, 1758	23,9	40,7	53,2	+	+	+
Libellula fulva O.F. Müller, 1764	6,8	6,5	8,5	0	0	0
Libellula quadrimaculata Linnaeus, 1758	65,8	56	64,5	0	0	0
Ophiogomphus cecilia (Fourcroy, 1785)		0,2	0,3	++	+	++
Orthetrum brunneum (Fonscolombe, 1837)		1,6	1,2	++	-	++
Orthetrum cancellatum (Linnaeus, 1758)	42,1	80,2	81,6	+	0	+
Orthetrum coerulescens (Fabricius, 1798)	1,7	4,1	3,2	++	0	++
Platycnemis pennipes (Pallas, 1771)	17,2	18,6	18,4	+	0	+
Pyrrhosoma nymphula (Sulzer, 1776)	69,4	47,8	61	-	+	0
Somatochlora arctica (Zetterstedt, 1840)		0,2	0,4	++	++	++
Somatochlora flavomaculata (Vander Linden, 1825)	0,1	0,7	1,7	+	++	++
Somatochlora metallica (Vander Linden, 1825)	18,7	15,7	15,1	0	0	0
Sympecma fusca (Vander Linden, 1820)	0,4	6,2	8,3	++	+	++
Sympecma paedisca (Brauer, 1877)		0,3	1	++	++	++
Sympetrum danae (Sulzer, 1776)	51,4	45,6	45,7	0	0	0
Sympetrum depressiusculum (Selys, 1841)	1	0,5	0,1	0	-	-
Sympetrum flaveolum (Linnaeus, 1758)	24,4	38,4	20,2	++	-	+
Sympetrum fonscolombii (Selys, 1840)	0,4	4,8	6	++	0	++
Sympetrum pedemontanum (Allioni, 1766)	1,4	1	1,7	0	+	+
Sympetrum sanguineum (O.F. Müller, 1764)	37,1	64,3	58,3	+	0	+
Sympetrum striolatum (Charpentier, 1840)	13,2	39,2	41,8	+	0	+
Sympetrum vulgatum (Linnaeus, 1758)	38	44,5	48,3	0	0	+

more prone to negative influences of other environmental factors. Five out of seven northern species occur in mesotrophic lake and bog habitats, while there are no northern species occurring in running waters. It is clear that habitat degradation is an important factor to explain the results of the northern species group, possibly climate change makes this decrease more severe.

The northern distribution of many southern species seems to be directly limited by the summer temperatures, resulting in a direct expansion of their range when temperature permits (Appendix1). The southern border of northern species on the other hand does not seem to be limited directly by temperatures, but seems to be determined by habitats being absent more southerly and by competition with other species prevailing in warmer climates.

The decrease of northern species as a result of increasing temperatures would in that case be caused by degradation of habitats and by increasing competition from southern species. This would result in a slow decline, which is far more difficult to detect than the rapid increase shown by southern species.

Another negative effect of increasing summer temperatures is increasing evaporation, resulting in lower surface and ground water tables. This can lead to desiccation of

All species, period 1-2   **All species, period 2-3**   **All species, period 1-3**

□ increased ■ decreased □ stable
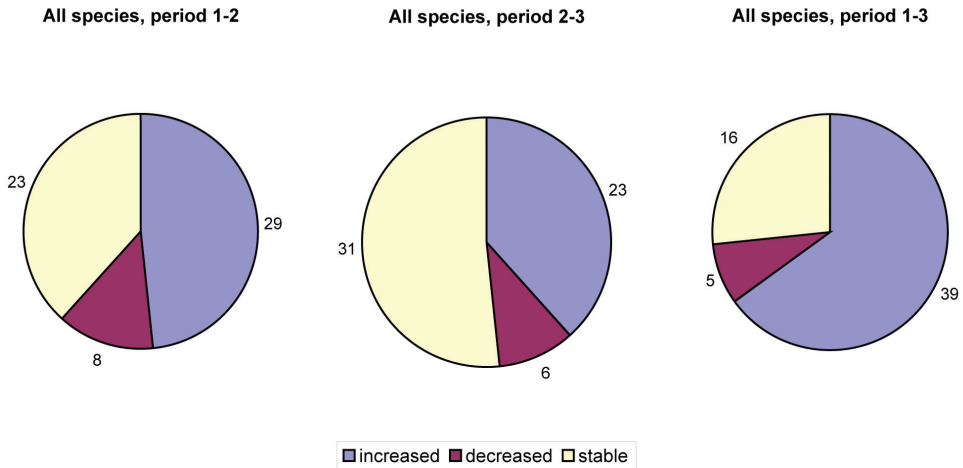
Figure 1. Distribution of all tested species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

important vegetation structures in the riparian zone of lakes and the upstream stretches of streams. This happens especially in late summer, when the first and most vulnerable larval instars of most species are present in the water. Furthermore, desiccation leads to the stagnation of ground water in seepage fed lakes and streams, causing acidification. Also the turn-over rate of organic matter increases when lake shores dry out, causing nutrient enrichment.

Coenagrion hastulatum, *Cordulegaster boltonii* and *Somatochlora arctica* are examples of threatened species which are known to react negatively on desiccation caused by human influences (e.g. intensive drainage in agricultural areas and drinking water collection) (Groenendijk 2002; Groenendijk 2005; Ketelaar 2001a; Ketelaar 2001b; Wasscher 1999). It is expected that hot summers contribute to this problem. On the other hand, temporary water specialist like *Lestes barbarus* and *Sympetrum flaveolum* might have profited from waters becoming shallower.

Changes in quality of habitats

The test failed to show that the species group of running water contains a significantly higher portion of increasing species than the all-species group. However, this is probably due to the low number of species included in the group, making it difficult to find significant results. Of the ten included species five show a strong increase, two a moderate increase, one is stable and two show a decrease when the first period is compared with the third. Most striking is the comeback of *Gomphus flavipes*, which from 1996 onwards reoccupied all large river systems in the Netherlands (figure 5), after an absence of more than 90 years (Kleukers and Reemer 1998;

Table 5. Results of χ2-tests of the observed proportions of trend categories within the different species groups. *****p<0,05; ******p<0,01.

	All species n=60	Southern species n=19			Northern species n=19		
		Ob-served	Ex-pected	p	Ob-served	Ex-pected	p
Period 1 compared to period 2							
Number of increased species	29	14	9.2	0.027*	4	3.4	0.641
Number of stabel / decreased species	31	5	9.8		3	3.6	
Number of decreased species	8	1	2.5	0.301	3	0.9	0.022*
Number of stabel / increased species	52	18	16.5		4	6.1	
Number of stabel species	23	4	7.3	0.121	0	2.7	0.037*
Number of increased / decreased species	37	15	11.7		7	4.3	
Period 2 compared to period 3							
Number of increased species	23	8	7.3	0.735	5	2.7	0.072
Number of stabel / decreased species	37	11	11.7		2	4.3	
Number of decreased species	6	2	1.9	0.939	1	0.7	0.705
Number of stabel / increased species	54	17	17.1		6	6.3	
Number of stabel species	31	9	9.8	0.708	1	3.6	0.048*
Number of increased / decreased species	29	10	9.2		6	3.4	
Period 1 compared to period 3							
Number of increased species	39	19	12.4	0.001**	4	4.6	0.663
Number of stabel / decreased species	21	0	6.7		3	2.5	
Number of decreased species	5	0	1.6	0.189	2	0.6	0.053
Number of stabel / increased species	55	19	17.4		5	6.4	
Number of stabel species	16	0	5.1	0.009**	1	1.9	0.459
Number of increased / decreased species	44	19	13.9		6	5.1	

	All species n=60	Species of running waters n=10			Species of lakes and bogs n=24			Species of fenlands n=19		
		Ob-served	Ex-pect-ed	p	Ob-served	Ex-pect-ed	p	Ob-served	Ex-pect-ed	p
Period 1 compared to period 2										
Number of increased species	29	6	4.8	0.460	8	11.6	0.141	7	9.2	0.316

	All species n=60	Species of running waters n=10			Species of lakes and bogs n=24			Species of fenlands n=19		
		Ob-served	Ex-pect-ed	p	Ob-served	Ex-pect-ed	p	Ob-served	Ex-pect-ed	p
Number of stabel / decreased species	31	4	5.2		16	12.4		12	9.8	
Number of de-creased species	8	2	1.3	0.535	6	3.2	0.093	1	2.5	0.301
Number of stabel / increased species	52	8	8.7		18	20.8		18	16.5	
Number of stabel species	23	2	3.8	0.233	10	9.2	0.737	11	7.3	0.079
Number of increased / decreased species	37	8	6.2		14	14.8		8	11.7	
Period 2 compared to period 3										
Number of increased species	23	4	3.8	0.914	10	9.2	0.737	5	7.3	0.281
Number of stabel / decreased species	37	6	6.2		14	14.8		14	11.7	
Number of de-creased species	6	2	1.0	0.292	2	2.4	0.785	0	1.9	0.146
Number of stabel / increased species	54	8	9.0		22	21.6		19	17.1	
Number of stabel species	31	4	5.2	0.460	12	12.4	0.870	14	9.8	0.055
Number of increased / decreased species	29	6	4.8		12	11.6		5	9.2	
Period 1 compared to period 3										
Number of increased species	39	7	6.5	0.740	10	15.6	0.017*	12	12.4	0.866
Number of stabel / decreased species	21	3	3.5		14	8.4		7	6.7	
Number of de-creased species	5	2	0.8	0.182	2	2.0	1000	0	1.6	0.189
Number of stabel / increased species	55	8	9.2		22	22.0		19	17.4	
Number of stabel species	16	1	2.7	0.233	12	6.4	0.010*	7	5.1	0.316
Number of increased / decreased species	44	9	7.3		12	17.6		12	13.9	

Bouwman and Kalkman 2005). One extinct species (*Ophiogomphus cecilia)* and one absent species (*Onychogomphus forcipatus*) were found reproducing in the 1990's, in the river Roer in the south of the Netherlands (Geraeds 2000; Geraeds and Van Schaik 2004). *Platycnemis pennipes, Gomphus vulgatissimus, Orthetrum coerulescens, Orthetrum brunneum* and *Sympetrum pedemontanum* increased (van Eijk and Ket-

Southern species, period 1-2
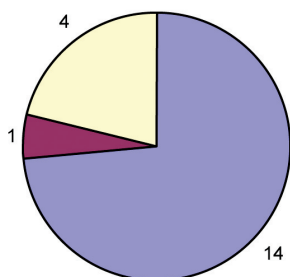
Southern species, period 1-3
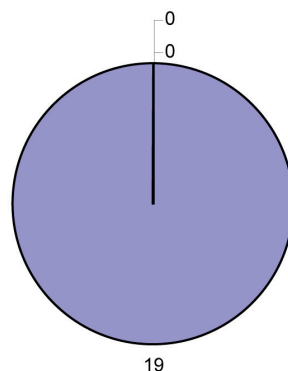
Figure 2. Distribution of the tested southern species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

Northern species, period 1-2
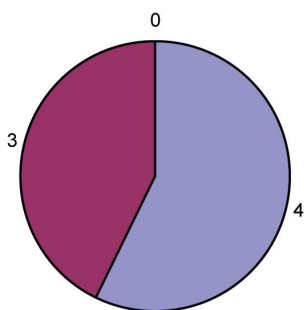
Northern species, period 2-3
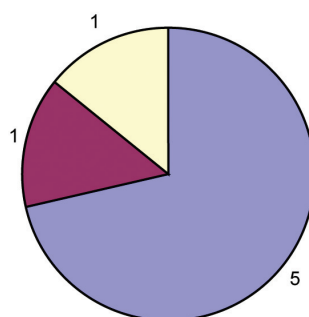
Figure 3. Distribution of the tested northern species over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

elaar 2004; van Delft 1998; Mensing 2002), while *Calopteryx splendens* remained stable. *Calopteryx virgo* and *Cordulegaster boltonii* are the only rheophilic species showing negative trends, however the observed numbers of these species have increased recently and several new localities were found (Groenendijk 2002; Termaat

Species of mesotrofic lakes and bogs, period 1-3
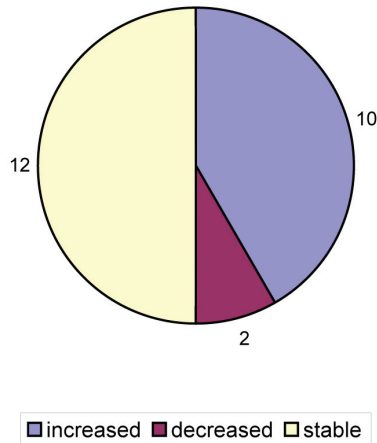
Figure 4. Distribution of the tested species of mesotrophic lakes and bogs over the trend categories. Three different periods were compared. Period 1 = 1980–1993, period 2 = 1994–1998, period 3 = 1999–2003.

and Groenendijk 2005). In our opinion, these findings leave no doubt that species of running water have increased strongly since 1980. Water quality improvement and restoration of the natural morphology of streams and rivers are likely to be the important causes for it. Some species probably profited from the higher summer temperatures as well. This is at least very likely for *Orthetrum brunneum, O. coerulescens* and *Sympetrum pedemontanum.*

Whereas the quality of running water habitats has improved, the threats for stagnant water habitats such as mesotrophic lakes and bogs are still present. Eutrophication, dessication and habitat fragmentation are still factors which explain why relatively few species in this species group show a positive trend. The intensity of eutrophication has reduced in recent years (RIVM 2003), but in many cases this has not lead to the recovery of lakes and bogs that have already been spoiled. The results of our analyses suggest that the negative trend of the species group of mesotrophic lakes and bogs stopped, but that they fail to recover. Especially *Coengrion hastulatum*, a species of mesotrophic lakes and bogs, is still declining in the Netherlands and is becoming increasingly endangered (Termaat 2006).

Conclusions

The analyses of the trends in the period 1980 to 2003 shows that the 55 Dutch dragonfly species for which a trend could be calculated remained stable or increased during
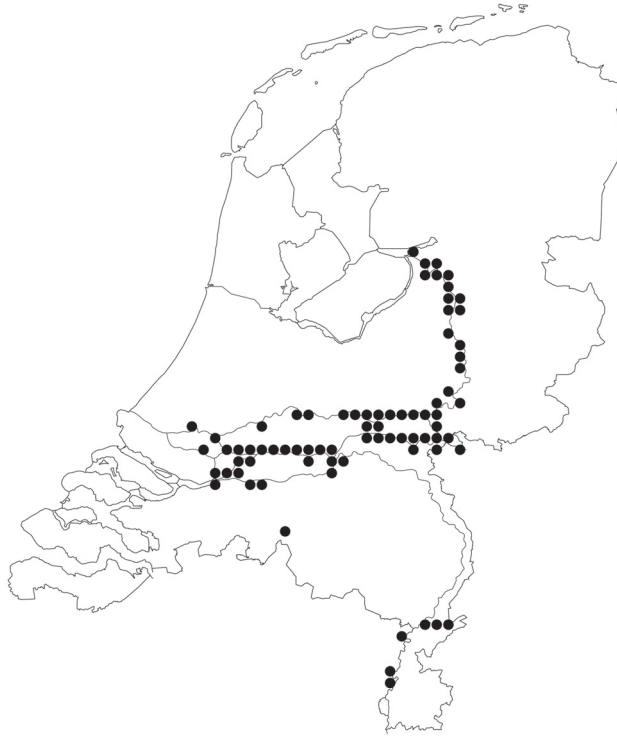
Figure 5. The distribution of *Gomphus flavipes* in the period 1996–2005. The species was not found in the Netherlands from 1902 to 1995.

that time period and that only 5 species have declined. Habitat degradation during the larger part of the 20th century resulted in a degradation of the dragonfly fauna in the eighties of that century. Improved water quality and increasing summer temperatures in the last two decades resulted in a revival of the Dutch dragonfly fauna.

Although our analyses failed to show that the species group of running water contains a significantly higher portion of increasing species than the all-species group, it is clear that especially species of running water have increased since 1980. This is probably largely due to the improved water quality of running waters and the restoration of the natural morphology of these systems.

The average temperature in the last twenty years of the 20th century was 0,7 °C higher than those of the first twenty years of the 20th century. As a result significantly more species with a southern distribution show a positive trend when compared with the all-species group.

Seven species very rare or absent prior to 1990 became established in the Netherlands, probably due to the increase in temperature. Three of these established themselves by means of large invasions. These invasions were very effective, showing once more that dragonflies are highly capable of colonising new areas. No evidence could

be provided to state that species with a northern distribution are decreasing due to the higher temperatures. The habitats where these species live (mostly mesotrophic lakes and bogs) have been strongly influenced by eutrophication, acidification and desiccation in the 1960th and 1970th resulting in a decline of most of these species. This decline might have masked the influence of climate change.

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Appendix 1

Southern species and invasions

Six southern species rare or absent in the 1980's are now well recognised members of the Dutch odonate fauna: *Lestes barbarus*, *Erythromma lindenii*, *Aeshna affinis*, *Crocothemis erytraea*, *Orthetrum brunneum* and *Sympetrum fonscolombii*. *Anax parthenope* is expected to become established in the coming years, as it recently became a regular guest and has reproduced successfully. The way in which southern species became established in the Netherlands differs among the species. *E. lindenii*, *C. erytraea* (figure 6) and to a lesser extent *O. brunneum* gradually expanded the northern border of their range. The other three species *L. barbarus*, *A. affinis*, and *S. fonscolombii* became established after invasions, being rare in the years preceding these invasions (see table 6). The invasion of *Lestes barbarus* started in July 1994 (Ketelaar 1994) During the invasion records were made in most areas of the country with a strong emphasises on the dunes and the Pleistocene areas. At the majority of these localities several (up to 40) individuals were found. Almost all records were made at shallow, warm waters such as dried-out bogs and smaller dune lakes. In many cases the species established itself at these localities. Probably several smaller invasions occurred since 1994 but these went largely unnoticed as the species was already established. In the period since 1994 the species is found yearly in suitable habitat all over the Netherlands. Preceding the 1994 invasion the northern border of the distribution of *L. barbarus* was situated to the south of the Netherlands. The invasion in 1994 therefore resulted in a northwards expansion of its range of well over 300 km.

The invasion of *A. affinis* started mid July 1995. All 39 records from 1995 came from the southern part of the Netherlands, most of them from the coastal dunes or from the Pleistocene areas. Almost all individuals were found at drying or dried-out waters, with low reeds or bulrushes. Of the 81 sexed specimens only four were females. This might be partly due to the inconspicuous behaviour of the females. Since the 1995

Figure 6. The distribution of *Crocothemis erythraea* in the periods 1980–1993, 1994–1998 and 1999–2003, showing its gradual northwards expansion.

Table 6. Southern species rare during the eighties which have become established since 1990. The second column states whether or not the species became established during a large invasion or gradually expanded northwards.

Species	Established due to	Number of records in the 10 years prior to invasion	Number of records in year of invasion
Aeshna affinis	Invasion in 1995	1	39
Anax parthenope	Gradually (1)		
Crocothemis erythraea	Gradually		
Erythromma lindenii	Gradually		
Lestes barbarus	Invasion in 1994	14	79
Orthetrum brunneum	Probably gradually		
Sympetrum fonscolombii	Invasion in 1996	1	135

(1) *Anax parthenope* is not yet established but has become a regular guest and is likely to become established in the future.

invasion the species is found several times a year in all parts of the Netherlands. The first proof of successful reproduction was found in 2005 (Wasscher 2005) although it is likely that small (temporary) populations have existed since 1995.

In end May and begin June of 1996 a massive invasion of *Sympetrum fonscolombii* reached Northwestern Europe (Lempert 1997; Dijkstra and Van der Weide 1997). As with *Lestes barbarus* the species was recorded all over the country with a strong emphasises on the dunes and the Pleistocene areas. Most records were made at unshaded, standing waters with sparse vegetation and often sandy banks. The species managed to establish itself at many of these localities. Since 1996 the species is found every year at numerous localities across the country, although it has become less abundant than in 1996.

The invasions of *L. barbarus*, *A. affinis*, and *S. fonscolombii* have two things in common:

1　During the invasion almost all specimens were found at suitable habitats and not seldom successful reproduction was noticed in later years;
2　Most records during the years of the invasions referred to more than one specimen.

The three species which invaded The Netherland in 1994, 1995 and 1996 were rarely seen at unsuitable sites. This stresses the fact that these species are highly capable of localising suitable habitats. This is further emphasised by the fact that in most cases more than one individual was found at a locality. These species do not fly in clustered groups making it likely that the individuals from one locality all located the habitat on their own.

Probably these species used their ability to recognise polarized light combined with visual cues on vegetation structure to detect suitable habitat from some height as has been shown for some species of dragonflies (Corbett 1999). This makes that a relatively high portion of the individuals taking part in the invasion is able to reproduce at a potentially suitable location. These examples show that at least these species are capable of taking advantage of favourable circumstances in an extremely effective way.

Monitoring the effects of conservation actions in agricultural and urbanized landscapes – also useful for assessing climate change?

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Abstract

Various methods for measuring the success of conservation actions and for evaluating aquatic habitats are outlined, based on quantified dragonfly monitoring. They are discussed with respect to their practicability and information value, counts of adult males and especially of exuviae yielding the most valuable results. These are presented by actual examples of mire ponds, streams, ditches and rivers from central Europe, making allowance for the dynamics of the habitats and their dragonfly community. Records of detailed data, if repeated subsequently at the same localities with the same methods, are considered a useful basis for preparation of distribution maps and for comparison of the fauna over the time. Fauna shifts in horizontal and vertical distribution over the time should be judged critically with respect to climate change as they could also be caused by anthropogenic habitat changes.

Keywords

measuring conservation effects, species conservation, monitoring, dragonflies, Odonata

Introduction

The results of any efforts toward conservation and promotion of species become apparent in the development of species richness and population size of plants and animals. This does not only apply to the protection of more or less undisturbed ecosystems but is especially true for constructional measures in nature reserves aiming at the promotion of species diversity. On principle, there are two ways to measure the effect of

conservation actions: (1) to survey the number and diversity of species and (2) to follow up the long-term development of the local populations by counting individuals. In practice it will always be necessary to focus on selected groups of organisms or even on single species. Thereby, the choice of the focus organisms depends on the type and size of biotopes. For rather small oligotrophic grassland communities, orchids, grasshoppers or butterflies will be suitable, whereas for large marshes birds and amphibians would be a reasonable choice. Dragonflies (Odonata) have proved to be suited for many types of water bodies as the larval stage is spent under water. After completion of their development they emerge as imagines above water, mostly on riparian substrates, leaving the larval skins (exuviae) that can be collected for identification and census. Furthermore, reproductive activities of the adults occur at the breeding sites thus allowing easy determination of the species' variety. Since it is possible to carry out quantified odonatological field studies, dragonflies can be used for measuring the success or failure of conservation activities in wetland habitats. Here, a short account is given, mainly based on the author's experience, on methods, collection of data, analysis, and conclusions with respect to the development of dragonfly communities following wetland management mostly in nature reserves within agricultural and urban landscapes of central Europe.

What can be counted?

Quantitative studies require counts of species and individuals. Besides mature imagines these may comprise various developmental and maturation stadia, possibly combined with records of reproductive activities. A combination of various data will supply the best information, as they provide different evidence for the assessment of species richness, indigeneity, and population size. In this context the following single variables are of different importance:

Number of species. The number alone is little informative. It should be combined with the listed names of the species, possibly supplemented by indication of those belonging to respective regional Red Lists. Unless the list of species is based on a minimum of repeated counts scattered over the flying season and critically annotated with respect to the specific habitat requirements of the rare spp., it is of only limited informational value. There is no point in assigning numerical values to the different spp. in order to assess the effects of conservation actions or the importance of a biotope. This should be done by qualitative argumentation.

Number of individuals (mature imagines). Because of the male biased operational sex ratio at the breeding sites, counts of mature males yield a better basis than those of females for the estimate of the size of a breeding population at a certain locality. However, in territorial species that competitively space out conspecifics or temporally share a breeding site as in many Libellulidae, Corduliidae or Aeshnidae, the population size may be strongly underestimated. The number of recorded individuals at a specific site can also be indicated by abundance classes. In Baden-Württemberg/Germany the

following classes are used (cf. Sternberg & Buchwald 1999: 183): I = 1 individual, II = 2-5, III = 6-10, IV = 11-20, V = 21-50, VI = <50 individuals. Another method for measuring the colonization of a habitat is to determine the weekly or seasonal largest number of adult males at small ponds (Moore 2002) or the mean highest steady density of males per 100 m shore or bank stretch of large water bodies (Moore 1991). In any case, adults should be counted systematically, i.e. as often as possible or at least at regular intervals at about the same time, on sunny days with little or no wind, and between two hours before and past solar noon. Moore and Corbet (1990) even recommend counts within one or at most two hours of solar noon. The results yield a reasonable but rather unprecise idea of the real population size. A much better approach would be using capture-recapture. However, this requires marking of tenerals or adults and the application of mathemathical models. As for this method rather great expenditure is needed it is not practicable for surveys.

Presence throughout the flying season. Alternatively or in addition to counting the individuals simply the presence of the species may be noted on each visit. The sum of days with their presence – the frequency sum (FS) – can then be compared with that of the syntopic species. Consequently, the absolute and relative frequency sum (FS_a and FS_r [%]) may give a quantitative idea of the actual colonization of a water body (for more information and examples see below). In addition, the data may be used for computations applying simple or more sophisticated mathematical models.

Exuviae. They are the best evidence for successful breeding and the value of larval cases for semi-quantitative ecological studies cannot be overestimated. Thanks to the keys available for nearly all European species (e.g. Gerken and Sternberg 1999; Heidemann and Seidenbusch 2002), the identification is possible with certainty up to species level even for most Zygoptera. Exuviae of many species are found on plants emerging from a water body or on vegetation near its edge, while others cling to stones, sand, rocks, concrete walls, tree trunks, roots or posts. Larvae ready for emergence may walk ten metres or more over land and even climb on trees. However, most of them emerge near the water's edge. In *Somatochlora alpestris*, e.g., 91% of the exuviae were collected within a strip of one metre on each side of the water line (Knaus 2000). The total number of exuviae collected at a site throughout one emergence season, designated emergence sum (ES), should be indicated for every year separately. Generally, counts in Anisoptera are easily practicable. However, the exuviae of Zygoptera are small, delicate and often hidden among vegetation to an extent that it will be very difficult to detect relevant numbers. Although larval skins may persist for months under dense sedge vegetation or other sheltered places like rocks or parts of buildings like bridges or boathouses, they should be collected throughout the entire emergence period and as often as possible, especially before inclement weather, because rain or wind may displace or destroy them. Small and easily accessible ponds with well defined edges and emergent vegetation confined to a narrow riparian belt are most suited for quantitative exuviae collecting. On the other hand, at water bodies with large areas or wide zones of emergent vegetation it is most difficult or even impossible to come close to the effective seasonal emergence sum. Therefore, at more or less homogeneous breeding waters,

counts must be restricted to selected riparian sections or areas of largely overgrown water bodies and the total emergence number has to be assessed by projection. Some lake shores and river banks may only be accessible by raft or canoe. In large rivers with low water temperatures swimming with protective neoprene diving suit provided a most successful method for collecting exuviae of Gomphidae (Osterwalder 2004, 2007).

Larvae. They give also strong evidence for successful breeding of the respective species at certain sites. However, compared with exuviae, there are several disadvantages. Quantitative sampling of larvae requires special equipment and experience (e.g. Suhling and Müller 1997: 152–154). Furthermore, the sampling technique in dense submerged vegetation is completely different from that on sand or gravel ground. In addition, the larvae of many species, especially damselflies, are only identifiable under the miscroscope and for practical reasons they often have to be preserved in ethanol unless they are identified quickly and taken back to their habitat. Finally, stadia younger than F-0 or F-1 of many European species cannot be identified with the keys so far available. Even if all the larvae of a water body could be determined, the sum would not represent the reproductive population as only a small part of the larvae will survive.

Tenerals. A census of freshly emerged imagines, featured by pale colours and their bodies and wings still being soft, is especially recommended for Zygoptera as they are easier to find and to count than exuviae (Moore and Corbet 1990). Their presence indicate successful development at the place where they have been found with high probability. However, in some cases it may be difficult to identify the species in the field, especially in females of Coenagrionidae. Furthermore, many individuals are only present at water for a short time after emergence and subsequently disperse in the hinterland (e.g. Lestidae). Nevertheless, counting teneral Anisoptera (e.g. *Sympetrum striolatum*) may be an adequate method for estimating the size of mass emergence, provided the right moment – before the maiden flight – is chosen.

Additional indications for reproduction: For practical reasons it is not always possible to provide evidence for reproduction success of certain species by exuviae findings or observation of tenerals. Indications for reproduction at a water body, although weaker than those mentioned, are records of territorial males, tandems, copulation wheels, and ovipositing females. According to Höppner (1999), observed copulation or oviposition combined with the presence of minimal 2–5 adults may indicate indegeneity in many species.

Short-term and long-term studies at small stagnant water bodies

In order to assess the success of conservation measures and the future needs for management, as much information as possible is desirable on the dragonfly community of a site. Thorough short-term studies provide appropriate data on the actual state of species diversity and population size, and may be sufficient for immediate decisions of small operations or corrections in the habitats. However, biotopes and their biocenoses are dynamic systems to be considered in medium and long-term management plan-

ning. Therefore, besides data on the actual situation of a local dragonfly fauna, there is need for information on the development of their diversity and population size as pointed out in the following examples of small moorland ponds.
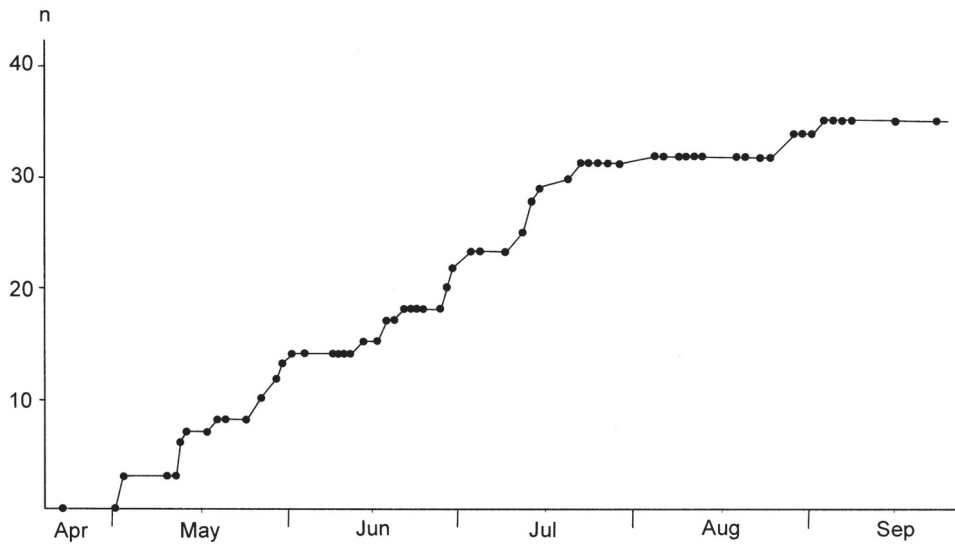
The water bodies are situated in the nature reserve 'Drumlinlandschaft Zürcher Oberland' on the Swiss plateau near Zurich (47°19'N, 08°48'E), ca. 500 m above sea level. The area is characterized by a number of small shallow valleys running parallel on turf ground between rolling, oblong and largely wooded hills (Wildermuth et al. 2001). In this region peat had been exploited extensively during three centuries. Around 1950 peat cutting, having been practised throughout extensively, was abandoned and subsequently the water filled peat holes and drainage ditches that functioned as secondary habitats for aquatic organisms for a long time became widely overgrown. Hence, the diversity and population sizes of dragonflies declined. From 1970, in the frame of conservation actions, about 30 peat diggings were successively restored or freshly created and maintained according to the rotational principle (Wildermuth and Schiess 1983; Wildermuth 2001). Monitoring of the dragonfly fauna also started in 1970 and has been continued up to the present with varied intensity according to the aims and the time available (Wildermuth 1980, 2005, 2008).

In 2005 an intensive short-term survey was carried out at 11 ponds varying in succession stage and in size between ca 10 and 80 m^2, situated within about 5 hectares moorland with fen and bog vegetation of the 'Böndlerried/Ambitzgi'. The site was visited on 63 days throughout the emergence and flying season, following approximately the same transect, but sometimes extended to some additional water bodies like ditches and puddles. Exuviae were collected systematically merely at 6 selected ponds, and of Anisoptera only. One of the ponds, no. 6d, was in the pioneer stage with bare peat at shallow edges, and so were two shallow ditches and a large puddle on turf ground. In total 35 dragonfly species were recorded (Table 1), i.e. 71% of the 49 spp. found between 1970 and 2005 within the entire nature reserve. As shown in Fig. 1 the cumulative number of species raised continuously during the flying season until its end. Only 30 of the 35 spp. frequented the 11 ponds (Table 2), the other 5 were mainly encountered at fresh ditches or puddles. The highest relative frequency sum was recorded in *Coenagrion puella*, followed by *Lestes sponsa* and *Libellula quadrimaculata*, with *C. puella* probably constituting the largest population. Out of the 30 spp. at least 16 are considered indigenous according to exuviae findings or the observation of tenerals, copulating pairs or ovipositing females. Two spp., *Lestes virens* and *Leucorrhinia pectoralis*, both indigenous in the sampling area, deserve special interest as they are critically endangered in Switzerland (Gonseth and Monnerat 2002) and threatened in most parts of Central Europe (e.g. Ott and Piper 1998). The relatively high frequency sum in *L. pectoralis* (FS$_r$ = 8.6%) and the finding of more than 100 exuviae indicate the conservational importance of the site. This is underlined by the regular occurrence of *Somatochlora flavomaculata*, *Orthetrum coerulescens* and other spp. that are nationally rare (Wildermuth et al. 2005). Most spp. are not confined to moorland ponds. In some of them a large FS may not conclusively signify high reproductive success and vice versa as shown at pond no. 7d for two aeshnids, with FS$_a$ = 7 and ES = 0 in *Anax imperator*

Table 1. Presence of adults of dragonflies on the ‚Böndlerried/Ambitzgi‘ during the flying season 2005. (Orig.)

date 2005 →	02.5.	12.5.	13.5	17.5.	19.5.	20.5.	24.5.	26.5.	29.5.	01.6.	03.6.	08.6.	09.6.	10.6.	11.6.	13.6.	16.6.	17.6.	18.6.	21.6.	22.6.	23.6.	24.6.	27.6.	28.6.
Calopteryx splendens																									
Calopteryx virgo									•					•	•					•	•				
Lestes sponsa														•				•		•	•	•	•	•	•
Lestes virens																									
Lestes viridis																									
Sympecma fusca	•							•																	
Platycnemis pennipes																									
Pyrrhosoma nymphula	•	•		•	•	•	•	•	•	•	•		•	•	•	•	•			•	•	•		•	•
Coenagrion puella		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Coenagrion pulchellum				•	•	•								•											
Enallagma cyathigerum								•												•			•	•	
Ischnura elegans																									
Ischnura pumilio								•																	
Aeshna cyanea																									
Aeshna grandis																									
Aeschna isoceles									•									•							
Aeshna juncea																								•	•
Aeshna mixta																									
Anax imperator									•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•
Anax parthenope																									
Cordulegaster boltonii																									
Cordulia aenea		•	•	•	•	•	•	•	•		•			•	•			•							
S. flavomaculata										•	•			•	•	•	•	•	•	•	•	•	•	•	•
Somatochlora metallica																									
Leucorrhinia pectoralis		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Libellula depressa		•		•		•	•	•	•					•				•	•	•			•	•	•
L. quadrimaculata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Orthetrum brunneum															•			•	•					•	•
Orthetrum cancellatum																		•							
O. coerulescens																									
Sympetrum danae																									
Sympetrum flaveolum																									
S. sanguineum																				•		•	•	•	•
Sympetrum striolatum																									
Sympetrum vulgatum																									

29.6.	03.7.	04.7.	09.7.	12.7.	13.7.	14.7.	15.7.	20.7.	22.7.	23.7.	25.7.	27.7.	28.7.	04.8.	05.8.	08.8.	09.8.	10.8.	11.8.	18.8.	19.8.	24.8.	29.8.	30.8.	31.8.	01.9.	03.9.	04.9.	05.9.	07.9.	15.9.	22.9.
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Figure 1. Development of the cumulative number of dragonfly species in the course of 63 visits during the flying period at 'Böndlerried/Ambitzgi'. (Orig.).

and FS$_a$ = 4 and ES = 43 in *Aeshna cyanea*. Similar observations had been made in earlier years. *Libellula depressa* and *Orthetrum brunneum* as pioneer spp. typically colonized pond no. 6d where mating and oviposition were repeatedly recorded. *Calopteryx splendens*, *C. virgo* and *Cordulegaster boltonii* bred in a small brook some hundred metres away from the pond area and regularly visited the stagnant waters. Therefore, they do not belong to the fauna of the ponds of the survey area. The same holds true for *Enallagma cyathigerum* that is regionally common but needs larger and deeper ponds with only little overgrown water surface. It will disappear as soon as the succession is proceeded. For a number of spp. that generally are not rare, e.g. *Ischnura elegans*, *Platycnemis pennipes*, and *Aeshna grandis*, the mire ponds seem to be unsuited. They are considered guest species as are *A. isoceles*, *Somatochlora metallica*, and *Sympetrum flaveolum*. This is in contrast to *Coenagrion pulchellum*, another sp. with very low FS. It has declined much in the area for unknown reasons but is still breeding in small numbers.

Small ponds and their dragonfly community may change in short time, especially in the early succession stages of a habitat. This is shown in a two years-study at the 'Oberhöflerried', at a different area of the same nature reserve as described above. Four new ponds, ca 50-125 m^2 in size and up to 1 m deep, were created within 1.5 hectares of fenland in autumn 2003. The late summer species *Sympetrum striolatum* and *Aeshna cyanea* oviposited immediately after the water holes were finished and their eggs overwintered. Monitoring was performed rather intensively in 2004 (23 visits) and in 2005 (34 visits). In both years 28 spp. were recorded but with different species composition. The list comprised 34 spp. for 2004 and 2005 in total and its composition resembeled that of the 'Böndlerried/Ambitzgi'. On the other hand, there were striking differences not only

Table 2. Presence of adults of the dragonfly spp. encountered at 11 ponds of the ‚Böndlerried/Ambitzgi‘ in 2005. The figures indicate the number of days with presence of the spp. on 63 visits throughout the flying season. FS$_a$ and FS$_r$ = absolute and relative frequency sum (see text). * = evidence for reproduction (exuviae, tenerals) (Orig.).

	2a	2b	3	4	6	6a	6b	6c	6d	7d	8a	FS$_a$	FS$_r$
Calopteryx splendens	1									8	1	10	0.6
Calopteryx virgo			3						1	2		3	0.2
Lestes sponsa	15	9	19	14	26	35	22	32	27	37	25	261*	16.5
Lestes virens	1	3	3	6		6		2	3	5	4	33*	2.1
Lestes viridis	2		1		6	1	1	2	3	5	3	24*	1.5
Sympecma fusca						1		3				4	0.3
Platycnemis pennipes										1		1	0.1
Pyrrhosoma nymphula	4	1	1	2	8	2	2	2		2	8	32*	2.0
Coenagrion puella	42	41	41	33	25	34	27	32	35	38	34	382*	24.2
Coenagrion pulchellum				1	3							4	0.3
Enallagma cyathigerum									13			13	0.8
Ischnura elegans									1			1	0.1
Ischnura pumilio									1			1	0.1
Aeshna cyanea		2	2	1	1	2			1	4	3	16*	1.0
Aeshna grandis		2				1				1		4	0.3
Aeshna isoceles		1										1	0.1
Aeshna juncea	2	2	1	1	8				1	7	1	25	1.6
Anax imperator	5	15	16	1	2	3		3	21	7	1	75*?	4.7
Cordulegaster boltonii						1				2		3	0.2
Cordulia aenea	5	4	3						1	5		18*	1.1
Somatochlora flavomaculata	6	4	3		5	4	7	2	1	12	3	47*	3.0
Leucorrhinia pectoralis	24	19	10	7	9	11	7	14	14	15	6	136*	8.6
Libellula depressa			4						18	1		19	1.2
Libellula quadrimaculata	23	30	20	22	15	17	19	24	36	28	14	248*	15.7
Orthetrum brunneum									8			8	0.5
Orthetrum cancellatum								1		11	1	13	0.8
Sympetrum danae			1				1	1		2		5	0.3
Sympetrum striolatum	7	5	3	2	9	7	5	5	8	15	12	88*	5.6
Sympetrum vulgatum						1	1		1	1		4	0.3
Sympetrum sanguineum	10	6	1	2	7	8	6	13	5	18	28	104*	6.6

in the species composition but also in the FS. Exactly these features changed impressively from the first year to the second, demonstrating the vivid dynamics of habitats and their dragonfly community throughout the pioneer stages of the ponds (Table 3). During the first year besides exclusive pioneer spp. such as *Libellula depressa* several other spp. that typically breed in advanced succession stages arrived in numbers: *Coenagrion puella, Enallagma cyathigerum, Ischnura elegans, Anax imperator, Libellula quadrimaculata*, and *Sympetrum striolatum*. All three *Lestes* spp. of the region were already present: They probably immigrated from the 'Böndlerried/Ambitzgi' that was situated 1.5 km

Table 3. Presence of adults of the dragonfly spp. in two subsequent years at 4 ponds that were created in autumn 2003 at the ‚Oberhöflerried‘. The figures indicate the number of days with presence of the spp. on 23 and 34 visits, respectively, throughout the flying seasons in 2004 and 2005. FS_a and FS_r = absolute and relative frequency sum (see text). * = evidence for reproduction (exuviae, tenerals) (Orig.).

	2004 (n = 23)						2005 (n = 34)					
	O1	O2	O3	O4	FS_a	FS_r	O1	O2	O3	O4	FS_a	FS_r
Calopteryx splendens	1	1			2	0.5	1				1	0.2
Calopteryx virgo	2	1		1	4	1.0	1	1		1	3	0.6
Sympecma fusca				0	0	0	13	6	2		21*	4.0
Lestes sponsa	2	3	2	1	8	2.0	2	7	1		10	1.9
Lestes virens	1				1	0.3			2		2	0.4
Lestes viridis	5	6	3	5	19	4.9	2	2	3	6	13	2.5
Platycnemis pennipes	1	1	2	3	7	1.8					0	0
Pyrrhosoma nymphula	3		3	1	7	1.8	9	6	8	5	28*	5.4
Coenagrion puella	10	10	14	15	49	12.6	17	28	18	15	78*	15.0
Enallagma cyathigerum	15	14	12	5	46	11.8	28	31	23	4	86*	16.5
Erythromma viridulum				4	4	1.0					0	0
Ischnura elegans	11	7	6	2	26	6.7	17	20	4		41*	7.9
Ischnura pumilio	2	1			3	0.8	1				1	0.2
Aeshna cyanea	2		3		5	1.3	4	3	2	1	10*	1.9
Aeshna grandis	1				1	0.3					0	0
Aeshna juncea	1			1	2	0.5	1	7	2	1	11	2.1
Aeshna mixta				1	1	0.3	2	1			3	0.6
Anax imperator	8	10	8	6	32	8.2	15	11	10	5	41*	7.9
Brachytron pratense					0	0	1			1	2	0.4
Cordulia aenea	3	5	2	3	13	3.3	11	7	6	2	26	5.0
Somatochlora flavomaculata				1	1	0.3	2	1		2	5	1.0
Somatochlora metallica					0	0			1		1	0.2
Libellula depressa	7	7	10	2	26	6.7			1	3	4	0.8
Libellula fulva					0	0			1		1	0.2
Libellula quadrimaculata	13	11	9	7	40	10.3	13	17	16	10	56*	10.8
Orthetrum brunneum			4	2	6	1.5		1	1		2	0.4
Orthetrum cancellatum	4	1	4		9	2.3	5	6	4		15	2.9
Orthetrum coerulescens	1		3		4	1.0					0	0
Crocothemis erythraea					0	0	2	4	1		7	1.3
Sympetrum danae	7	8	1		16	4.1					0	0
Sympetrum striolatum	11	13	9	10	43*	11.0	10	10	10	7	37*	7.1
Sympetrum vulgatum	2		1		3	0.8					0	0
Sympetrum sanguineum	7	3	2	3	15	3.8	1		1	1	3	0.6
Leucorrhinia pectoralis					0	0	6	4	1		11	2.1

away in the northwest. *Platycnemis pennipes*, *Erythromma viridulum*, *Ischnura elegans* and *Orthetrum cancellatum* presumably originated from a large pond 1.5 km apart in the southeast, *Calopteryx virgo* and *C. splendens* as guests from a nearby ditch with slowly running water. *Sympetrum striolatum* already emerged in the summer of the first year: Many exuviae and tenerals were found at three of four ponds, and *Aeshna cyanea* was recorded in the larval stage. Other spp. like *Pyrrhosoma nymphula* and *Orthetrum coerule-*

scens had already bred in the vicinity, but only the former sp. will establish at the ponds while the latter will remain an accidental visitor. *Aeshna mixta*, *A. grandis* and *Libellula fulva* are also considered guests as long as aquatic vegetation has not developed yet.

Looking back to the records of continuation and changes in the dragonfly community in the course of the first two years, some tendencies emerged. *C. puella*, *E. cyathigerum*, *I. elegans*, *A. imperator*, *L. quadrimaculata* and *S. striolatum* – all are at least partly univoltine spp. in this region – were expected to establish definitely breeding populations. *Sympecma fusca* arrived in spring of the second year, and immediately produced a new generation that emerged during late summer in numbers. For the reserve it was a new breeding sp. that is expected to colonize the ponds for many years to come. Others as *C. aenea*, *S. flavomaculata* and *O. cancellatum* will follow, while the pioneer spp. *I. pumilio*, *L. depressa* and *O. brunneum* will soon disappear. *Leucorrhinia pectoralis* was of special interest. As several males appeared at three of the four new ponds, *L. pectoralis* can be expected to become a breeding sp. here, hence the management actions are considered successful. Finally, from the species list it could be inferred that the species richness and the composition of the dragonfly community largely depends on the potential of the regional fauna.

Long-term monitoring (35 years) in the entire reserve yielded the following results:
– In total 49 dragonfly spp. were recorded, about half of them considered indigenous. The populations of most spp. could be maintained or promoted by appropriate management of the water bodies. Two breeding spp. became extinct, at least one sp. is considered a new permanent colonizer.
– Newly created ponds were immediately colonized by a relatively large number of spp. Some of them bred only in the pioneer stage of their habitat and disappeared already in the second or third year (e.g. *Libellula depressa*), while others established stable populations during the subsequent succession (e.g. *L. quadrimaculata*).
– The first univoltine pioneer species to colonize a newly created water body depended on the seasonal time of construction. In spring it typically was *Libellula depressa*, in autumn *Sympetrum striolatum*.
– In any species the seasonal number of emerging individuals varied enormously between different ponds and years up to a factor of >100 as shown for *Leucorrhinia pectoralis* in Table 4.
– *Leucorrhinia pectoralis* colonized only fishless water bodies on turf ground in medium succession stages, i.e. when the water surface was partly overgrown. Pioneer and late stages were avoided (Wildermuth 1992, 1994). The local population was promoted by rotational management of the breeding ponds (Wildermuth 2001, 2005).
– Some spp. emerged only four or five years after the construction of a water body, although adults were regularly present in the pioneer stage (*Cordulia aenea*, *Somatochlora flavomaculata*).
– Some spp. had to be considered as guests. They only appeared sporadically as individuals and never bred (e.g. *Aeshna affinis*, *Anax parthenope*, *Crocothemis erythraea*, *Sympetrum flaveolum*).

Table 4. Emergence sum (ES, number of exuviae) of *Leucorrhinia pectoralis* from 1984–2005 at six selected mire ponds (no. 2a-8a) in the 'Böndlerried/Ambitzgi'. (From Wildermuth 2005, completed).

	2a	4	6	6b	7d	8a
1984		78	39			
1985		28	11			
1986	1	5	6		1	
1987	42	2	2		29	30
1988	84		21	3	139	93
1989	9		13	3	31	8
1990	3	41	18	6	147	152
1991	18	102		20	1	2
1992	19	15		25	6	
1993	105	24		2	1	26
1994	177	6		30		3
1995	15	12		85	13	13
1996		15	1	7		1
1997		61		35	13	1
1998	521	40		64		
1999	66	9		1	10	
2000	50	17			5	
2001	59	101		13	17	
2002	6	31	6		5	
2003	23	50	18	8	11	
2004		1	4		7	
2005	3	2	3	3	55	
Total	1198	638	139	302	436	309

– A few spp. reproduced only temporarily with merely small numbers of offspring, the larvae mostly confined to a single water body (*Aeshna grandis*, *Aeshna mixta*, *Brachytron pratense*, *Somatochlora arctica*).
– The populations of at least two spp. declined, possibly due to climatic change (*Aeshna juncea*, *Sympetrum danae*).
– *Nehalennia speciosa* became extinct in the course of the study period, most probably due to desiccation and overgrowth of the habitat (Wildermuth 2004). *Coenagrion hastulatum* vanished before habitat management in the reserve had begun, possibly due to the loss of open water in the peat diggings.

Census at linear biotopes: ditches, brooks and rivers

Monitoring the dragonfly populations of small draining ditches and brooks is little problematic because the habitats are easy to survey, provided their banks are open and unhinderedly accessible. If their structure varies in different sections the suitability as habitat for the dragonfly fauna can be checked simultaneously

by regular collection of exuviae and counts of teneral and mature adults along the water course.

The results of simple counts of *Orthetrum coerulescens* at small draining ditches in a fen on a stretch of ca. 150 m are summarized in Fig. 2. There is strong evidence for reproduction at the site, and the annual population size may be assessed by the highest recorded number of males. In addition the seasonal development of the adult population can be followed up. The population exists for many years and had been established by restoration of ditches and fenland that was completely overgrown with shrubs. By subsequent maintainance of the ditches, always performed in spacial and temporal sections, the population increased. The highest daily number ever recorded during a five year period amounted 33 territorial males.

The second example concerns *Calopteryx virgo* that typically inhabits small and well oxygenated streams characterised by open running water, sunny patches, perches for territorial males, and water plants or rootlet felts as oviposition substrates. The species was monitored at a ditch-like water course 1 km in length running between a forest edge and a railway line, along a fen and through agricultural land. For hydraulic reasons, i.e. to enable the drain-off in periods with high precipitation, the river-bed was cleared sporadically. In order to preserve the benthic fauna, the works were carried out in sections and spread over a few years. As it was unknown if the method would prove successful, the effects on the aquatic biocoenosis was examined by a survey of the *Calopteryx virgo* population (Wildermuth 1986). A census of adult males and females was conducted on nine days during the flying season. The results from 1986 are represented in Fig. 3. They clearly show that some sections of the stream were more densely populated than others, obviously due to differences in habitat quality. Males and females concentrated mainly on sections III and IV where the creek was bordered by open fenland. However, from mid-July the number of individuals declined rapidly, especially at section III, probably because the water surface became covered with lush riparian vegetation and therefore was no longer visible for the dragonflies.

At rivers Gomphidae, typical inhabitants of large running waters, are suited for assessing the naturalness of the biotopes and the effects of restoration. The investigation methods may comprise mapping of adults and exuviae from the bank or by canoe and plotting the results in squares of 1 km² (e.g. Schlumprecht et al. 2004). The most accurate method in deep, fast running and cold rivers is certainly the collection of exuviae at the bank from the water side by swimming in a diving suit (Osterwalder 2004). This was also successful at newly created alluvial habitats like oxbows and cut-off meanders on the Swiss plateau (Osterwalder 2005, 2007). In the 'Foort'-example near Bremgarten (CH) the works were carried out in winter 2003/04 and 2004/05, respectively, and the survey of Gomphidae started in June 2005. Exuviae were collected at three new side branches as well as at two adjacent river sections upstream and downstream. Three Gomphidae spp. were recorded at the stretches in different numbers, surprisingly all of them also at the new habitats and in some cases in numbers (Table 5). It is assumed that the larvae were drifted from the main river bed into the new side branches where they found a suitable habitat for completing their development and emergence.
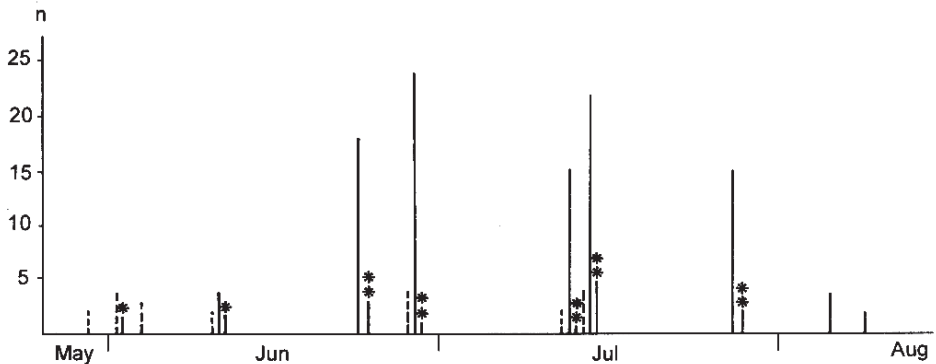
Figure 2. Development of a small population of *Orthetrum coerulescens* at 'Oberhöflerried' in 2005. Bars: adult males, broken bars: tenerals, * = exuviae, ** = copulae. (Orig.).

Summary, conclusions and outlook on faunal distribution shifts with respect to climate change

From the experience of survey and monitoring procedures the following conclusions are drawn:

(1) Dragonflies (Odonata) are suitable organisms for quantitative studies to measure the effects of conservation actions and to rate the value of aquatic habitats: They are conspicuous and attractive insects, restricted in species number, relatively easy to identify and to count, and they colonize a great variety of water bodies. Many species are habitat specialists.

(2) For the evaluation of biotopes all dragonfly species should be considered, not only those of the Red Lists. Regional common spp. may have a flagship role or they are important bioindicators, e.g. *Calopteryx virgo* for streams in urban landscapes, *Libellula depressa* for stagnant waters in pioneer stages, *Leucorrhinia dubia* for mire habitats, and *Cordulegaster bidentata* for seepage springs and headstreams.

(3) Methods of monitoring comprise counts of the number of species and individuals: larvae, exuviae, tenerals and mature adults. The latter can be indicated by the abundance classes, the weekly or seasonally largest number of adult males, the mean highest steady density, or by the frequency sum. Best method is the semi-quantitative collection of exuviae and the determination of the emergence sum. Additional indications for reproduction at a water body are obtained by records of territorial males, tandems, copulation wheels, and ovipositing females.

(4) Monitoring should consider the dynamics of biotopes and dragonfly communities, because species richness and its composition may change rapidly according to succession, especially in the early stages. Therefore, both short-term and long-term-studies are needed. Although the latter are uneconomic and require persistence they are of invaluable importance.
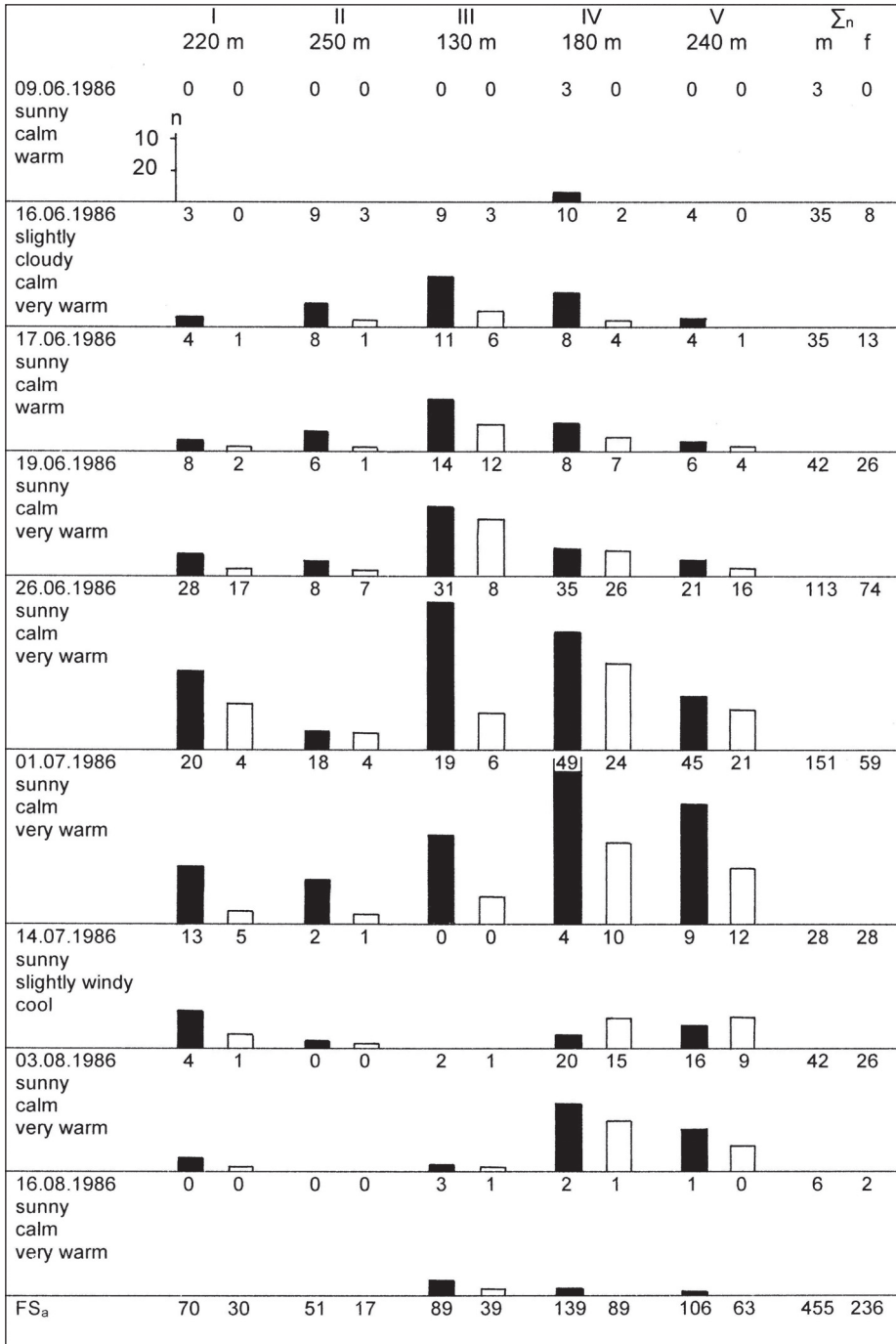
Figure 3. Development of a population of *Calopteryx virgo* in 5 sections (I-V) of a 1 km-stretch of a small brook near Wetzikon (CH) in 1986. Bars: number of adults per 100 m, black: males, white: females. The absolute number of recorded individuals is given above each column. Σ_n = total number of recorded males (m) and females (f) per count, FS_a = absolute frequency sum. (Orig.).

Table 5. Number of exuviae findings of three Gomphidae species at two sections of the river Reuss at ‚Foort' near Bremgarten (CH) and three adjacent side branches that had been created in winter 2003/04 and 2004/05. Numbers in each column: left *Onychogomphus forcipatus forcipatus*, middle *Gomphus vulgatissimus*, right *Ophiogomphus cecilia*. (Osterwalder 2007).

date of census	river Reuss section 1.331 1 × 1250 m			new side branch 1.348 2 × 475 m			new side branch 1.349 2 × 495 m			new side branch 1.350 2 × 140 m			river Reuss section 1.332 1 × 1250 m		
01.06.2005	0	31	0	0	94	0	0	16	0	0	64	1	0	1	0
23.06.2005	9	0	39	1	9	29	15	3	38	5	1	30	5	0	9

(5) Provided high quality and corresponding comprehensiveness, the monitoring data can be used as basis for distribution maps. The records with as much details as possible (see point (3), including those on geographical situation, altitude, date, weather, type of habitat) should be stored in central data banks.

(6) Dragonflies may serve as indicators for climate change. This can be assessed by comparison of data over the time. However, this method requires exact data on the species community of many localities, including abundance of species, geographical position, altitude, and habitat quality. Because exact historical data are usually not available, it is necessary to ascertain the present state of local faunas for future comparison. Yet the results of comparison between actual and former data should be interpreted with caution and refer to the complete regional fauna, i.e. not remain restricted to one or two species. Furthermore, it should be considered that changes in the dragonfly fauna may also be caused by biogeographic fluctuations for unknown reasons or by habitat alterations.

For central Europe, is expected that climate change will be become manifest in higher temperatures, increase of winter precipitation and decrease of summer rainfall. This will result not only in horizontal and vertical shift of many faunal elements but also in habitat changes. Shallow and tiny water bodies in moorlands, e.g., may dry up regularly in summer and therefore become unsuitable for larval development of habitat specialists. Furthermore, the periodically formed astatic habitats in prealpine alluvions filled up by melting water during the spring months could completely disappear due to the lack of high waters. The same may happen in gravel pits, ditches and other secondary habitats in the vicinity of river courses. On the other hand, lowering of the water table could also be caused by extraction of ground water for human requirements. Therefore, while assessing the effects of climate change on the dragonfly fauna, it is important to distinguish between climatic factors and other reasons affecting or improving the larval habitats. On this account, faunal surveys should always be paralleled by records of the local habitat conditions. So far only few regional long-term investigations complying with these requirements are available, an exceptional example being the studies by Vonwil and Osterwalder (1994, 2007). The more important it is to imply ecological data in future census studies.

Acknowledgements

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Anthropogenic climate change impacts on ponds: a thermal mass perspective

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Abstract

Small freshwater aquatic lentic systems (lakes and ponds) are sensitive to anthropogenic climate change through shifts in ambient air temperatures and patterns of precipitation. Shifts in air temperatures will influence lentic water temperatures through convection and by changing evaporation rates. Shifts in the timing, amount, and intensity of precipitation will alter the thermal mass of lentic systems even in the absence of detectable ambient air temperature changes. These effects are likely to be strongest in ponds (standing water bodies primarily mixed by temperature changes than by wind), for whom precipitation makes up a large component of inflows. Although historical water temperature datasets are patchy for lentic systems, thermal mass effects are likely to outweigh impacts from ambient air temperatures in most locations and may show considerable independence from those trends. Thermal mass-induced changes in water temperature will thereby alter a variety of population- and community-level processes in aquatic macroinvertebrates.

Keywords

climatic changes, lentic systems, ponds, dragonflies

Introduction

Little research has focused on freshwater biological impacts from anthropogenic climate change. Gaps in theoretical and observational perspectives on freshwater ecology stand in high relief in comparison with the amount of climate change impact research on marine and terrestrial systems (e.g., IPCC 2001; Parmesan and Yohe 2003; Root et

al. 2003; Thomas et al. 2004). Worldwide, freshwater aquatic systems account for 15 % of all known animal species even though freshwater covers only about 1.7 % of the world's land surface.

Most of the world's liquid freshwater is located in lakes, here defined as standing water bodies that are mixed primarily by wind. Ponds generally have less surface area than lakes (and thus fetch for wind) and have no more than a few meters of depth. They are here defined as standing water bodies mixed primarily by temperature shifts in the water column. Given their smaller size, ponds are generally more prone to drying than lakes. For the purposes of this chapter, I will divide them into (a) short hydroperiod ponds that are ephemeral and in normal-precipitation years dry up, most often in summer in temperate areas or in dry seasons in tropical zones, and (b) long hydroperiod ponds that persist throughout the annual precipitation cycle and disappear only in dry years. In most instances, ponds of both types require – and are defined by – precipitation patterns (Brönmark and Hansson 2005). And changes in precipitation patterns are likely to have a powerful impact on the inhabitants of ponds.

That said, anthropogenic climate change is probably not seen as the most widespread or pressing issue for lentic systems at the beginning of the 21st century (e.g., Poff et al. 2002). Habitat destruction, increasing withdrawals of surface water for human use, eutrophication, degradation of water quality as a result of industrial and agricultural pollution, acidification and nitrification of precipitation from industrial emissions, the transfer and invasion of exotic species, and many other consequences of human activity have been threatening the biota of freshwater systems for decades and even centuries (Williams 1997; Abell et al. 2000; Brönmark and Hansson 2002; Poff et al. 2002; Williams et al. 2003; Nicolet et al. 2004). Some critics have suggested that biologists studying climate change impacts are alarmists; climate change itself is not a new process, they correctly point out, and regional and global climate patterns shift naturally (e.g., Lomborg 2001). We can infer from the paleontological and paleoecological record that "natural" climate shifts resulting from a variety of nonhuman factors have contributed to the extinction of populations and species over ecological and evolutionary timescales (IPCC 2001). Why is the current period of human-induced change important for species, populations, and communities?

There are good reasons to suspect that the current era of human-induced changes are biologically significant and represent novel challenges to human resource management and ecological resilience and resistance. Past climate changes occurred in the context of relatively intact ecosystems. Species ranges could therefore respond in a plastic manner as the abiotic components of a niche shifted. The current period of human-induced climate change is thus occurring in across heavily modified (and often severely damaged) landscapes, with many fewer acceptable ecological and evolutionary escape paths that might have been open in the past (IPCC 2001; Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004). Perhaps most alarming, climate modeling suggests that global mean temperatures will continue to increase, and the rate of that increase is likely to quicken — perhaps considerably — over coming decades and centuries. At high latitudes and altitudes this era of rapid climate change may already have

begun for terrestrial systems (IPCC 2001; Thomas et al. 2004). Thus, climate change will creep up the list of important influences for most ecosystems; lentic ecosystems should prove no exception (Brönmark and Hansoon 2002).

Since we can expect climate changes to continue and increase in magnitude, the lack of scientific attention to realized lentic impacts from anthropogenic climate change is unfortunate, particularly given their role as important biodiversity reservoirs (Abell et al. 2000, Poff et al. 2002, Williams et al. 2003). I believe that understanding climate impacts on lentic systems will require approaches that will differ in important respects from those used to monitor and untangle terrestrial systems.

Basic to these new approaches is understanding the role of changes in thermal mass occurring as a result of climate shifts. Ambient air temperature is likely to be less important for aquatic biota than terrestrial species since lentic systems buffer aquatic species from air temperature and liquid water is far more difficult to heat/cool than the gases of the atmosphere. The physical properties of aquatic systems will be especially notable in short-hydroperiod ponds, which have small volumes, high variance in volume, and limited inflows; their temperature dynamics respond to water volume and thus thermal mass (Vannote and Sweeney 1980; Brönmark and Hansson 2005). The timing and amount of precipitation inflows for such systems are thus likely to be more important than ambient air temperature in determining seasonal temperature patterns. As a result, water temperatures may follow nonintuitive seasonal trajectories compared to mean air temperatures (Covich et al. 1997), and aquatic biological impacts may be similarly out of sync with surrounding terrestrial systems.

How might these impacts become manifest? Several global analyses have established that recent rises in mean global air temperature are correlated with terrestrial and marine species range and phenology shifts (e.g., IPCC 2001; Parmesan and Yohe 2003). Freshwater biological impacts have received much less attention than terrestrial and marine systems (Brönmark and Hansson 2002; Poff et al. 2002). Small lentic systems are dominated by poikilothermic species such as fish and aquatic macroinvertebrates that are metabolically sensitive to shifts in climate normals. Impacts on several lentic taxa have already been observed even though the realized effects attributable to anthropogenic climate change are small relative to predicted impacts (reviewed in IPCC 2001; Poff et al. 2002). This chapter will focus on the trends in changing precipitation patterns, the role of water volume on temperature shifts in small lentic systems, and (to a lesser extent) how these shifts might alter populations and communities of macroinvertebrates (particularly odonates) and present challenges for future research into climate change impacts on ponds.

Background: Trends in the Seasonality of Precipitation Patterns

Ponds receive inflows from direct precipitation, runoff from their catchment area (including meltwater from snow and ice), connectivity with temporary or permanent streams, and groundwater sources. All four sources will be heavily influenced by pre-

cipitation patterns, although lag times between the latter three and particular precipitation events may be hours, days, weeks, or (in the case of spring meltwater and groundwater sources) months. The major outflow for ponds that are not connected to streams is evapotranspiration.

Specific impacts on precipitation inflows have proven to be more difficult to model than air temperature in global climate models (GCMs), which are the primary basis for predicting climate trends (IPCC 2001; Allen and Ingram 2002; Karl and Trenberth 2003). Nonetheless, some models have shown a close relationship between human forcing and precipitation changes, particularly since 1945 (Lambert et al. 2004). Predictive power for the models may be limited and seems likely to depend on the type of feedback provided by the trajectory of sea-surface temperatures, the influence of atmospheric aerosols and clouds on air temperatures, and the relationship between air temperature and atmospheric humidity at a range of altitudes (Trenberth et al. 2003; Yang et al. 2003; Dore 2005). Much debate also exists about the role of anthropogenic forcing on large storm systems such as hurricane and cyclone frequency/strength and the intensity and periodicity of global or large-scale weather engines such as the North Atlantic Oscillation, El Niño–Southern Oscillation (ENSO) (e.g., Hurrell and Van Loon 1997; Karl and Trenberth 2002; Zahn 2003; Dore 2005). The long-term data to ground GCMs for these major events and cycles is especially limited.

Given these uncertainties, global mean air temperatures are predicted by GCMs to rise between 1.8 and 4.5°C by 2100 . The equivalent range for precipitation by these same models is a global mean increase ranging between 0.6 and 18 % over the same period (Allen and Ingram 2003). Unfortunately, few GCMs examine shifts in intra-annual changes in precipitation patterns. Most of the analyses developed within the IPCC framework span coarse temporal scales that are hard to relate to ecological time-scales, particularly in the context of ephemeral habitats like short-hydroperiod ponds.

Regional predictions from GCMs are also limited. Until the modeling process becomes sufficiently clear to resolve regional processes, the best description of what may happen in particular places is probably observed trend data from the 19th and 20th centuries that has been tempered with short-term modeling outputs. In many cases, historical data is limited, especially in un- and underdeveloped regions of the world. Long-term precipitation data is particularly prone to data quality issues that may exaggerate precipitation patterns (Karl et al. 1995). Nonetheless, several historical and modeling studies have described a handful of both global and regional patterns that are relevant to this discussion. These include:

– Global mean precipitation has increased about 2 % for the 20th century (Karl and Trenberth 2003).

– Precipitation events have risen in their frequency and intensity, particularly with regard to rainfall (Easterling et al. 2000; Allen and Ingram 2002). However, as Dore (2005) summarizes, these changes have not been part of a wholesale shift in the distribution of precipitation intensity but at the cost of both moderate-intensity events and non-rain precipitation. Regionally, these increases have occurred even when total

precipitation has remained steady or fallen. This data is generally interpreted as a sign that the variability of precipitation is itself increasing.

– Regional patterns began developing in the 20th century. In the words of Dore (2005), the "wet areas become wetter, and the dry and arid areas become more so." The northern hemisphere has seen much greater increases (7 to 12 % between 30 and 85°N latitude) than the southern hemisphere (2 % between the equator and 55°S latitude), perhaps as a consequence of having more terrestrial surface area. South Asia appears to show higher amounts of precipitation but not the high central plateau region. East Asia has seen a small decrease in precipitation since the 1950s, and western Canada has declined slightly in contrast to eastern Canada. Australia is divided in a similar pattern. Europe shows a wetter north and a drying south. On these continents, the increases/decreases in precipitation have been as much as several 10s of percent since 1910 (Dore 2005; Milly et al. 2005). A few high-resolution regional precipitation analyses are now being generated (e.g., see Zhang et al. 2000; Schindler 2001).

– The tropics and subtropics seem to follow decadal or multi-decadal cycles that are difficult to correlate with what is seen at mid and high latitudes. The subtropics appear to be generally declining in precipitation. Africa and South America are especially difficult to characterize, particularly northern Africa, which has seen both multi-decade severe droughts and multi-year wet periods and shows few significant large-scale patterns (Mann et al. 1998; Dore 2005).

– Accurate records of snowfall and snow cover extent (SCE) are quite rare worldwide, but SCE has been declining in the northern hemisphere's spring generally while winter SCE seems to be increasing. The spring SCE decrease has been closely correlated with spring ground temperatures in North America. Similar spring/winter patterns appear to be developing in Europe and Asia. Tropical SCE has seen rapid declines. Improved satellite data will improve the resolution of this data over coming decades (Karl et al. 1995; Karl and Trenberth 2003; Dore 2005).

– Pond and lake ice is breaking up two weeks earlier in spring in North America (Magnusson et al. 2000). This trend is likely widespread, but data is generally lacking.

– Comparable drought and flood data are also rare for the 20th century. Several sources believe both categories are becoming more frequent, and if the trend is confirmed it would support the interpretation above that precipitation patterns are becoming more variable. However, clear and widespread data to determine if their intensities have changed over the past century is still scarce. Mixed data also exists about whether trends exist regarding droughts as either a complete absence of rainfall or a decrease in the intensity in rainfall (Allen and Ingram 2002; Klein Tank and Können 2003; Trenberth et al. 2003).

– Evaporation rates are perhaps even more difficult to untangle than precipitation patterns, but they are generally expected to increase with higher air temperatures as the atmosphere becomes a potential larger reservoir for moisture. While mean global air temperatures have increased over the past century, they have not done so evenly, and some areas show little or no rise in air temperatures. Variation also exists in which intra-annual periods increases are occurring. However, within decades the pulse of

climate change is expected to be strong enough to induce air temperature increases worldwide, pulling higher evaporation rates in their wake (Allen and Ingram 2002).

Hydroperiod Impacts from Precipitation and Evaporation Shifts

Large-scale observational and modeling data suggest that seasonal pond volume dynamics (that is, pond hydroperiod) are likely to be shifting in many areas (Milly et al. 2005). For instance, intra-annual variation may result in significant shifts in seasonal precipitation-evaporation deficits. For the Canadian prairie provinces, for example, modeling based on a variety of possible climate impacts to lentic systems in this region suggests that elevated evapotranspiration rates might outweigh higher precipitation amounts in summer and fall (increases up to 10%), effectively shortening hydroperiods (Akinremi and McGinn 1999; Zhang et al. 2000). These increases are on the order of magnitude seen at this latitude in North America (Dore 2005). It has also been suggested that spring precipitation increases could extend short hydroperiods into the summer and fall (Akinremi and McGinn 1999, Schindler 2001). Another study suggested that ponds that were ephemeral only in dry years might desiccate in all years with a doubling of CO_2 levels (Manabe et al. 2004). Effectively, these are shifts in the seasonality of precipitation and evaporation.

Increased precipitation variability exists at two levels: individual precipitation events (more events overall, more intense and heavy events, and fewer moderate events), and in multi-month and multi-year scales in the frequency of droughts and floods. Both types of variability have strong implications for hydroperiod patterns. We begin to enter a more speculative area here since little observational data has been collected on ephemeral ponds over the 20th century (e.g., see Williams 1997), but we can follow the implications from predictions of changes in precipitation variability.

High-intensity rainfall, for instance, tends to increase runoff patterns at the expense of soil moisture; large volumes of runoff are thus likely to enter streams, lakes, and ponds than the groundwater recharge system following such events (Karl et al. 1995; Karl and Trenberth 2003). Likewise, more frequent and more intense droughts will leach out pond volume through evapotranspiration (Akinremi and McGinn 1999).

In both cases, the duration of an ephemeral pond would thereby be altered. What is also interesting to consider is that changing the seasonality, the amount, and the variability of precipitation all have the potential to alter the relative volume of water during its hydroperiod rather than merely extending or attenuating its extremes.

Impacts from Changes in Seasonal Pond Volume Patterns

The amount of water that an ephemeral pond's basin is capable of holding has obvious implications for its hydroperiod, but pond volume also impacts a variety of other biologically relevant variables.

Water Quality: Solubility

One study suggested that relatively small rises in air temperature (1 to 2°C) or declines in precipitation (5 to 10 %) resulted in large impacts on water quality for small prairie pothole ponds (discussed in Covich et al. 1997). Water quality can be variously measured (e.g., see Brönmark and Hansson 2005). Many ponds, for instance, contain a variety of salts from dissolved minerals found in the surrounding in soil, bedrock, or catchment zone. Shifting pond volumes will alter these concentrations through either dilution or concentration; solubility is also a function of temperature. Indeed, human-derived contaminants — fertilizer, animal waste, agricultural herbicides — that wash into the pond will respond in the same way as natural-source substances. Shifts in the concentration of soluble ionic compounds are also likely to alter pond pH. Turbidity changes should result as well since higher rates of precipitation (especially high-intensity events) will trigger higher rates of terrestrial erosion.

Water Quantity: Thermal Mass and Pond Water Volume

Most heat energy enters ponds as solar radiation (Brönmark and Hansson 2005). Increases in precipitation will be associated with increases in water volume and thus pond thermal mass (Brönmark and Hansson 2002). With a relatively constant set of energetic inputs acting on a greater thermal mass, pond temperature should decrease. Calculating the amount of cooling that would occur in a given pond from a particular change in volume is difficult to calculate in the field since many factors modulate temperature. The storm that delivered the precipitation itself, for instance, is likely to alter ambient air and ground temperature, and the storm's cloud cover may reduce solar radiation inputs into the pond for some days. Nonetheless, the pond should be cooler with more water, assuming the same amount of solar inputs. A trend towards a seasonal or annual increase in water volume is thus also a trend towards a cooler pond.

The reverse is also true: the lack of precipitation — either through an absence of rain or runoff or a decrease in the amount or frequency of precipitation events — leaves an unfrozen pond to the mercy of evaporative outflows and a subsequent loss of volume. Evaporation itself is a cooling process (Trenberth et al. 2003), but evaporation is perhaps most importantly a means of reducing pond volume and pond thermal mass (Brönmark and Hansson 2005). Again, given a constant set of solar inputs with a trend of less precipitation, the resulting smaller thermal mass will increase pond temperatures. Indeed, this warming process may proceed in a nonlinear fashion as higher pond temperatures facilitate evaporation (e.g., see modeling discussion in Covich et al. 1997).

Interestingly, these shifts may lead to trends in water temperature that are in opposition to ambient air temperatures. Such patterns may be at work in southern Ontario, Canada (Matthews, unpublished data). Since the late 1960s, spring precipitation amounts have increased several 10s of percent in this area while late-summer precipitation has declined

a corresponding amount. Even though Environment Canada and IPCC (2001) data suggest that air temperatures here have grown 1 to 2°C warmer in spring and remain flat in summer, pond volume trends suggest that water temperatures have declined in spring with increased precipitation and risen in August and September with rainfall declines. As a result, long-hydroperiod ponds may actually be shifting to a short hydroperiod cycle, attenuating regional hydroperiod (Covich et al. 1997; Akrinremi and McGinn 1999). Analogous patterns of regional hydroperiod and volume shifts should become common worldwide. Coming decades may come to prove that pond water temperatures are following trajectories that bear little or no correlation with local air temperatures.

Pond Volume and Thermal Stratification

A far more difficult synergy to predict is the interplay of climate change and thermal turnover processes in ponds. The turnover process is important to a wide range of organisms as it redistributes nutrients and gases within the water column (for a more thorough discussion, see Brönmark and Hansson 2005). Between turnover periods, relatively stable microhabitats are established within two thermal zones (the epilimnion and hypolimnion) separated by a steep temperature gradient in the water column (i.e., a thermocline). By definition, ponds are primarily mixed by thermal processes rather than wind; few ponds could therefore be called meromictic (i.e., of such a depth that there are regions that do not mix). Most ponds are therefore either polymictic (experiencing turnover more than twice a year, a pattern more common in regions without significant pond freezing) or bimictic (with spring and fall turnovers in temperate zones). One study suggests that temperate bimictic ponds can be expected to see a seasonally earlier onset of spring turnover and a later onset of all turnover. In some regions (e.g., ponds currently near the transition between subtropical and temperate latitudes), bimictic ponds may even become polymictic, although Covich et al. (1997) suggest that thermal stratification may prove more stable in spring and summer under elevated temperatures.

Between turnover periods, mixing does occur in the water column but most of this mixing is confined within each thermal zone. In effect, two ponds are formed. During warm seasons, one pond (the epilimnion) is near the surface and contains most of the photosynthetic organisms, high oxygen levels (at least during daytime hours), and higher temperatures. The second pond (or hypolimnion) is cooler and darker; high decomposition rates from detrital rain into this zone fuel aerobic decomposition and deplete oxygen levels. During cool periods, temperature differences are often less extreme within a pond, particularly when surface ice is present. The epilimnion then holds lower temperatures than the hypolimnion, which effectively forms a reservoir or refuge of warmer, denser water.

Climate change is likely to impact these zones in different ways. Increased evapotranspiration rates and higher temperatures will alter the upper thermal zone (Covich et al. 1997). Dissolved oxygen levels (DO) tend to decline as water temperature increases, and these trends may be exacerbated in eutrophic ponds when photosynthesis

ceases at night; in extreme cases, the epilimnetic zone may become hypoxic, killing organisms unable to disperse to more oxygenated regions of the pond (Brönmark and Hansson 2005).

Characterizing the Biota of Ephemeral Ponds

Short hydroperiod ponds frequently lack fish populations, especially large and piscivorous species (Williams 1997). Given that ephemeral pond are often small (<20 hectares), isolated, and show patchy distributions, fish-free ponds demonstrate both high species richness and high abundance of a wide range of taxa (Williams et al. 2003; Nicolet et al. 2004; Scheffer and van Geest 2006). Comparably sized long-hydroperiod ponds, especially those with fish, tend to lower species richness and abundances for overlapping groups; their community composition is often more typical of lakes in the same region (Williams 1997; Williams et al. 2004). Short-hydroperiod ponds are thus reservoirs of high alpha and beta biodiversity embedded in the terrestrial landscape (Scheffer and van Geest 2006). The short-lived nature and rapid successional cycling of ephemeral ponds suggests these communities may have much in common with other patchy environments with high disturbance rates such as forest treefall gaps or host plant clusters associated with specialist herbivores. Such systems have received much attention in recent decades via metapopulation and metacommunity theoretical approaches (e.g., see Hanski 1999; Holyoak et al. 2005) and by studies of life-history evolution, particularly explorations of the trade-offs associated with residential versus dispersal strategies (Harrison 1980; Roff 1986; Bilton et al. 2001).

Species adapted for patchy, ephemeral habitats generally face a choice between dispersing before a particular patch disappears or using some mechanism to remain in place and await the patch's reappearance (Bilton et al. 2001). Ephemeral ponds are no exception to this pattern. Many aquatic insects, for instance, have terrestrial stages in which dispersal occurs (e.g., most Ephemeroptera and Odonata), or they have behaviors or life-stages capable of resisting desiccation (a strategy more typical of larvae unable to disperse). Bet-hedging strategies are also common, such as distributing eggs or seeds across a variety of ponds or having offspring with a range of developmental and emergence rates. Similar strategies are also seen in vertebrates, mollusks, and plants adapted to ephemeral ponds (reviewed in Bilton et al. 2001; Bronson and Hansson 2005). Only a few studies have examined odonates in this regard (see Johannsen & Suhling 2004; review in Corbet 1999).

These strategies also imply that the timing (phenology) of major life-history events is critical to understanding the link between hydroperiod, habitat selection, and adaptational strategy (Jarvenin and Vepsalainen 1975; Hopper 1999). An adult dispersal strategy, for instance, is not effective from an evolutionary perspective if a pond dries up before an aquatic larva metamorphoses into a winged adult form. The birth and death of a water body mark clear and absolute boundaries for the organisms within. From this perspective, a short hydroperiod is useful in so far as it is regular and pre-

dictable. Indeed, Williams has identified the ecological predictability of hydroperiod as a critical and widespread adaptation for species that specialize in short-hydroperiod ponds (1997). A largely unexplored issue in this regard is the relationship between species richness and hydroperiod regularity at large spatial scales. A network of ponds, for instance, differ in their roles as population sources or sinks based solely on hydroperiod.

Biotic Impacts from Changes in Precipitation

Broadly speaking, population and species level effects from anthropogenic climate change have been lumped into shifts in seasonal behavior (phenology) and range shifts. Community-level effects includes changes in relative abundance, richness, and composition (e.g., Parmesan and Yohe 2003). These are coarse, general categories, yet they may be too specific for examining the impacts of changes in precipitation patterns on small ponds given the current small base of knowledge. Too few climate change studies have focused on the particular organisms that specialize in these habitats.

Not all aquatic environments have been so neglected. A handful of studies have explored the thermal constraints of lotic (flowing water) specialists, particularly those of low-order streams (e.g., Sweeney and Vannote 1978; Vannote and Sweeney 1980; Bêche et al. 2006). Some connections have been made between lotic species phenology and large-scale climate cycles (Briers et al. 2004). Experimental manipulations of streams have even been attempted in a number of instances (Hogg et al. 1995; Hogg and Williams 1996; Hogg et al. 2001; Smith and Collier 2005). Some researchers have also begun to examine warming impacts on long-hydroperiod lentic systems such as large lakes (e.g., McKee et al. 2002). Only a handful of studies have examined lentic species-level thermal impacts (Gillooly and Dodson 2000; Van Doorslaer and Stoks 2005a,b). Not all aquatic taxa have been ignored either. A substantial literature devoted to thermal tolerances of fish — particularly commercially important species — long predates the climate change impact literature (for a recent review, see Xenopoulos et al. 2005).

Given the isolation of ephemeral ponds from other water bodies and their relatively small amounts of water volumes, small lentic systems are especially sensitive to changes in precipitation patterns. Fish species are likely to be poor proxies for impacts on most of the invertebrate taxa present in short-hydroperiod ponds. I will focus here on areas I feel that biologists should be aware of as potential impacts or impacts already in progress that merit attention in the field and laboratory, with some highly speculative attention to odonates in particular.

Inter-annual Precipitation Variability

Climate variability stands in direct contrast to the maintenance of hydroperiod regularity (Williams 1997), particularly in the sense of variability in the frequency of droughts

and floods that will dramatically lengthen, delay, or abbreviate hydroperiod. Particularly destructive may be droughts that shift long-hydroperiod periods into short-hydroperiod cycles or extremely wet periods that alter the competitive environment of short-hydroperiod ponds in favor of long-hydroperiod species. Greater rainfall, for instance, may increase pond connectivity and lead to higher rates of pond dispersal by fish, substantially changing pond community composition and structure.

Adjustments to New Thermal Regimes

Regional trends in hydroperiod are likely to have widespread effects on the thermal regime of small ephemeral ponds beyond hydroperiod alone (Covich et al. 1997; Brönmark and Hansson 2002). For aquatic invertebrates, temperature appears to be a major source of community and species level niche differentiation in freshwater systems, whether in a linear context along a stream or river's watershed (Vannote and Sweeney 1980) or within a thermally stratified pond or lake (Sanderson et al. 2005). Poikilothermic invertebrate organisms dominate these systems in richness, abundance, and (in most cases) biomass (Brönmark and Hansson 2005). Given their sensitivity to temperature, such species often show thermal influences on growth rate and size, fecundity, metabolic rate, activity levels, phenology, behavioral strategy, and emergence rates (Vannote and Sweeney 1980; Brönmark and Hansson 2002), which together have second-order effects on range limits, abundance, and interactions with competitors, predators, and conspecifics (Williams 2003; Scheffer and van Geest 2006).

Climate change impacts in all of these areas have been widely documented in terrestrial, marine, and a few freshwater aquatic species. What has not been appreciated previously, however, is that water temperatures in small lentic systems may not correlate with neighboring terrestrial systems very closely. Indeed, given observed shifts in precipitation to date, the temperatures of small bodies of waters may be quite unlikely to track air temperature trends in coming decades. Increases in precipitation may be a global trend, but the result of more rain on small ponds may be decreases in water temperature. For aquatic insects, cooler temperatures tend to result in reductions in growth and development and lower metabolic and activity levels, all of which could alter the phenology of adult dispersal and reproduction. The resulting climate mismatch may be an example of an ecological trap being slowly set and tripped (Battin 2004).

Direct thermal modulation of the traits listed above may be best described as ecological responses to climate change. These are expected to occur over ecological timescales, ranging from one generation to (perhaps) several dozen or hundred generations. Evolutionary responses are also possible to climate change. Evolutionary responses are much harder to characterize or predict than ecological shifts, though a handful of convincing cases have been posited for insects (e.g., Rodríguez-Trelles and Rodríguez 1998; Thomas et al. 2001). In the case of ephemeral ponds, more frequent droughts might shorten pond hydroperiod regionally and provide a source of directional selection to complete development more quickly (Covich et al. 1997).

A microevolutionary response in this context implies that natural selection is sorting through differential and heritable phenotypes based on their relative fitness in a changed environment. While such responses are theoretically possible for all populations and species threatened by deleterious climate change impacts, in fact most populations are highly constrained by such factors as the rate of climate change, by the magnitude of change in environmental factors, by the lack of genetic variation associated with variation in phenotype, or the degree of phenotypic elasticity. A species may thus be unable to complete development in response to shorter hydroperiods because hydroperiod is advancing several weeks per decade and over a large spatial scale, or because the little or no genetically based phenotypic variation in development time exists within the species.

Potential Thermal Impacts on Odonates

Based on the limited work on the subject of thermal mass shifts to date, any speculation applying this perspective to odonates must serve as an example of scientific recklessness. Nonetheless, given the constraints of this volume, I will plunge ahead boldly. Several categories of change particular to odonates seem likely given the impacts described above:

– So-called "spring" species in temperate and subtropical zones are likely to reflect mismatches between water and air temperatures. Two impacts appear possible. First, in regions with less spring and winter precipitation, the thermal mass of small freshwater systems will decrease, resulting in warmer water and faster rates of development that may outpace observed shifts in the phenology of nearby terrestrial systems. Second, regions with more spring and winter precipitation (especially more winter rain) will see the opposite effect: more thermal mass and slower development, resulting in phenological delays relative to nearby terrestrial systems. Evolutionary impacts resulting from either shift may be driven more by community-level processes, such as food availability for teneral adults.

– "Summer" species in temperate and subtropical zones may see even more pronounced impacts as widespread warm-season trends of higher air temperatures and evapotranspiration rates, combined with decreased precipitation, reduce the amount and thermal quality of available habitat. Abbreviated hydroperiods will serve as a hard ecological boundary that could serve to limit the ranges of many species, with few evolutionary responses possible. Summer species may be forced to shift range boundaries when possible.

– Trends towards warmer temperatures are likely to facilitate increases in the number of odonate generations per year in many species. Such shifts have already been observed in North American freshwater plankton (Daniel Schindler, personal communication) and British butterflies (Roy and Sparks 2000) but historical data are limited for comparisons between periods of relative climate stability (roughly 1850 to 1970) and periods of rapid warming (since 1970). Thus, we may have few opportunities to record the occurrence of these shifts in odonates.

– Far more likely to be recorded are changes in the historical range boundaries of long-observed species. These changes have been widely observed in many taxa (e.g., Parmesan and Yohe 2003). Recent reports suggest that "tropical" odonates have entered subtropical zones such as Florida, USA (Paulson 2001) since the late 1960s. There are also intriguing reports that the overwintering larvae of bivoltine species with both slow-developing overwintering larvae and fast-developing summer larvae may have separate ranges that are shifting independently (Catling 2003; Westover 1999). In high-latitude zones such as northern Canada, the combination of rapidly increasing temperatures and ample water supplies could result in dramatic poleward shifts as these regions effectively trade exotic temperate odonates for native Arctic taxa. Similar trends should be occurring in high-altitude areas as well.

Taking these trends in the aggregate, climate trends over the twenty-first century are likely to favor the species most capable of colonizing new habitats (i.e., high-dispersing species and species that specialize in short-hydroperiod systems), species that are tolerant of extreme temperature conditions, and temperate and subtropical species whose range is primarily limited by winter cold.

Research Needs for Ephemeral Pond Species and Communities

Profiles of how small single ponds have changed over long temporal periods are probably the most important gap in how understanding of how ponds may be changing in coming decades. Data linking water volume, water temperature at several depths, ambient air temperature, and the relationship between particular precipitation events and changes in water volume are essential parameters for creating a new generation of models. In essence, we need to develop a thermal life-history of small lakes and ponds.

Closely related is the issue of regional hydroperiod and precipitation trends. Can we make generalizations between a measurable shift in regional precipitation and hydroperiod regularity? Moreover, how does climate variability alter regional hydroperiod?

The biological impacts of changes in water temperature should also be a major research focus. Ephemeral ponds possess high variance in biotic and abiotic qualities seasonally and regionally, requiring substantial tolerance for variation on the part of their specialist denizens. Will future conditions remain within these tolerances, or will new levels of environmental variation extend beyond the limits of resilience and resistance? This area is ripe for species and community level experimental manipulations.

Some impacts on aquatic species can already be associated with a changing climate; indeed, other chapters with this volume provides ample documentation for effects on odonates alone. This research must extend over two levels. First, what large-scale patterns can we observe? What directions do we see in phenology or range shifts, and how are richness and abundance being modified at the community level? This level of detail is descriptive and observational. Second, we need proxy studies that reveal the specific mechanisms of change at population, species, and community levels. Can we

find proxy species for particular habitats and regions that allow us to untangle the complex elements that may be driving climate change impacts? This second approach will help determine why the changes we are observing at large scales are occurring, and it may ultimately assist in developing strategies to mitigate and untangle adverse impacts through policy shifts and more effective resource management.

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Expansion of *Crocothemis erythraea* in Ukraine

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Abstract

A noticeable expansion of some Mediterranean species takes place in Europe during last several decades and this data are related to climatic effects clearly. The present work is a review of literature and original data on distribution of *C. erythraea* in Ukraine. In the beginning and middle of XX century in Ukraine the Scarlet Dragonfly was observed in southern area at Dnieper valley, in outmost southwest at Danube delta at the west of Ukraine in Transcarpathian and Forecarpathian. Next, this species was registered at the foothills of Carpathian Mountains. During last three decades *C. erythraea* was also recorded at the north and east (central regions, eastern, northern and northeastern areas). Since 2000 new points have been registered in Odessa, Kherson,Vinnytsya, Cherkasy, Chernihiv, Kyiv administrative regions and in Crimea.

Keywords

dragonflies, range expansion, *Crocothemis erythraea*, Ukraine, monitoring

Introduction

Crocothemis erythraea is Palaearctic-Afrotropical-Oriental species, which distributed in Europe, Transcaucasus, Near East, Mid- and Central Asia, Northern and Tropical Africa, Madagascar and Northwestern India. In Western Palearctic the Scarlet Dragonfly occurs in the south and middle parts, reaching the Netherlands (Hermans and Gubbels 1997), Belgium (Knijf 2003), south of England (Jones 1996; Butler and Butler 1998; Parr 2001, 2002). The map of distribution C. erythraea in Western Palearctic region was made due to analysis of recent literature (fig. 1). In Europe it was found in Austria (Schweiger 1983; Chwala 1990; Raab et al. 1996; Ehmann 1998), Bulgaria
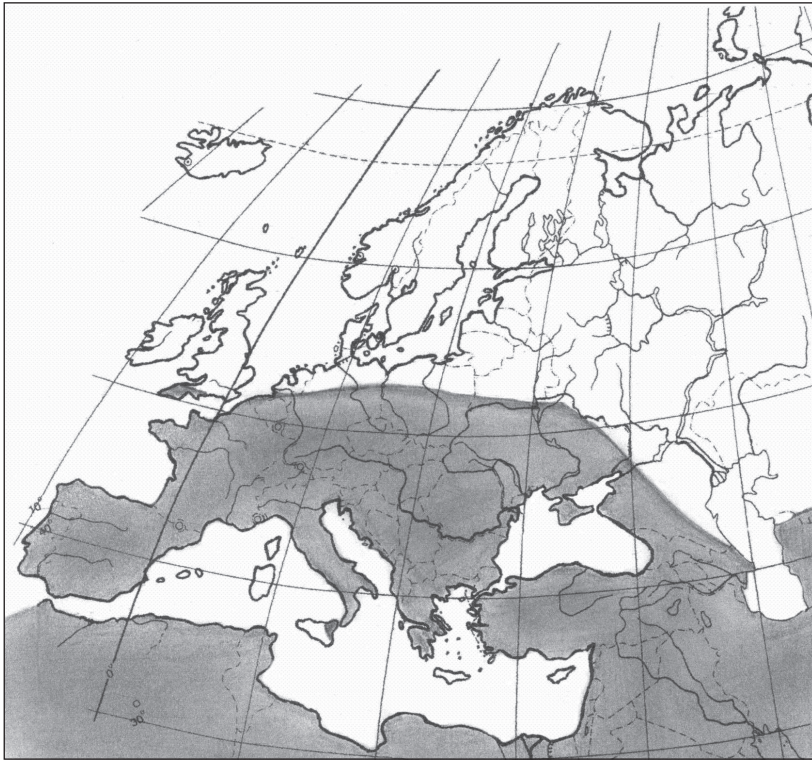
Figure 1. Distribution of *Crocothemis erythraea* in Western Palearctic.

(Beshovsky 1964a, 1964b, 1965, 1968; Scheffler 1973; Mauersberger 1985, 1990; Beutler 1987; Donath 1987; Beshovsky and Marinov 1993, 1998), Croatia (Trilar and Bedjanič 1999), Czech Republic (Mocek 1998; Waldhauser 2001), France (Rehfeldt 1991; Hazet 1992; Convey 1992; Papazian 1994, 1998; Wildermuth 2005), Germany (Müller 1987; Ott 1988, 1996, 2001; Stenberg 1989; Schorr 1990; Malkmus 1993, 1998; Bauhus 1996, 2001; Xylander et al. 1998; Donath 2001, 2003; Lohr 2003; Horn 2004; Schlumprecht et al. 2004; Heidecke and Lindemann 2004, Mauersberger 2004), Hungary (Ambrus et al. 1996a,b,c,d,e), Italy (Letardi and d'Auria 1991; d'Antonio 1996, Terzani and Lo Cascio 1997), Moldova (Artobolevs'ky 1929; Andreev 1998), Poland (Czekaj 1994; Bernard 1999; Kalkman and Dijkstra 2000; Theuerkauf and Rouys 2001; Dolny 2003; Dolny et al. 2003), Slovakia (David 1990; 1998; Sibl 2001), Romania (Lehrer and Bulimar 1979), Spain (Aguero and Ferreras 1994; Cordero 1996; Pedrocchi and Ferreras 1996; Torralba and Ocharan 2003), Switzerland (Kiauta and Kiauta 1984; Weidmann 2001; Kunz and Hunger 2003; Gonseth and Monnerat 2003; Graf et al. 2004). *C. erythraea* also was registered in Asian part of Western Palearctic: Azerbaijan (Bartenev 1901), Jordan (Schneider 1985), Kazakhstan (Chaplina 2004), Tajikistan (Borisov 1987), Turkey (Hacet and Aktaç 1997; Kalkman et al. 2003; Van Pelt 2004), Saudi Arabia (Schneider 1995), Uzbekistan (Bartenev 1912) and northern Africa: Tunisia (Jodicke 2003).

A noticeable expansion of some Mediterranean Odonata species like *C. erythraea* occurred in Europe, beginning around 1980. Because the northward spread of these species is especially well documented, it seems worthwhile trying to correlate it with detailed climatic data now at hand (Ott 2001; Dijkstra, 2006). Scarlet Dragonfly colonizes the new biotopes mostly on initial stages of succession. Investigators registered the increasing of population sizes in higher altitudes as well. For example, in Germany *C. erythraea* have spread over several hundreds kilometers to the north and about 400 meters in altitude for last two decades (Ott 2001). Investigators consider this phenomenon as consequence of global climatic changed and propose *C. erythraea* as good indicator species.

Material and methods

The present work is a review of literature data on distribution of *C. erythraea* in Ukraine. Author use the data of own collection and observation during 1999–2009 and data of collection of colleagues entomologists which were kindly lent for author as well.

Results and discussion

In the beginning and middle of XX century in Ukraine the Scarlet Dragonfly was observed in southern area at Dnieper valley (Artobolevs'ky 1929; Brauner 1902), at Danube delta (Brauner 1903; Bezvali 1932) and in Western Ukraine in Transcarpathian and Forecarpathian (St. Quentin 1933; Grabar 1933) and Crimea (Artobolevsky 1929b; Pliginsky 1913). Pavlyuk (1990) collected this species in 1968 and 1973 at the foothills of Carpathian Mountains. During last two decades *C. erythraea* was recorded in Ukraine in outermost southwest at Danube delta (Gorb and Ermolrenko 1996; Dyatlova 2005, 2006), in Crimea peninsula (Kiseleva and Vershitsky 1998; Prokopov 2003), in the west (Vizslán and Huber, 2001) and towards to north and east, namely central regions (Barsov 1987), eastern (Martynov and Martynov 2003), northern (Tytar 2003; Matushkina 2006) and northeastern regions (Khrokalo 2000). In 2000–2007 new points were registered in Vinnytsya, Chernihiv, Kyiv administrative regions and in Crimea. Detailed data of all records are presented in regional order in the table 1. These points are mapped on the fig. 2 as well with numbers according to table 1 and years of records in parentheses.

Thus, *C. erythraea* is abundant in south areas, in other territories it occurs rarer. It expansion in Ukraine toward the north and east has been observed obviously. The flight period in Ukraine was registered from the end of May to end of September. Larvae were collected in different type of waters, such as lakes, ponds, rivers, brooks and pools, brackish waters. One of aspects which define this species is its ability to colonise the waterbodies on initial stages of succession. *C. erythraea* is characterized by R-strategy of population development, preference for higher temperature of environment, good flyers in adults, exophytic oviposition and other features of "winners" spe-

Table 1. Records of *Crocothemis erythraea* in Ukraine

№	Location	Date of records	References	Number of specimens, notes
Northern and Northeastern Ukraine				
1.	Sumy region, Yampil' distr., Nature Park "Prudysche"	17.07.1999	Khrokalo 2000	1 female - in Ulichka river valley at the derivation canal
2.	Chernihiv region, Borzna distr., env. vill. Yaduty	10.06.2002	Sheshurak P unpublished data	1 male
3.	Kyiv region, Vyshhorod distr., env. vill. Osischyna	27.06.2004, 6.08.2004, 2.07.2005	Matushkina 2006	2 males, 6 female, 1 exuviae were found at the lotic waterbodies. Tandems and oviposition were observed.
4.	Kyiv, Dnieper River, Trukhaniv Island		Tytar 2003	
5.	Env. of Kyiv, lake Ped'kine	4.07.2004	Khrokalo 2005	1 male
6.	Kyiv, lake Malynivka	23.06.2005	Khrokalo L unpublished data	2 males
7.	Kyiv, Golosiivsky Park, pond	25.07.2006	Khrokalo L unpublished data	1 male
8.	Kyiv region, Boryspil distr., env. of vill. Devichki, Dnieper river	12.07.2005	Matushkina 2006	1 female
9.	Kyiv region, Obukhiv distr., env. Kozyn, Kozynka river.	14.09.2003	Khrokalo L unpublished data	larva 1 female
Western Ukraine				
10.	Zakarpats'ka region, env. of Uzhhorod		Grabar 1933	
11.	Zakarpats'ka region, env. of Khust, lake in Tissa River valley	14.06.1968	Pavlyuk 1990	1 male
12.	Zakarpats'ka region, Mukacheve town, pond	26.09.1973	Pavlyuk 1990	1 male
13.	Zakarpats'ka region, Latorytsya river, env. of Mukacheve	28.07.1997	Vizslán and Huber 2001	1 male, floodplain of the Latorytsya river, *Reunoutria japonica* in some places.
14.	Zakarpats'ka region, env. of Velykaya Dobron', canals	25-30.07.1997	Vizslán and Huber 2001	7 males, slowly flowing almost stagnant water, silty bed and macrovegetation, on banks *Salix*.
15.	Chernivtsi region, Storozhynets' distr., vill. Jadova	13-20.07.1931	St. Quentin 1933	Common species.
16.	Vinnytsya region, Shargorod distr., vill. Klekotyne	24.06.2004	Stolbchaty V unpublished data	1 male

№	Location	Date of records	References	Number of specimens, notes
Central Ukraine				
17.	Cherkasy region, Kanivs'ky reserve, Dnieper River, Zmiyni Islands	11-12.06.2004	Matushkina 2006	2 male, 2 female
18-20.	Central Ukraine, Dnipropetrovs'k region, valleys of Dnieper, Samara, Mokra Sura, Vovcha rivers.		Barsov 1987	
East Ukraine				
21.	Donets'k region, Artemovsk distr., env. vill. Dronovka, valley of Sivers'ky Donets' River	27.07.2002	Martynov and Martynov 2003	1 female was found at the bogged bank of lake
South Ukraine				
22.	S Ukraine, Mykolayiv region, bank of Ingul river	June 1914	Artobolevs'ky 1929a	1 female
23.	S Ukraine, Zaporizhzhya region. Between Zaporizhzhya and vill. Bilen'ke	23-24.07.1927	Artobolevs'ky 1929a	2 males
24.	Kherson region, env. of Kherson		Brauner 1902	Numerous records. Emergence took place from end of May with duration about month. Copulation started from end of June.
25.	Kherson region, Gola Prystan town, Dnieper delta, Konka river	4.08.2004	Dyatlova 2006	Abundant
26.	Kherson region, Gola prystan distr., Stara Zburiivka vill	2.08.2004	Dyatlova 2006	2 females
Southwestern Ukraine				
27.	Odessa region, env. of Izmayil	26.06.1902	Brauner 1903	1 male, 1 female
28.	Odessa region, env. of Izmayil		Bezvali 1932	
29.	Odessa region, Kiliya distr., vill. Prymors'ke	15-28.06. 1995	Gorb and Ermolenko 1996	9 males, 1 female
30.	Odessa region, Kiliya distr., Vilcove town	14-19.09. 1995	Gorb and Ermolenko 1996	1 male, 2 females
31.	Odessa region, Kiliya distr., west bank of Sasyk Lake	12.09.1995	Gorb and Ermolenko 1996	1 female
32.	Odessa region, Kiliya distr., Vilcove town	25.05.1996, 7,10.07.1997	Dyatlova 2005, 2006	2 males, 3 female3

№	Location	Date of records	References	Number of specimens, notes
33.	Odessa region, Kiliya town, Danube delta	24.05.2003, 24.05.2005	Dyatlova 2005	larva 1 male; in May 2005 author observed mass emergence
34.	Odessa region, Kiliya distr., env vill. Kyslytsya, Danube flood-lands	21.08.1999	Dyatlova 2005	1 male, 1 female
35.	Odessa region, Reni distr., env. vill. Novosil'ske, lakes	9.07.2004	Dyatlova 2005	1 male, 1 female
36.	Odessa region, Bolgrad distr., vill. Vynogradivka, Yalpug lake	21.06.1999 13.07.2003	Dyatlova 2005	2 females
37.	Odessa region, Izmayil distr., Danube delta "Izmayil Islands", Tataru Island	6.07.2005	Dyatlova 2005	1 male, 1 female
38.	Odessa region, Izmayil distr., Danube delta, Tataru Island	1-10.07. 2003	Matushkina 2006	7 males, 19 females
39.	Odessa region, Stambul's'ky Island	7.07.1997	Dyatlova 2005	2 females
40.	Odessa region, Izmayil distr., Kugurly lake	17.08.1996	Dyatlova 2005	1 male
41.	Odessa region, Bilyaivka vill, branch of Bystry Turunchuk river	26.06.2005, 28.07.2005	Dyatlova 2006	2 males
42.	Odessa region, Bilyaivka distr, Mayaki vill.	19.06.2003, 12.06.2004, 26.06.2005, 30.06.2005	Dyatlova 2006	4 males, 3 females
43.	Odessa region, Ovidiopol distr., env.of Prilimanskoye vill., Sukhoy liman	3,15.06.2003, 15.05.2004, 5.06.2004, 4, 18.07.2004, 17.08.2004	Dyatlova 2006	9 males, 6 females
44.	Odessa region, Ovidiopol distr., Dnistrovsky firth, Nadlymanske vill.	5.06.2005	Dyatlova 2006	1 male, 1 female
45.	Odessa city	17.07,8.08. 2004, 18.08. 2005	Dyatlova 2006	2 males, 3 females
46.	Odessa region, Berezivka town, Tyligulsky firth	8.06.2005	Dyatlova 2006	1 male
Crimea				
47.	Steppe part of Crimea peninsula		Kiseleva and Vershytsky 1998	Larvae in waterbodies of different types
48.	South coast of Crimea, env. Sevastopol' city	09.07.1906	Artobolevsky 1929b, Prokopov 2003	1 male Larvae in different lentic and lotic water, springs

№	Location	Date of records	References	Number of specimens, notes
49.	South coast of Crimea, env. Inkerman town	30.06-09.07.1912	Pliginsky 1913 Prokopov 2003	Adults Larvae in different lentic and lotic water, springs
50.	West coast, Bakhchisaray dist, env. vill. Beregove, Bulganak river	23.08.2001	Khrokalo and Prokopov 2009	larva 1 ♀
51.	Bakhchisaray dist, env. vill. Plodove, pond on river Al'ma	08.08.2008	Khrokalo and Prokopov 2009	1 male
52	Saky dist. lake Donuzlav	25.08.2008	Khrokalo and Prokopov 2009	2 females
53	env. of Bilogirsk, Rusanovsky pond	26.07.2007	Khrokalo and Prokopov 2009	2 males
54	Simferopol'	1898 30.06-09.07.1912	Artobolevsky 1929b, Pliginsky 1913	1 male Adults
55	Simferopol' dist., vill. Poznanske, pond on river Bukganak	06.08.2008	Khrokalo and Prokopov 2009	2 males
56	South coast, Alushta distr., env. Rybache, Kanaks'ka gully	6.05.2005	Khrokalo and Prokopov 2009	larvae 2 juv. were found in small pool near road
57	Yalta, pond in Mys Mart'yan reservation	08-10.07.2008	Khrokalo and Prokopov 2009	2 males
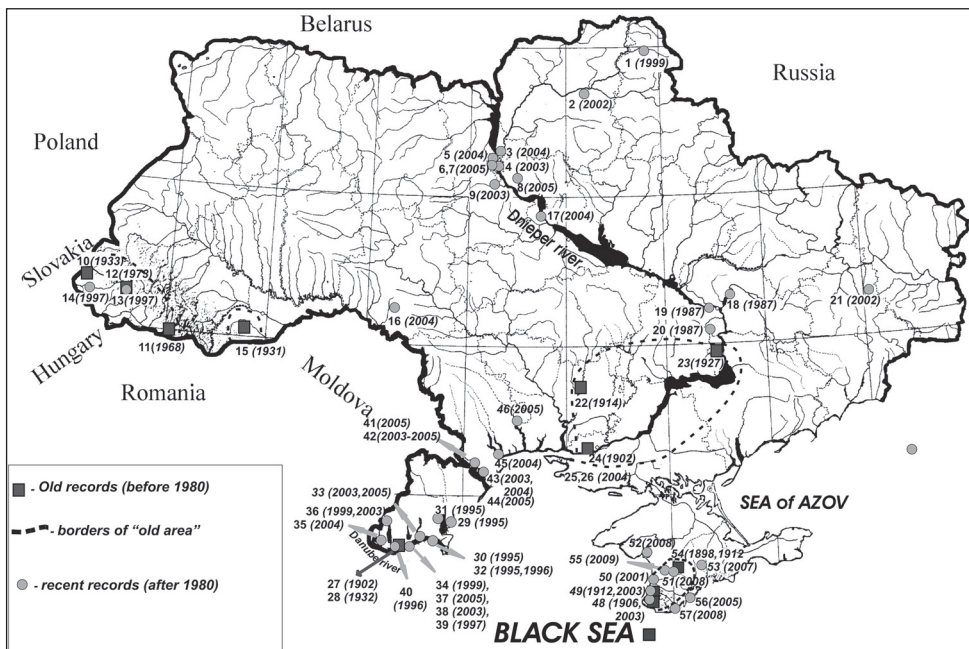
Figure 2. Records of *C. erythraea* in Ukraine.

cies (in competition). Most northern point of it breeding in Ukraine was registered in the north in Kyiv region (№ 3 in tab. 2). As climatic changes taking place, in Ukraine the average temperatures increases on 0,2–0,3°C during last two decades (Bilyavs'ky et al, 2004)), so more intensive expansion of Mediterranean species could be expected in future.

Acknowledgements

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RESEARCH ARTICLE

Dragonfly and Damselfly (Insecta, Odonata) Distributions in Ontario, Canada: Investigating the Influence of Climate Change

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Abstract

We analysed temperature data and odonate distribution data collected in the province of Ontario, Canada, over approximately sixty years. Analysis of temperature data from 31 weather stations collected in the years 1945–2000 showed an overall significant increase in the minimum, maximum and mean monthly temperatures; these trends were not adjusted for changes in urbanisation. Comparison of county level presence/absence data for odonates from the 1950´s and 2002 found a slight decrease in the northernmost distributions of some species, although no significant patterns were evident. Lower sampling coverage in the larger, more northerly counties in Ontario, as well as the assessment of distributions based on county records may limit the sensitivity of our approach in detecting changes in odonate species distributions over time. Future work should focus on increasing the coverage, uniformity and geographic detail of available datasets, as well as evaluating range change through testing predictions based on the ecology and biogeography of odonate species.

Keywords

temperature, Odonata, climate change, range extension, Ontario

Introduction

Climate Change, Ecological Responses & Odonates

Compelling evidence for a global trend in environmental warming continues to accumulate (IPCC 2007, Karl and Trenberth 2003). Likewise, researchers have found ecological and evolutionary responses to the effects of climate change in a number of plant and animal groups (Huntley 1991, Hughes 2000), with a range of data specifically from arthropods (Parmesan et al. 1999, Warren et al. 2001). Further study of the ecological and evolutionary responses of a number of plant and animal groups is necessary to better understand and predict future climate change responses, and to potentially mitigate the detrimental effects of climate change.

Organisms can respond to climate change in a number of ways: by going extinct, by adaptation *in situ*, by range change or expansion (Coope 1995), and/or through plastic changes in life-history patterns (Butterflied and Coulson 1997, Hassall et al. 2007, Paremesan 2007). The type of response observed will likely be a function of both the type of organism involved (based on its ecology and life-history), as well as the home-range conditions of that organism. Dragonflies and damselflies (Insecta: Odonata), offer great potential as an indicator group for anthropogenic disturbances, such as habitat alteration, and climate change (Corbet 1999 Chapter 12 and sources therein). The majority of dragonfly species have an obligate aquatic larval stage, linking their ecological success to the distribution and quality of a range of aquatic habitat types throughout the landscape. As an aerial adult, odonates demonstrate a potential for dispersal and recolonization (Conrad et al. 1999), with some species migrating great distances in response to seasonal changes in weather and climate (Wikelski et al. 2006). As such, the possibility of range change and expansion is high in this group, if other ecological factors (such as the distribution of appropriate habitat for specialist species) allow for such responses.

Recent work has investigated the change in range size of dragonflies and damselflies to detect the effects of climate change (De Knijf et al. 2001, Ott 2001, Ott 2007). Work published by Hickling et al. (2005) detected a significant expansion of the total range, as well as the northernmost range extent, of non-migratory odonates in Britain. Hassall et al. (2007) have also found significant changes in the phenology of British odonates, with advances of 1.51±0.060 days per decade (or 3.08±1.16 days per degree rise in temperature) in the leading edge (first quartile date) of the flight period between 1960 and 2004. As odonates are a ubiquitous group of organisms, found on many continents and in many biomes, investigation of the response of this group could prove a useful indicator for the effects of climate change in regions throughout the world.

In this current study, we have assessed data on the distribution of dragonflies and damselflies in the province of Ontario, Canada, using surveys at different time periods (1950´s and 2002) to evaluate potential changes in species ranges. We compare these

preliminary results to recorded changes in climatic conditions in Ontario that have arisen over this same time period. As with any survey work, one of the important interpretive constraints is knowing whether a recorded absence actually corresponds to a genuine absence. We discuss our results and their implications in the light of these constraints, and we suggest potential directions for future research.

Habitat and Climate in Ontario

Ontario is a large province, covering an area of 1,076,395 km² (approximately 15% of which is covered with water) divided among three geographic regions: the Precambrian Shield (a rocky region with many lakes and wetlands that comprises over half of the province) in the northwestern and central regions, the Hudson Bay lowlands in the extreme north and northeast and the Great Lake/St. Lawrence Valley region in the south. The northernmost point of the province lies at 56°51'N, extending south to 41°54'N at the end of Point Pelee in Lake Erie, a distance of over 1600 km (the west-east extent of Ontario is from 95°10'W on the border with the province of Manitoba to 74°19' where it adjoins the province of Quebec, along the St. Lawrence River, just over 1500 km). There are a total of 47 administrative counties in the province (see Figures 1 and 2).

The climate of the province ranges from a moderate humid continental climate in the southernmost regions of southern Ontario (Peel et al. 2007) to a more severe humid continental climate in the central portions of the province. These regions have relatively hot summers and cold winters, though summers are shorter in the north. Northern Ontario (especially above 50°N latitude) has a much longer and more severe winter.

The Odonate Fauna of Ontario

Ontario has a rich odonate fauna, attributable at least in part to the diversity of habitat types distributed on a north-south gradient within the province. Many species that are associated with more southerly habitats in the United States, such as the Carolinean forests, are found in southern Ontario, while more northerly-distributed species, such as those found within the boreal forests, are common to the northern regions of the province (Dunkle 2000, Catling et al. 2004). As such, species ranges within this region may be more significantly affected by climate change than in other geographies.

The data used for these analyses (see below) indicate the presence of 134 species of Odonate, distributed over a total of 9 families: Aeshnidae, Cordulegastridae, Corduliidae, Gomphidae, Libellulidae and Macromiidae in the suborder Anisoptera (dragonflies); Calopterygidae, Lestidae and Coenagrionidae in the suborder Zygoptera (damselflies) (see Table 1). The species within these groups utilize a large range of habitat types, from large lakes, ponds and marshes to small streams and large rivers.
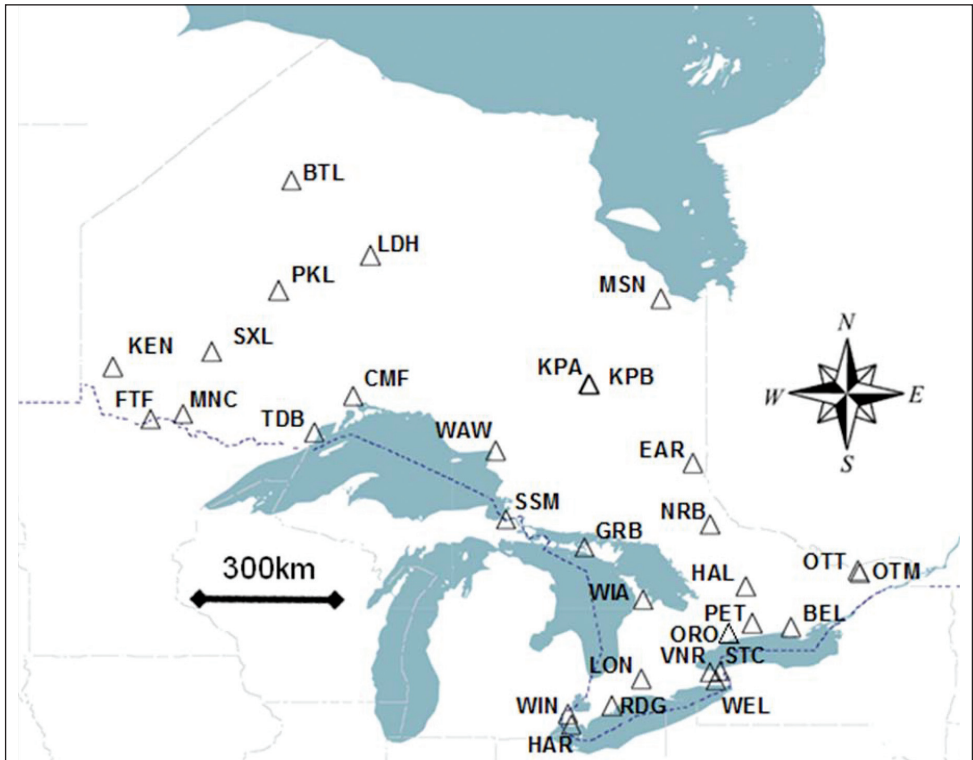
Figure 1. Map of the Province of Ontario, showing weather station locations. Stations are labelled as follows: Belleville (**BEL**); Big Trout Lake (**BTL**); Cameron Falls (**CMF**); Earlton (**EAR**); Fort Frances (**FTF**); Gore Bay (**GRB**); Haliburton (**HAL**); Harrow (**HAR**); Kapuskasing A (**KPA**); Kapuskasing B (**KPB**); Kenora (**KEN**); Lansdowne House (**LDH**); London (**LON**); Mine Centre (**MNC**); Moosonee (**MSN**); North Bay (**NRB**); Orono (**ORO**); Ottawa (**OTT**); Ottawa MacDonald (**OTM**); Peterborough (**PET**); Pickle Lake (**PKL**); Ridgetown (**RDG**); Sault Ste Marie (**SSM**); Sioux Lookout (**SXL**); St. Catharines (**STC**); Thunder Bay (**TDB**); Vineland Ritterhouse (**VNR**); Wawa (**WAW**); Welland (**WEL**); Wiarton (**WIA**); Windsor (**WIN**).

Many species are habitat generalists, while some, such as *Nehalennia gracilis*, specialize in specific habitats (in this case, sphagnum bogs, similar to *N. speciosa* in Europe (Lam 2004, Dijkstra 2006)).

Due to their range of habitat preferences, some species are found in only a single region of the province; for example, many species, such as *Sympetrum vicinum* and *Celithemis elisa*, are found only in the southermost regions of the province, while species such as *Aeshna juncea* and *Somatochlora whitehousei* are found only in the north. Still other species, such as *Leucorrhinia hudsonica*, are found throughout the province. Some species, while found over a large area, have a patchy distribution, due to the limited presence of their preferred habitat type. Finally, some species, such as *Anax junius*, are migratory: in this case, individuals will fly south in the fall, and the offspring they produce will return to Ontario in the spring. In the case of *A. junius*, only some
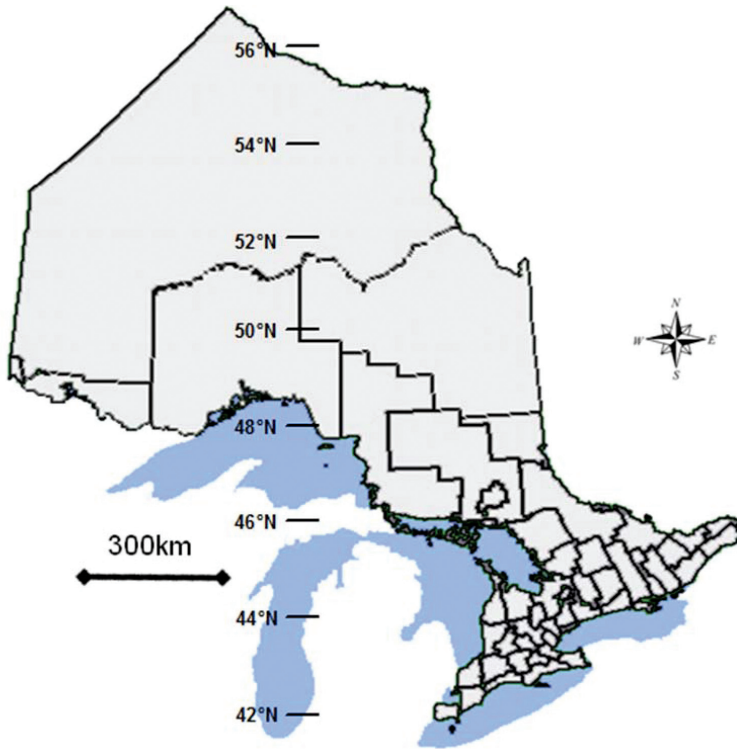
Figure 2. Map of the Province of Ontario, showing county boundaries and latitude (°N). Odonate presence/absence was recorded and analysed on a county by county basis. Northern range extensions were calculated by assessing the mean and northernmost extent of the counties in which each species was found.

populations are migratory; others, often found in the same habitats with individuals that migrate, remain in Ontario throughout the year, completing their entire life cycle in these lakes and ponds.

Methods and results

Unadjusted estimates of climate change in Ontario

We assembled data on maximum and minimum monthly temperatures collected at 31 weather stations throughout Ontario (Canadian Centre for Climate Modelling and Analysis, http://www.cccma.ec.gc.ca/data/data.shtml), starting in January 1945 and continuing through 2000, (Figure 1, Table 2). These data approximately coincide with the time period of our odonate distribution data (see below). Fluctuations in the mean monthly temperatures of three winter months and three summer months over these decades are shown in Figure 3a and 3b.

Table 1. List of Ontario odonate species found in datasets used in this analysis. Species are grouped by suborder and family. The change in northernmost latitude by county between the 1950´s and 2002 is listed as increased (+), decreased (-) or unchanged (U).

SUBORDER/ Family	Change	SUBORDER/ Family	Change
ANISOPTERA		*Somatochlora septentrionalis*	U
Aeshnidae		*Somatochlora albicincta*	U
Boyeria vinosa	+	*Somatochlora hudsonica*	U
Boyeria grafiana	U	*Somatochlora cingulata*	U
Basiaeschna janata	U	*Cordulia shurtleffi*	U
Nasiaeschna pentacantha	-	*Dorocordulia libera*	-
Epiaeschna heros	+	**Gomphidae**	
Aeshna eremita	U	*Hagenius brevistylus*	U
Aeshna interupta interupta	U	*Ophiogomphus colubrinus*	U
Aeshna interupta lineata	-	*Ophiogomphus carolus*	-
Aeshna canadensis	U	*Ophiogomphus rupinsulensis*	+
Aeshna clepsydra	U	*Ophiogomphus anomalus*	-
Aeshna tuberculifera	+	*Lanthus albistylus*	-
Aeshna sitchensis	U	**Gomphidae (cont´d)**	
Aeshna umbrosa	U	*Gomphus lividus*	-
Aeshna constricta	+	*Gomphus graslinellus*	U
Anax junius	+	*Gompus exilis*	U
Cordulegastridae		*Gomphus quadricolor*	+
Cordulegaster maculatus	+	*Gomphus spicatus*	U
Cordulegaster diastatops	-	*Gomphus villosipes*	-
Cordulegaster obliquus	U	*Gomphus furcifer*	+
Corduliidae		*Gomphus cornutus*	U
Neurocordulia yamaskanensis	-	*Gomphus descriptus*	-
Epitheca princeps	U	*Gomphus fraternus*	U
Epitheca cynosura	+	*Gomphus vastus*	U
Epitheca spinigera	U	*Gomphus brevis*	U
Epitheca canis	U	*Gomphus scudderi*	+
Helocordulia uhleri	U	*Gomphus notatus*	U
Williamsonia fletcheri	-	*Dromogomphus spinosus*	U
Somatochlora walshii	-	**Libellulidae**	
Somatochlora minor	U	*Nannothemis bella*	-
Somatochlora elongata	-	*Perithemis tenera*	+
Somatochlora williamsoni	+	*Celithemis eponina*	U
Somatochlora tenebrosa	-	*Celithemis elisa*	U
Somatochlora franklini	U	*Libellula quadrimaculata*	U
Somatochlora kennedyi	-	*Libellula/Ladona julia*	U
Somatochlora forcipata	+	*Libellula lydia*	-
Somatochlora whitehousei	U	*Libellula luctuosa*	-

SUBORDER/ Family	Change	SUBORDER/ Family	Change
Libellula pulchella	U	*Lestes inequalis*	-
Libellula semifasciata	-	*Lestes congener*	U
Libellula incesta	+	*Lestes unguiculatus*	-
Libellula vibrans	U	*Lestes dryas*	-
Erythemis simplicicollis	+	*Lestes disjunctus*	U
Pachydiplax longipennis	+	*Lestes forcipatus*	+
Sympetrum corruptum	-	*Lestes rectangulais*	-
Sympetrum vicinum	+	**Coenagrionidae**	
Sympetrum costiferum	U	*Argia moesta*	U
Sympetrum semicinctum	-	*Argia apicalis*	-
Sympetrum danae	U	*Argia tibialis*	+
Sympetrum rubicundulum	-	*Argia sedula*	U
Sympetrum internum	U	*Agria translata*	U
Sympetrum obtrusum	U	*Argia violacea*	U
Leucorrhinia hudsonica	U	*Chromagrion conditum*	-
Leucorrhinia patricia	U	*Amphiagrion saucium*	+
Leucorrhinia glacialis	U	*Nehalennia irene*	U
Leucorrhinia proxima	U	*Nehalennia gracilis*	+
Leucorrhinia frigida	U	*Coenagrion resolutum*	U
Leucorrhinia intacta	U	*Coenagrion interrogatum*	U
Tramea carolina	-	*Enallagma carunculatum*	U
Tramea lacerata	+	*Enallagma civile*	-
Pantala hymenea	-	*Enallagma boreale*	U
Pantala flavescens	+	*Enallagma cyathigerum*	-
Macromiidae		*Enallagma vernale*	U
Didymops transversa	U	*Enallagma hageni*	U
Macromia illinoiensis	U	*Enallagma ebrium*	-
ZYGOPTERA		*Enallagma geminatum*	+
Calopterygidae		*Enallagma exsulans*	-
Calopteryx maculatum	-	*Enallagma antennatum*	-
Calopteryx aequabilis	U	*Enallagma apersum*	-
Hetaerina americana	+	*Enallagma vesperem*	-
Lestidae		*Enallagma signatum*	+
Lestes eurinus	+	*Ischnura posita*	+
Lestes vigilax	-	*Ischnura verticalis*	*U*

To test whether overall temperatures in Ontario have changed over this period, and estimate the size of these changes we fitted a General Linear Model (GLM) to the climatological data with year as a covariate and site as a random factor. These analyses indicated a significant increase in minimum, mean and maximum temperature over the period 1945 to 2000 (see Table 3 for results), as well as a significant site effect. The rates of temperature

Table 2. List of Ontario weather stations with their latitude and longitude coordinates.

Station Name	Latitude (N)	Longitude (W)
Belleville	44.15	77.40
Big Trout Lake	53.82	89.90
Cameron Falls	49.15	88.35
Earlton	47.70	79.85
Fort Frances	48.65	93.43
Gore Bay	45.88	82.57
Haliburton	45.03	78.53
Harrow (Aut)	42.03	82.90
Kapuskasing A	49.42	82.47
Kapuskasing B	49.40	82.43
Kenora	49.78	94.37
Lansdowne House	52.20	87.93
London	43.03	81.15
Mine Centre	48.77	92.62
Moosonee	51.27	80.65
North Bay	46.37	79.42
Orono	43.97	78.62
Ottawa	45.38	75.72
Ottawa MDonald	45.32	75.67
Peterborough	44.23	78.37
Pickle Lake	51.45	90.22
Ridgetown	42.45	81.88
Sault Ste Marie	46.48	84.52
Sioux Lookout	50.12	91.90
St Catharines	43.20	79.17
Thunder Bay	48.37	89.33
Vineland Ritterhouse	43.17	79.42
Wawa	47.97	84.78
Welland	43.00	79.27
Wiarton	44.75	81.10
Windsor	42.27	82.97

increase were relatively consistent throughout the year such that temperatures in Ontario have increased at the rate of about 0.02°C per year (1°C in 50 years) in both summer and winter months (Figure 3a and 3b, Figure 4). These results are in line with larger-scale assessments of climate change, which have found increases in mean annual temperatures throughout southern Canada ranging from 0.5°C to 1.5°C over the 20th Century (Bonsal et al. 2000, Zhang et al. 2001). Our analysis does not account for important effects such as urbanisation (Prokoph and Patterson 2004), which could artificially increase estimates of rates of change of temperature at many of our locations where weather stations are situated. The significant differences in temperatures among sites are not unexpected, since sites in the northern regions of Ontario are consistently colder throughout the year.
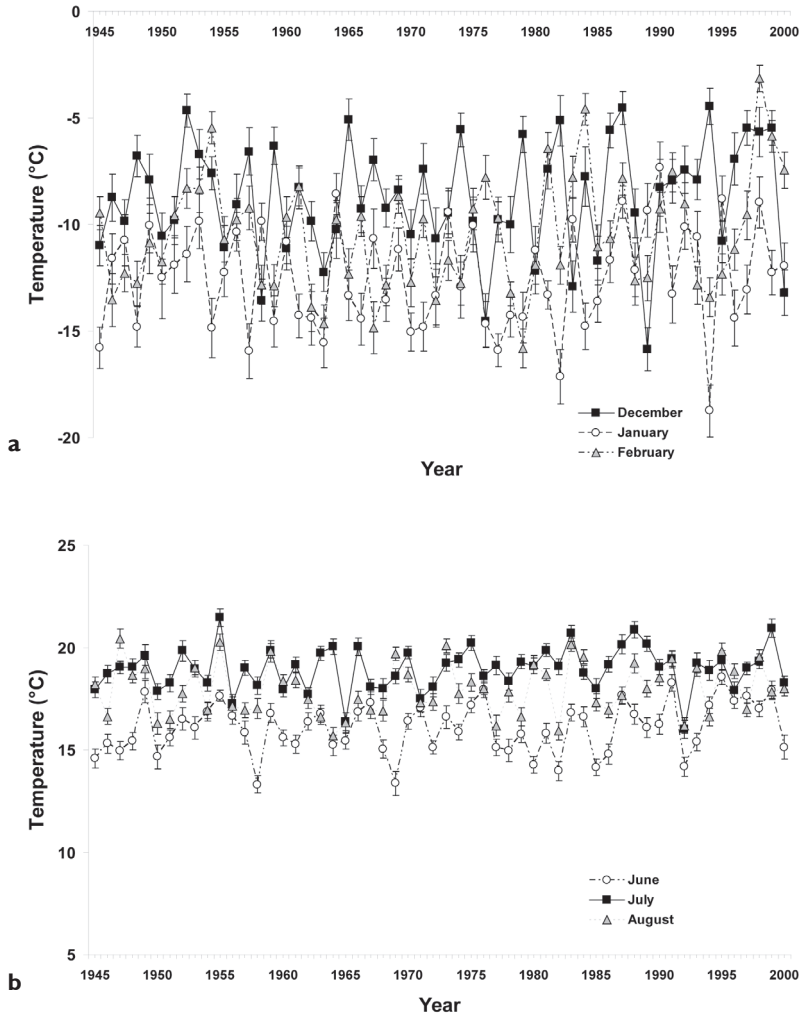
Figure 3. Mean annual temperature across each of 31 Ontario weather stations for **a** the months of December, January and February and **b** June, July and August from 1945 to 2000.

Changes in Odonate Distributions in Ontario

To assess potential responses to the changing climate of Ontario, we assembled county distribution data for dragonflies and damselflies from two sources. First, historical distributions were gleaned from the volumes of *The Odonata of Canada and Alaska* by Walker (vol. 1, 1953, vol. 2, 1958) and Walker and Corbet (vol. 3, 1978). Data for suborder Zygoptera (damselflies) in volume 1 were collected from 1906 through 1952. For the Anisoptera (dragonflies), volume 2 provided data on the families Aeshnidae, Petaluridae, Gomphidae and Corduligatridae from 1906–1955, while volume 3 contained information on the anisopteran families Macromiidae, Corduliidae and Libellulidae from 1907–1973.

Table 3. Mean estimated yearly rate of temperature increase in degrees Celsius (°C) over 31 weather stations in Ontario in the years 1945–2000 (un-adjusted for factors such as urbanization).

	Minimum Temp.	Mean Temp.	Maximum Temp.
January	0.022**	0.017**	0.012*
February	0.033**	0.029**	0.026**
March	0.020**	0.017**	0.014**
April	0.010**	0.013**	0.016**
May	0.034**	0.037**	0.040**
June	0.021**	0.016**	0.012**
July	0.017**	0.010**	0.003
August	0.018**	0.011**	0.004
September	0.018**	0.013**	0.008**
October	0.011**	0.024**	0.037**
November	0.005	0.004	0.004
December	0.032**	0.028**	0.024**

*Denotes significant departure from 0 at P ≤0.005; **P ≤0.001
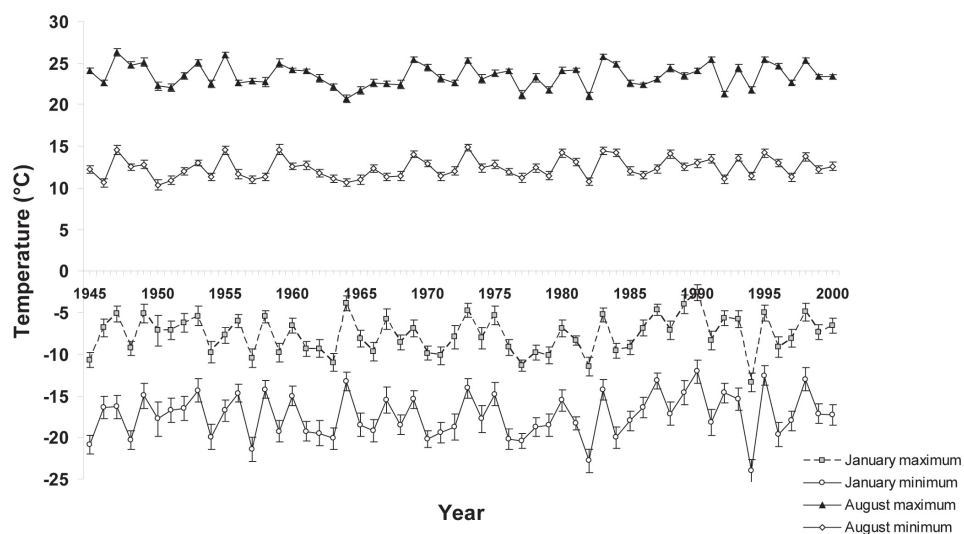
Figure 4. Maximum and minimum temperatures (°C) in January and August averaged across 31 weather stations in Ontario from 1945 to 2000.

For current distributions we have synthesized data from volume 4 of Ontario Odonata by Catling, Jones and Pratt (2004). These recent data represent known distributions as of 2002 and comprise 6,700 recorded sightings by 43 different contributors. Records were compiled into databases at the regional level and then passed to a provincial complier to create a single database. Unusual records were discussed with contributors to ensure a level of certainty. Voucher specimens were required for the most
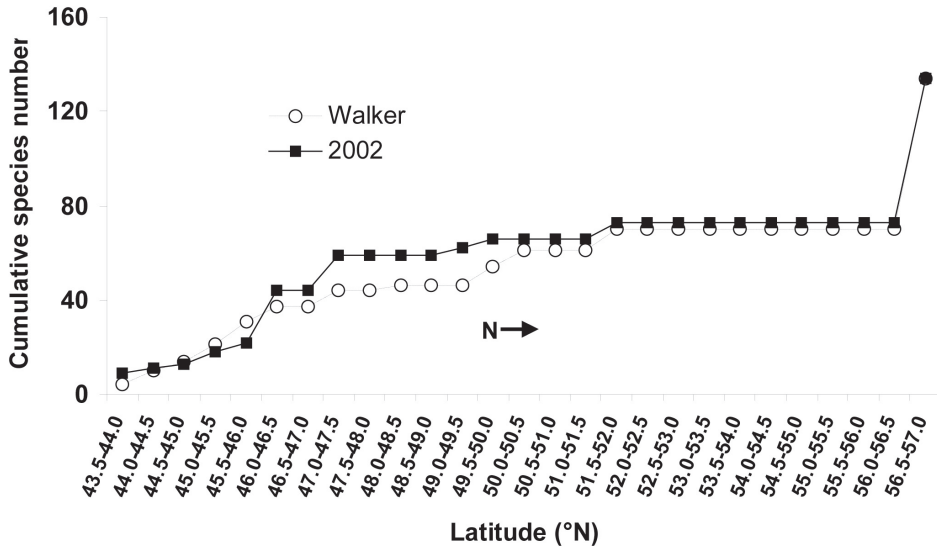
Figure 5. Cumulative number of species that have reached their northernmost extent in each of our two datasets, as a function of increasing latitude. Both datasets include the same 134 species of odonate. Between latitudes of 46°N and 50°N, a higher number of species were detected at their northernmost extent in 2002 than were detected in the 1950′s. This reflects a marginal overall decrease in the maximum extent of several species in the 2002 dataset – the opposite trend would be expected for a pattern of climate-driven northward range expansion. The final increase in species number in the highest latitude range represents those species whose latitudinal extent reaches the northern border of Ontario.

significant records. Included in these different surveys over several decades are data on 134 species, with 39 damselflies (suborder Zygoptera) and 95 dragonflies (suborder Anisoptera) (see Table 2 for species list).

Since the records of occurrence were only at the county level, some analysis was required to match historic and current distributions of Ontario odonates to geographical latitudes. For each county, the geographic boundaries were used to determine the northern extent of the county in terms of latitude, which allowed for an estimate of the maximum northerly latitude of a species based on the northern-most county observation. The median latitude of each county was also determined given the geographical boundaries of the county. The median latitude of the county enabled an estimation of the average latitude of the range of the species within Ontario given its presence in a number of counties. Some counties that had been sampled by Walker were not sampled in the 2002 data; when historic and current data were matched, data from a total of 41 counties could be assembled, though inevitable variation exists as to the extent of sampling within different counties.

Of the 134 species of odonate included in the study, 29 showed an increase in northern range extension between the two datasets (based on the northernmost latitude of the northernmost county in which the species was detected), while 40 species actually showed a decrease. Sixty-five species showed no change in their
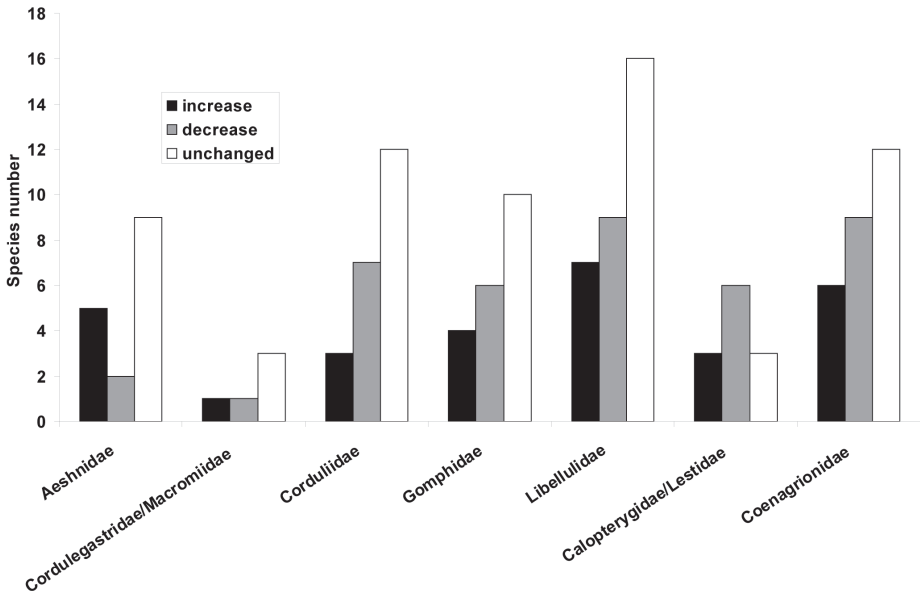
Figure 6. Differences in northern latitudinal extent between 1950′s and 2002 of Ontario odonate species, showing species broken down into family groups. For most groups, the number of species with increased and decreased ranges in not significantly different; the majority of species remain unchanged.

most northerly distribution. Comparing the total number of species at their northernmost extent in each survey as a function of latitude (Figure 5) we do not see, as might be expected, an increase in the northern ranges of species in the 2002 dataset. In fact, a larger number of species in the 2002 dataset reach their latitudinal maximum between 46° N and 50°N than in the Walker dataset, indicating a slight trend toward a decrease in the latitudinal ranges for some species between the 1950′s and 2002.

To determine whether differences could be found among taxonomic groups, we compared family-level distributions between datasets. We found similar patterns within family to those for the overall order (Figure 6) – thus, even at the family level, no significant overall increase (or decrease) was detected for any group.

It has been suggested that odonate species which inhabit lentic habitats (non-moving water, such as lakes and ponds) have larger and more northern distributions than those that inhabit lotic (river and stream) habitats (Hof et al. 2006). Hof and colleagues found this to be the case for odonates throughout Europe and North America, suggesting that the lower stability of lakes and ponds through time (in comparison to streams and rivers) require lentic species to have higher dispersal rates. As such, lentic species might be quicker to respond to increasing temperatures, and thus might expand their ranges northward more rapidly than lotic species. We compared lentic to lotic species (92 species versus 42 species, respectively), but found no difference in the pattern of latitudinal extent between these two groups (Figure 7).
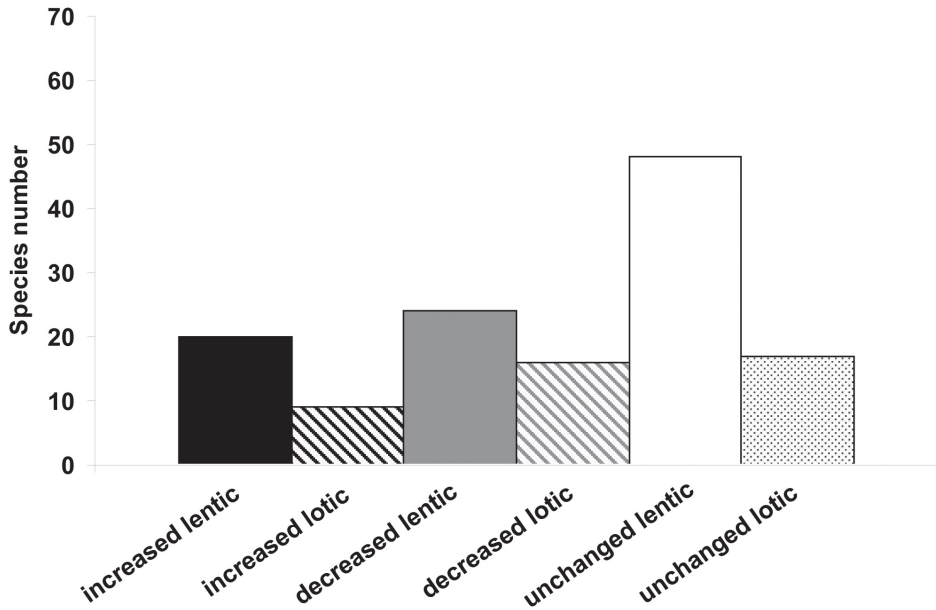
Figure 7. Differences in northern latitudinal extent between 1950´s and 2002 of Ontario odonate species, showing species that are found in lentic (lake, pond and marsh) habitats versus lotic (stream and river) habitats. Species are listed based on whether they have shown an increase in latitudinal extent, a decrease in latitudinal extent, or no change.

Discussion

Preliminary conclusions

Our first-step analysis of evaluating the responses of Odonates to changes in climate has concentrated on temperature, although we recognise that rainfall may also have the potential to influence the breeding ecology (and hence distribution) of Odonates (Cannings and Cannings 1998). We have found that, while increases in the recorded minimum, maximum and mean monthly temperatures in Ontario have been observed over the time interval between 1945 and 2000, no consistent pattern of change in the northern extensions of our studied odonate species is detectable. This is surprising, as changes in range size and northward extent, as well as changes in life history, have been observed in odonates in a warming European climate (Hickling et al. 2005, Hassall et al. 2007, Ott 2007).

A number of difficulties often arise in the collection of time-series data such as those used for these analyses. First, uneven sampling effort may lead to differences in levels of detection at different times. For example, if a lower amount or intensity of sample effort (fewer sample events, or fewer collectors) takes place during a specific phase of the sampling, species may be underrepresented, and the full distribution of

some species—especially rare species—may not be determined (Southwood & Henderson 2000). As is often the case with survey data, later samples in our data (from the 2002 source) were done more consistently—by a large number of people—than our earlier data, which was collected by Walker and his colleagues. Thus, the detection of an expanded range for a species—particularly a species with low densities or a patchy distribution—may be an artefact of sampling.

Secondly, uneven sampling within a sample period (for example, our 2002 dataset) may lead to biased assessments of species distributions. Sampling may favour urban areas, with large numbers of collectors and with greater access to habitats. Large areas with low human population densities will likely be sampled less effectively and could result in uneven recordings of species distributions. This could be problematic in our dataset, in that the northernmost counties of Ontario are the largest, least populated and least accessible; these are also the most crucial to sample in the detection of northward range changes.

The use of county-level presence data is also problematic, in that there is a great range of sizes in county areas in Ontario (see Figure 2); thus, recording presence at the county level represents an uneven sample effort. Many modern surveys record latitude and longitude of the actual sample location – this is made all the more easy due to the availability of hand-held global positioning system (GPS) receivers. However, older data, such as those used here, often are not recorded with such accuracy. A potential problem with county record data when analyzing changes is distribution patterns comes if county sizes are clustered – that larger counties are grouped in an area together. In our data, the fact that larger counties in Ontario tend to be in the northern part of the province could lead to an inflated increase in northern range extensions in species, as any record within a large county could represent a considerable northward latitude increase for that species.

Future Work

We observe that, while we did not find a significant trend in the change of species distributions in our dataset, this may be due not to absence of a change, but an inability to detect such change with the current data. Ontario is a large province, with many remote areas that are difficult to sample. Still, increased interest has been seen in recent years in dragonflies and damselflies, reflected by the development of regional groups of odonate enthusiasts throughout North America, and the increased availability of field guides. We welcome this increase in public interest and awareness, and hope that it continues to contribute to the growing availability of data species distributions. We encourage our readers, in Ontario and elsewhere, to become involved in the collection and synthesis of dragonfly distribution data, which will improve our understanding of these organisms. Those specifically interested in Ontario odonata can become involved by contacting the Natural Heritage Information Centre with the Ontario Ministry of

Natural Resources, the Toronto Entomological Society, or other naturalist organisations in the region.

When considering the distribution patterns of odonate species, intriguing trends can be observed. While some species in this survey were found throughout the province, others are limited to a distinct region. While some species distributions can be explained by the extent of a habitat type (Precambrian Shield lakes, for example) other species show distinct distribution boundaries that do not match to discrete landscape features. For these species – such as *Aeshna canadensis*, *Erythemis simplicicollis* or *Enallagma civile* – range boundaries appear to be limited primarily by a maximum latitudinal extent. It may be that climatic patterns are the limiting factor in the distribution of these species; We propose, in future work focusing on species such as these and employing a larger and more robust dataset for North American odonates, to further and more rigorously explore the relationship between odonate distributions and climate change

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RESEARCH ARTICLE

The local species richness of Dragonflies in mountain waterbodies: an indicator of climate warming?

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Abstract

With climate warming, many Odonata species are extending their geographical area. In Switzerland, as in many parts of the world, this phenomenon may lead to a regional increase in species richness. The local richness (the richness of individual waterbodies) is also expected to increase, particularly in the alpine or subalpine areas where the waterbodies are particularly species–poor. Based on the species richness recorded in 109 waterbodies scattered all across Switzerland, a model is presented here relating the local species richness (adult dragonflies) to environmental variables, including the mean annual air temperature. This model predicts a sharp increase in species richness for alpine or subalpine waterbodies, which is expected to double or even treble before the end of this century. This increase would mainly be the consequence of the immigration of eurythermal species extending their geographical range, together with potential local extinctions of the cold stenothermal species.

Introduction

Global changes, and particularly climate warming, are likely to have various impacts on Odonata (see other chapters of this book), such as a shift in species' geographical distribution, an earlier timing of emergence, or a shorter duration of the aquatic live

stage. In the northern hemisphere, the northerly shift in the geographical distribution of several species will lead in many areas to an enrichment of the regional species pool, mainly resulting from an increase in the number of eurythermal species. Such an increase will largely encompass the associated decrease in the number of cold stenothermal species. A regional increase in species richness has already been reported in many European states such as Switzerland, Germany, Netherlands, Belgium, or UK. Similar changes are also expected to occur with altitude. Indeed, the elevation gradient is often claimed to mirror the latitudinal gradient (Rahbek 1995), hence conditions at higher altitudes resemble conditions at higher latitudes (Ricklefs 1990).

If the regional increase in species richness is now an evidence, changes in the local richness (richness of a given ecosystem, e.g. pond, stream, wetland) were at the moment poorly documented (but see the example of permanent vegetation plots, in Pauli et al. 2007). Nevertheless, such changes would undoubtedly occur, especially in areas where the local richness is low. This is particularly the case in altitude (or high latitude), where local species richness is clearly lower than in lowlands (or lower latitude) (e.g. Oertli et al. 2008). Many alpine ponds in Switzerland do not presently host any Odonata species (or only a few), whereas it is common to observe ten to twenty species in lowland ponds.

The present case study aimed to predict the expected changes in the local species richness as a consequence of various scenarios of temperature elevation. For this purpose, the species richness of adults Odonata was assessed in 109 ponds distributed in all altitudinal regions (and therefore thermal regions) of Switzerland. This data set is used to relate the species richness of the ponds with the mean annual air temperature.

Material and methods

Measure of local species richness and environmental variables

A set of 109 ponds scattered in the four altitudinal belts of Switzerland (collinean, montane, subalpine, and alpine; Figure 1) was investigated between 1996 and 2002. This set represents a broad range of thermal conditions with mean annual air temperature ranging from –2.2°C to 12.1°C (Figure 2). The sampling of adult Odonata and the assessment of species richness were standardised and followed the PLOCH method (Oertli et al. 2005), for which a representative species list is gathered during two sampling days (at the end of spring and summer). To account for sample-size inadequacies (i.e. it is unlikely to perform the same sampling effort on each pond), the measured species richness is further corrected by means of Chao estimator of true richness (see Oertli 2008; Oertli et al. 2002; 2005).

About a hundred of environmental variables were also measured, at the local and regional scales, including water physico-chemistry (e.g. pH, nutrients, conductibility, transparency), morphometry (e.g. pond area, depth), watershed characteristics (geology, land use), connectivity (isolation from other waterbodies), and climatic data (air
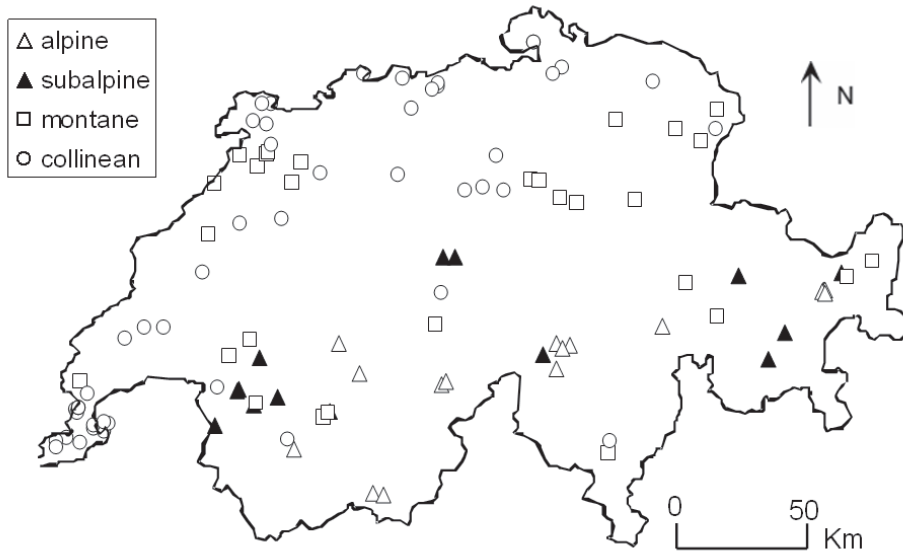
Figure 1. Distribution of the 109 sampled ponds in Switzerland, with indication of their altitudinal belt.
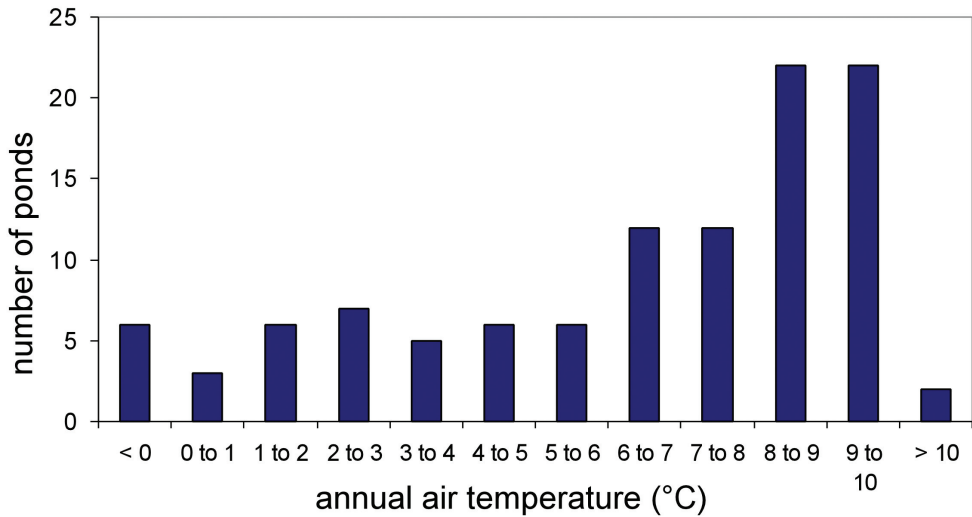
Figure 2. Range of mean annual air temperature covered by the 109 sampled ponds. Annual mean air temperature was calculated on the basis of monthly values from 115 climate stations and of a digital terrain model with a 25-m grid (data from the Swiss Federal Institute for Forest, Snow and Landscape Research).

temperature, quantity of precipitations, cloud cover, evapotranspiration, solar radiation). For additional information on sampling procedure and pond characteristics, see Oertli et al. (2002, 2005).

Statistical analyses

In a first descriptive step, correlation coefficients (Spearman's "ϱ") served to assess the relationships between species richness and mean annual air temperature, and each environmental variable.

A stepwise linear regression procedure (LR) was then used to model the relationship between estimated Odonata species richness and the annual mean air temperature (also including the other significant environmental variables), by setting the probability to 0.05. The model was used to predict the changes in species richness for two "virtual" alpine and subalpine ponds (each one with a surface area of 3300 m²) in response to global change. The typical alpine pond had a mean annual air temperature of 0.6°C and the typical subalpine pond of 3.4°C. The temperature increases ranged between +1.8°C to +4.0°C, and were based on seven emission scenarios: the six IPCC scenarios for 2090–2100 (IPCC 2007) and the CH2070 scenario for Switzerland in 2070 (Hohmann et al. 2007).

Results

Relation between pond species richness and mean annual air temperature

From the correlation analysis, it resulted that species richness best correlated with, first, mean annual air temperature (r= 0.72), and then with altitude (r= - 0.67). These two variables were highly correlated (r= 0.99). Other important variables were identified by calculating their correlation with the residuals of the linear regression between species richness and annual air temperature. This analysis highlighted a significant relation with pond area (r= 0.47), proportion of the environment covered by forest (r= - 0.32), fish presence (r= 0.30), and mean pond depth (r= 0.23).

Based on these preliminary analyses, a selection of 15 variables was used to build the model (stepwise LR) relating the Odonata species richness to the air temperature: mean annual air temperature, pond area, pond age, mean depth, shore development, water conductivity, water transparency, pond eutrophication state, proportion of pond shaded, fish presence, proportion of pond area covered by floating vegetation or by submerged vegetation, proportion of agricultural landcover in the catchment, and proportion of the environment covered by forest and the connectivity in a radius of 1000 m.

The final model selected two variables, mean annual temperature and pond area, and showed that species richness (S) increased with an increase of temperature (T, in °C) or/and pond area (A, in m²):

$$S = -4.65 + 1.34 * T° + 1.39 * \log(A)$$
$$r^2 = 0.51 \quad p < 0.0001$$

Prediction of the local species richness of mountain ponds as a function of different scenarios of temperature increase

The resulting model was used for the simulation of the impact of temperature increases on local species richness. For a given alpine or subalpine pond (fixed area of 3300 m²), we tested seven scenarios (Figure 3) representative of the trends predicted for the next 65 to 95 years. All seven scenarios evidenced a clear increase in Odonata species richness. The magnitude of this increase is particularly high, as the richness is likely to double, or even to treble in the case of alpine ponds. Whilst the species richness currently observed in an alpine pond is one species, this is expected to increase to three to six species during the next decades. In the case of a subalpine pond, species richness may rise from six (mean value currently observed) to 8–11 species.

Discussion

The predictions of climate warming presented here point out future drastic changes in the species richness of mountain waterbodies. For alpine ponds, the local richness of Odonata is likely to double or treble. This increase in local species richness of mountain waterbodies is the consequence of immigration events that will largely exceed extinction events. Indeed, in Switzerland, the present Odonata species pool is composed of 72 indigenous species (Gonseth and Monnerat 2002), the majority being eurythermal species associated with lowland waterbodies. Only seven species are restricted to altitude areas and can be considered as "cold stenothermal species". With the warming of the climate, many eurythermal species will extend their geographic distribution to higher altitudes, and will therefore be able to colonise mountain ponds from which they are currently absent. The extension of the geographical area to higher latitude has already been reported for European Odonata by Ott (2007). This phenomenon is likely to have also occurred along the altitudinal gradient through the highest elevations, though this has not been yet reported. Such altitudinal shift in geographical species distribution is also observed for plant species in the Alps (e.g. Pauli et al. 2007).

Beside the immigration of eurythermal species in waterbodies, it is noteworthy that extinction of currently established species will probably also occur. As a consequence of warming, the seven cold stenothermal species could disappear from their living waterbodies. The lower altitudinal limit of their geographical distribution could increase and could consequently lead to an upward shift of their habitats; in the long term, this could lead to species loss at a regional scale.

In Switzerland, the geographical area (and therefore the altitudinal distribution) of Odonata species is particularly well documented by the databases of the Swiss Centre for Fauna Cartography (CSCF) (see also the Swiss Atlas; Wildermuth et al. 2005). Odonata are absent of almost all high-elevation waterbodies (higher than 2500 m). Sixteen species are frequent above 1500 m (Figure 4), from which a first set of seven species can be considered as cold stenothermal due to their predominance in the upper
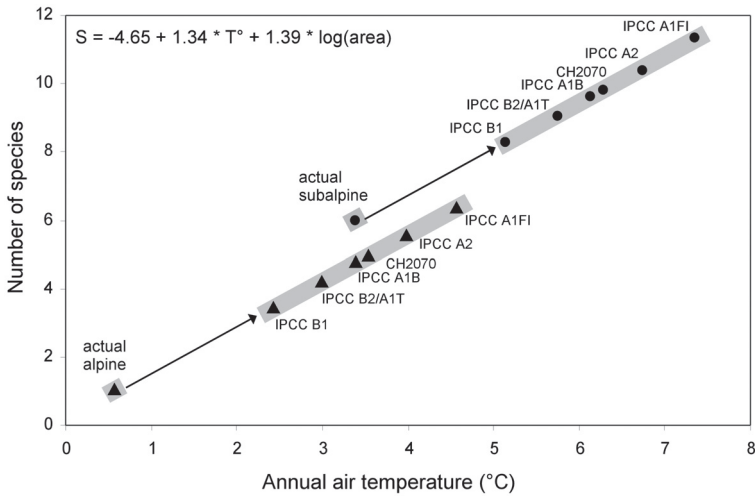
Figure 3. Potential change in the Odonata species richness (S) for an alpine and a subalpine pond as predicted by the stepwise LR equation according to seven climate change scenarios (six IPCC emission scenarios and the CH2070 scenario). "T°" is the annual mean air temperature. The two virtual ponds are typical of subalpine and alpine altitudinal belts, with a fixed area of 3300 m². For the alpine pond, present "T°" is 0.6°C, while it is 3.4°C for the subalpine pond

elevation areas: *Aeshna caerulea, A. juncea, A. subarctica, Coenagrion hastulatum, Leucorrhinia dubia, Somatochlora alpestris, S. arctica.* The most elevated altitudinal ranges are those of the boreo-alpine species *Aeshna caerulea* and *Somatochlora alpestris*, and are particularly narrow. Species belonging to this set are those presenting the highest risk of extinction at the local scale (waterbody), but also on the long range at the regional scale. A second set is composed by nine eurythermal species, characterised by a broad altitudinal distribution, mainly located below 1000 m. This set includes the candidate species to the colonisation of mountain waterbodies, and will be responsible for the increase of the local species richness.

The predictions of changes in local richness presented in this paper are potential values. They present a global trend that provides a baseline for describing biotic responses to warming. The magnitude of the changes, however, may be slightly different than that described here, being either higher or lower. Indeed, the predictive models are based on the change of only one parameter affected by climate change, i.e. mean annual air temperature. Other variables could interact with temperature and either diminish or increase the magnitude of the predicted changes. For example, variables such as the seasonal timing of warming (i.e. winter or summer), the quantity and frequency of precipitations, the number of days of ice cover, or the radiation (e.g. UVs), are factors potentially able to interfere directly with temperature, or to lead to secondary changes (e.g. hydrology, productivity, water chemistry). Land use, which could have many secondary consequences, is a relevant factor that is likely to greatly vary in mountain area (Maurer et al. 2006). Besides environmental factors, biotic variables should also be accounted for. The dynamics of the colonisation processes in both
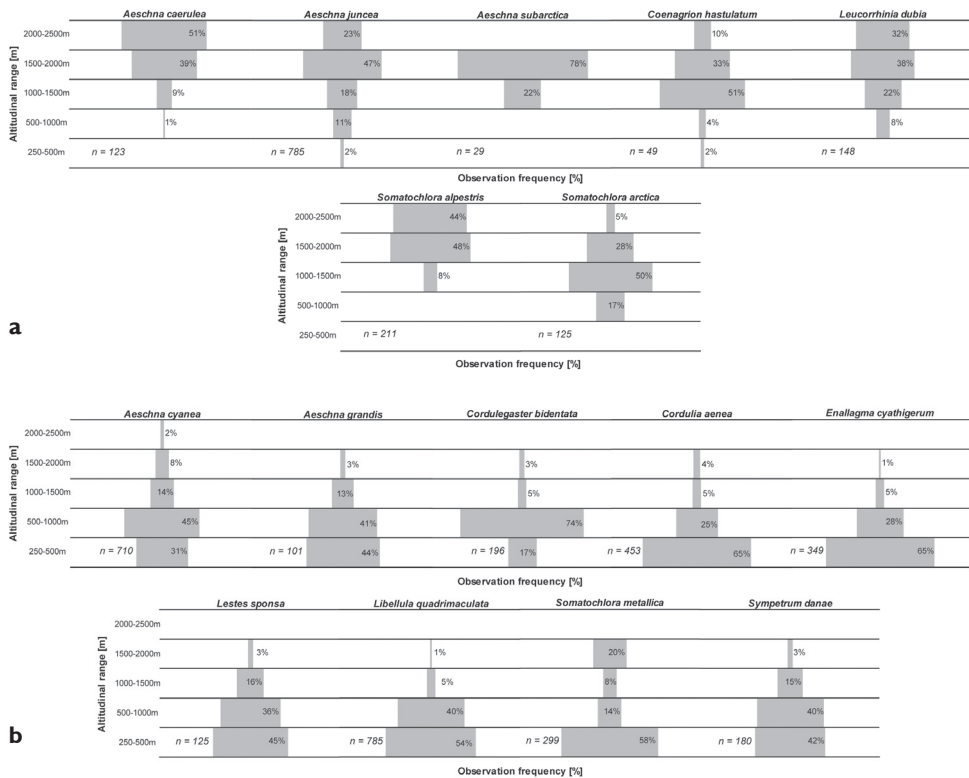
Figure 4. Altitudinal distribution in Switzerland of a set of 16 species frequently observed at high altitude (above 1500 m). **4a** The seven cold stenothermal species, expected to exhibit a decrease in their geographical area (at risk of extinction on the long range). **4b** The nine eurythermal species, likely to become more frequent at higher altitude. The data report observations of exuviae and subadults only, two life stages attesting the reproduction at the observed altitude. "n" indicates the number of observation. Data were gathered before 2003 (mainly between 1990 and 2002) by the Swiss Centre for Fauna Cartography.

space and time could be very complex, as they are species-specific. The time at which the upward dispersal begins, or the speed at which a species extend its distributional area, depend on its own biological or ecological characteristics. At the assemblage scale, this could result in a space-time overlapping and changing pattern of species distributions. As an example, Anisoptera are much more efficient fliers and active colonisers than Zygoptera. The latter group can nevertheless compensate this miss by an usually elevated number of individuals per population and by the passive dispersal by wind. Other biotic interactions, such as predation, may occur when an immigrant colonises a new pond. Local processes are therefore likely to present some resistance to immigration and to delay the increase in species richness.

With their small size and their relative simple community structure, ponds constitute ideal sentinel and early warning systems (De Meester et al. 2005). This is particularly true for alpine or subalpine ponds, characterised by species-poor communities (e.g. Oertli et al. 2007). Such systems should therefore be used for monitoring the

biotic impacts of climate changes. Monitoring should be conducted with a set of ponds situated at various altitudes and covering a large range of latitudinal scales, both in Switzerland and in other countries.

Among other invertebrates, Odonata is certainly one of the most suitable groups for conducting monitoring, either alone or, better, in conjunction with another indicator group (i.e. Oertli 2008). Indeed, the regional species pool of Odonata in altitude areas is small (e.g. Figure 4), but nevertheless large enough for conducting long range monitoring. Here, the local species richness has been shown to be a particular sensitive metric, hence being a good candidate to join the set of metrics used for long range monitoring. Local extinctions of cold stenothermal species, or colonisation of lowland species, are early warning events for mountain waterbodies that should be monitored.

Acknowledgement

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Dragonflies and climatic change - recent trends in Germany and Europe

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Abstract

In this paper the trends of dragonfly expansions during the last decades in Germany and Europe are summarized. It is shown, that there is a general expansion of many species to the north: Mediterranean species expanded to Central and Northern Europe, whereas some African species expanded to Southern Europe, some are even new to the continent. In general this means an increase of biodiversity, but looking at the ecological effects, in the medium term a decrease can be expected for mooreland and alpine species. Dragonflies can be regarded as a good indicator group for climatic change. Already now in some areas or regions negative effects on waters bodies and their dragonfly communities can be observed and more will occur if e.g. temperature rises or precipitation decreases. The consequences for nature conservation strategies – such as the NATURA 2000 network – are outlined and the general need for monitoring programmes is emphasised.

Keywords

dragonflies, climatic change, indicators, risks, ecological effects, nature conservation, monitoring

Introduction and some definitions

Since the 1990ies the discussions on the effects of climate change became increasingly intensive, in ecology as well as in nature conservation (e.g. Gates 1993). Climate change is now regarded as one of the most important factor threatening species, habitats, ecosystems and biodiversity in general (e.g., Lovejoy and Hannah 2005; IPCC 2007a,b; Settele et al. 2010a, 2010b; EEA 2010).

Subsequently an overview is given on the reactions of dragonflies following those climatic and habitat changes which have so far been observed. Finally some conclusions for the protection of dragonflies are drawn.

Oscillations versus Trends

The changes of species` ranges as a result of climatic changes – here the main focus is on expansion – is a normal process, but it is important to differentiate between "oscillation" and "trend".

Oscillation can be described as a regular movement from one side to the next or a regular cycle and for a species in a new area it means "coming and going". E.g., if the weather in some years is favourable for the species, it expands and later on, in years with unfavourable weather, it retreats its range back to the former extension.

A *trend* on the other hand is a gradual development – maybe including some small oscillations – but in general resulting for a species in "coming and staying" in a new area and a constant expansion of the species` range.

Tipping points, scenarios and ecosystem services

Tipping points are described as the moment, when an object or situation is displaced from a state of stable equilibrium into a new, different state; such a shift from one state to another is irreversible.

A scenario is a postulated sequence of possible events based on assumptions. In this context it is for example the increase of carbon dioxide emissions or temperature, as a consequence of economic growth, as it is worldwide coupled with the consumption and burning of fossil energy. It is projected on the basis of current circumstances and trends.

Natural as well as man-made ecosystems supply humans with a lot of different resources and processes and all these benefits are defined as ecosystem services, such as pollination, drinking water or the decomposition of organic material. Natural systems in particular are increasingly influenced and altered by human activities.

The expansion of southern species in Germany and Europe

Example: the expansion of *Crocothemis erythraea* in Germany and Europe

The best example of the expansion of a dragonfly is without doubt the Scarlet Darter (*Crocothemis erythraea* (Brullé, 1832), see fig 1). In the literature in Germany and other countries north of the Alps this species still was described as a "Mediterranean species",

Figure 1. A male of the Scarlet Darter (*Crocothemis erythraea*). Foto: J. Ott

until about three decades ago, also being regarded as a typical vagrant species which only in rare occasions could be observed breeding in northern countries (e.g. Jurzitza 1978).

But then it became permanently indigenous in Germany, in the beginning only in southern federal states and in the lowlands along the Rhine River (Ott 1988, 1996). In the following years it was expanding to the north – finally reaching the border to Denmark in 2009 – and it was registered also in higher altitudes (Ott 2001a, 2007a, 2010a, see also fig 2). Its expansion corresponded with the increase of temperature, even if it is still unclear which factor(s) is (are) the dominating one(s) (e.g. maximum temperature, mean temperature, duration of sunshine).

The positive temperature effect is also underlined by the observation, that in the extremely warm year of 2003 the species obviously had a second generation (Horn 2003).

This expansion was not only registered in Germany, but also in other European countries which is summarized for some countries in the following table (Table 1).

A comparable expansion was noted also for other European countries, like for the Ukraine (see Khrokalo, 2010) and Luxemburg. In the Ukraine – beside other Mediterranean species – *Crocothemis erythraea* expanded all over the country in the last three decades. In Luxemburg the species was first discovered in 1986 while in 2005 it was present in 17 % of the grid cells (Proess 2006).

This expansion in Europe over the last decades finally can be regarded as a clear *trend* of expansion rather than only an oscillation of its range.

Some more examples: other species expanding their range in Germany

The example of the Scarlet Darter, a very striking species which is easy to detect at the water (see fig. 1) is not the only one. Other "southern" species also expanded their
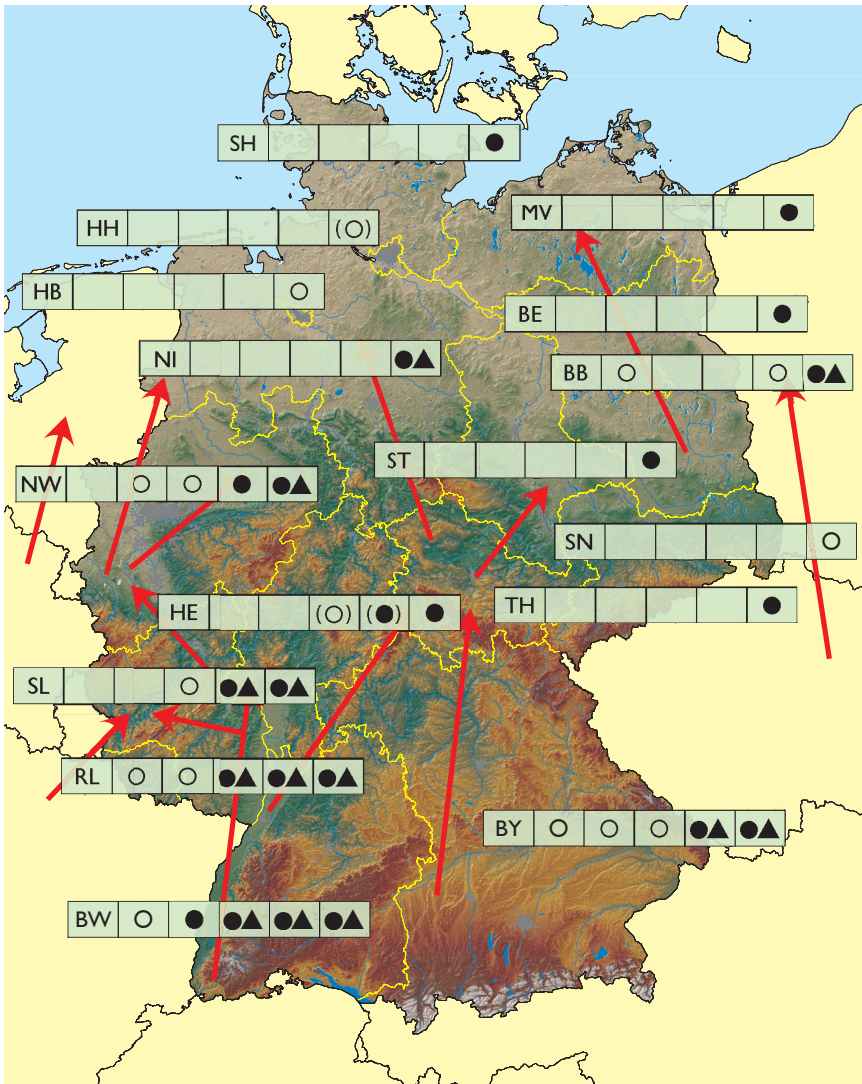
Figure 2. Expansion of the Scarlet Darter in Germany (Ott 2007a, updated)

range in Germany northwards or invasions were noted much more frequently. Besides species like *Erythromma viridulum* (Charpentier 1840), *Orthetrum brunneum* (Fonscolombe 1837) and *O. coerulescens* (Fabricius, 1798) which crossed Germany already some time ago or became much more abundant (see Ott 2001a, 2008a), some more recent examples are subsequently presented.

Anax parthenope Selys, 1839:

The species presently expands its range in central and north-east Germany (e.g. Mauersberger et al. 2002), but also in regions where it has previously established new populations it becomes more abundant. E.g., in some gravel pits in the Rhine Valley

Table 1. Expansion of *Crocothemis erythraea* in some European countries.

country	time	source	situation
France	1960–1986	Dommanget (1987)	known from 28 French *departements* out of 96, more frequent in the south and very abundant in the Mediterranean
	< 2000	Grand and Boudot (2006)	not known from 3 *departements*, in 18 rare or very rare, but in all the other *departments* common to very common, also in central and northern ones
The Netherlands	< 1983	Geijkens and van Tol (1983)	only one sure record from 1959 and 2 others from 1967 and 1968 have been confirmed
	< 2002	NVVL (2002)	steady expansion after the first population was discovered in 1993, thereafter several populations present and increasing
	< 2007	Bouwman et al. (2008)	between 1997 and 2007 registered in more than 250 localities (= 5 x 5 km grid cell)
UK	< 1995	Hammond (1977), Merrit et al. (1996)	no observation ever
		Parr (2005, 2008)	first record in 1995, thereafter until 2005 in total 6 accepted records confirmed, some others probable, regularly observed as breeding populations on the Channel Islands (e.g. 2007 on Jersey) and breeding
Poland	< 1989	Bernard et al. (2009)	only 6 accepted records, possibly only one of them from an indigenous population
	> 1990	Bernard et al. (2009)	broad expansion, species now widespread (even if still rare on the national scale) and indigenous up to 52° 38`N, in total ca. 50 localities
Czech Republic	1950–1989	Dolny et al. (2008)	found in 5 grid cells (out of 659)
	1990–2007	Dolny et al. (2008)	found in 105 grid cells (out of 659)
	2008–2009	Dolny pers. comm.	found in another 10 grid cells

near Ludwigshafen and north of Worms it is now more abundant than *Anax imperator* Leach, 1815, whereas in the mid 1980ies *A. parthenope* was very rare in this area and *A. imperator* was the dominating aeshnid in the summer (Ott unpubl. data).

Aeshna affinis Vander Linden, 1820:

A constantly increasing number of observations has been confirmed in the last two decades. In the Rhine Valley and Lower Saxony the species became, for the first time, indigenous in the mid 1990ies (Ott 1997; Drees et al.1996), later on in 2000 also in north-eastern Germany in the federal state of Brandenburg (Brauner 2005), where up to 2005 it was found breeding in 32 waters.

Boyeria irene (Fonscolombe, 1838):

This Mediterranean species inhabiting mainly running waters, but also big lakes, in Germany was found for the first time in 2002 and then again in 2004 (Schmidt 2005). As also in France northward expansion is registered (up to the region Champagne-Ardenne in 2006: Ternois 2008), without any doubt the species sooner or later will

populate more waters. Whether the new German population in Lower Saxony (river Ötze) - hundreds of kilometres north from the known sites – could already be regarded as a part of an expansion, needs further investigation (Clausnitzer et al. 2010).

Coenagrion scitulum (Rambur, 1842):

Also this damselfly is expanding its range and was found in Rhineland-Palatinate for the first time in 2006 (Glitz 2008), where in some areas it expanded very much (Lingenfelder 2008). Also it was newly discovered for Bavaria (Karle-Fendt 2006). In North Rhine-Westfalia, where it also was rarely seen in the past decades, it is now much more abundant and shows increasing populations (Grebe et al. 2006).

Beside these species mentioned above, several more Mediterranean species recently became much more abundant and even common in Germany, like *Sympetrum fonsco-lombii* (Selys, 1840) or *Orthetrum brunneum* and *O. coerulescens.*

It shall be noted that nearly all "southern" species expanding in Germany showed the same pattern: expansions show a clear northward direction and often individuals or populations are also found in higher altitudes.

On the other hand, no "northern" species showed a comparable expansion to the south. There are also some expansions, e.g. by *Gomphus vulgatissimus* (Linnaeus 1758) or *Gomphus flavipes* (Charpenties 1825), but this might rather be a consequence of a better water quality in rivers, than the effect of a change in temperature or climate. Whether the new and remarkable expansion of *Leucorrhinia caudalis* (Charpenties 1825), in northern Germany (Mauersberger 2009; Deubelius and Jödicke 2009) is an effect of climatic change definitely needs further investigation.

The effects on waters: changing climate – changing communities?

A practical example: the "Kolbental" monitoring-project

The changes in the fauna of an area can only be described in detail, if these changes can be followed permanently and over an extended period. This is the case for example in the "Kolbental" monitoring-project near Kaiserslautern (Ott 2001b). The nature reserve "Täler und Verlandungszone am Gelterswoog" (valleys and silted-up zone near lake Gelterswoog) is a ca. 55 ha wetland complex with a mosaic of very diverse biotopes (meadows, forests, abandoned land, lentic and lotic waters etc.). This reserve consists of 3 valleys with 11 standing waters (so called "Wooge") and some of these biotopes are protected according to national or international laws (EC habitat's directive: e.g. dystrophic waters and transition mires, Natura 2000-code: 3160 and 7140).

In this area a regional agency (ZWW/TWK) planned to extract about one million cubic meters of ground water for drinking water supply. This permission was only given by the regional authority under the prerequisite, that the agency is able to proof

the sustainability for the environment by means of hydrological and ecological monitoring. These two monitoring projects started in 1998, and the ecological monitoring consists of the collection and evaluation of abiotic data (climate, soil humidity, water analysis etc.), as well as investigations on the vegetation and the fauna. As indicator taxa for the monitoring project carabid beetles, butterflies, grasshoppers and dragonflies were chosen.

Whereas in the beginning flora and fauna remained relatively constant, dramatic changes occurred after the year 2003 with its extreme warm and dry summer. These changes are still ongoing, even if recently – as a consequence of an increasing precipitation (see tab. 2) – some waters recovered (see also fig. 3).

Still it is unclear, if and to which extent the extraction of ground water has additional impact on the wetlands. Hydrologists calculated a maximum additional lowering of the ground water table of 10–20 cm per year, which is much lower than the effects of a lack of precipitation. Thus they assume that extraction only has a minor effect (L.U.P.O. 2009). On the other hand, each additional lowering of the water table in the open waters as well as the ground water dependant ecosystems (GWDE) will prolong the periods of drought and consequently the stress on the species and ecosystems increases.

The "Kolbenwoog": an example for the effects of the extreme summer of 2003

During the summer of 2003 with its lack of precipitation the water table of the Kolbenwoog dropped and in the beginning only the shallow silted-up zone fell dry. This

Table 2. Important abiotic factors in the monitoring area: temperature and precipitation – extremes (>± 50% of mean per month) shaded in grey; l.-t.-mean = long-term mean (source: www.agrarinfo.rlp.de)

precipitation in [mm]	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	l.-t. mean
January	71	50	39	85	50	84	95	39	22	64	50	46	52
February	7	57	78	50	155	13	27	41	30	96	48	55	50
March	59	79	59	182	70	15	38	38	65	84	106	59	46
April	17	59	35	80	44	28	39	98	34	1	61	43	44
May	39	55	153	18	129	99	63	63	93	83	62	29	66
June	65	62	36	54	41	29	56	45	35	126	99	110	72
July	61	87	178	64	100	44	62	67	48	80	34	143	62
August	18	51	85	129	108	32	132	60	189	69	57	34	76
September	45	44	67	98	41	46	38	68	65	63	59	35	52
October	97	51	59	47	143	53	55	48	86	13	70	59	43
November	85	11	55	123	104	50	36	45	32	43	25	81	61
December	72	40	123	62	65	38	31	62	39	77	44	99	63
total / year	620	772	940	982	1051	530	673	672	738	799	713	793	692

Figure 3. Silt-up zone of the Kolbenwoog with rich – and now dry – vegetation: this important zone for larval development of sensitive species fell dry for years. Foto: J. Ott

zone is very important for the larvae of many dragonfly species: here they can hide and escape predation (in particular the sensitive *Leucorhhinia*-larvae – compare: Henrikson 1988). Also oviposition of many species takes place in these parts of the water with rich structured vegetation along the shoreline.

But also in the consecutive 3 years precipitation was very low (see tab. 2) and consequently the water level continued to fall. In summer 2006 the whole lake was nearly dry: only about 20 sqm of shallow water (nearly 40°C water temperature, no oxygen – own measurments) were left (see fig. 4). At this moment the water surface of the lake was reduced to ca. 0.25% (0.8 hectares under normal conditions) and the water body was reduced to ca. 0.07% (ca. 5400 cubic meters under normal conditions).

This nearly dry lake (see fig. 4), now having wide open shores with only scarce vegetation was colonized by several species, previously not registered at this water before: *Orthetrum cancellatum* (Linnaeus 1758), *Libellula depressa* Linnaeus 1758, *Gomphus pulchellus* Selys 1840 and also a few individuals of *Crocothemis erythraea* appeared. These species are typical for dynamic or secondary biotopes like gravel pits etc. and here – at dystrophic water bodies with mooreland biotopes (mires and bogs) – can be described as disturbance indicators.

Figure 4. The Kolbenwoog in July 2006: a dystrophic water nearly dry with wide open shores and no more vegetation in the water body (left) and in 2010 with a recovered water level (right). Fotos: J. Ott

Also the immigration of *Anax imperator* was noted, which became much more abundant and also indigenous. It is well known that this species has aggressive larvae which without doubt can have a strong influence on the other dragonfly species (see e.g. Beutler 1985), as in general dragonflies are important and prominent parts of the aquatic food chain (Turner and Chislock 2007).

In the same time period the typical mooreland species – *Coenagrion hastulatum* (Charpenties, 1825), *Somatochlora arctica* (Zetterstedt 1840), *Aeshna juncea* (Linnaeus 1758), *Leucorrhinia dubia* (Vander Linden 1825) – left the water and still did not return, even although the water table in the meantime recovered to its former level (see fig. 4).

For these species the Kolbenwoog lost its value, as the water was like a "small bathtub" with wide open shores and all the important habitat structures for larval development were gone: there were no more roots or other dense vegetation left, where larvae could hide or live and where the adults of the endophytically ovipositing species could lay their eggs (see fig. 3 and 5, also compare e.g. Henrikson 1993). It is well known and documented in many cases, that the complexity of the habitat structure is of general importance for the success of predators (see e.g. Warfe and Barmuta 2004).

Obviously this was a *tipping point* for the dragonfly community and it changed fundamentally.

Changes in other waters bodies

A similar change of the dragonfly fauna was observed in all the other waters of the three valleys of the monitoring area, only in two waters of the Erlental a small population of *Coenagrion hastulatum* and *Leucorrhinia dubia* survived (see fig. 5). *Somatochlora arctica* was not registered anymore and became extinct in the monitoring area, whereas *Aeshna juncea* disappeared also as an indigenous species, only single dispersing individuals were registered, but no population was left.
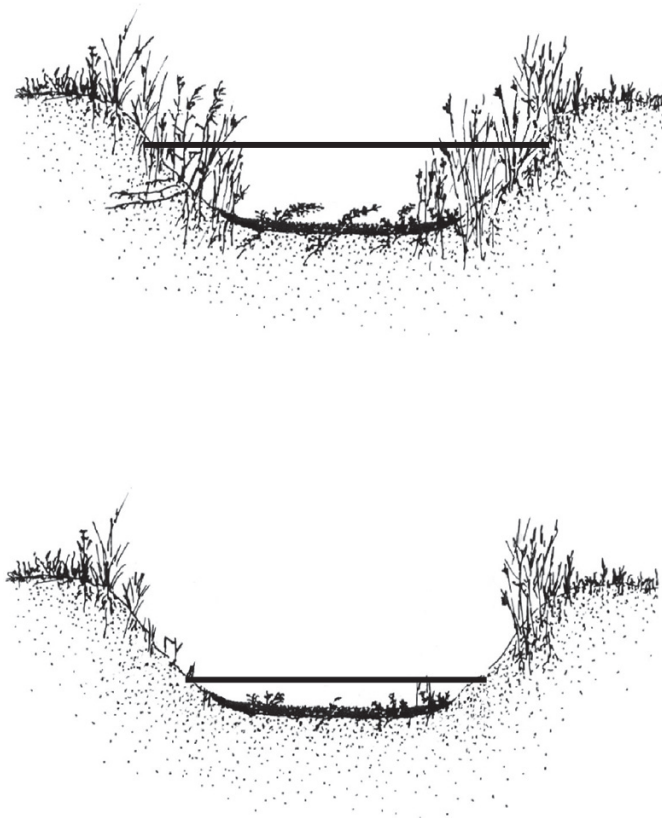
Figure 5. Different situations of the water – high and low water level (original)

As these two species in general became very rare in the Palatinate and the adjacent regions with only very few isolated populations remaining (see Ott 2006a, 2007b, 2007c, in press; Trockur et al. in prep. – see fig. 7) such extreme events may lead to a general extinction of the species on the regional level in the medium term.

A species which on the other side was profiting from this situation was the damselfly *Ischnura pumilio* (Charpentier 1825): all over the Palatinate it colonized these waters with open shores and extremely low water tables (Ott 2008b). Future investigation must show, whether this colonisation is successful for a longer period or whether the species becomes rare again, as it is normally found only in secondary waters.

Changes in the composition of regional faunas

The southern species did not only expand their range, they also increasingly dominated the regional faunas, as will be shown with the following examples.

species present in 1998–2007	waters or valleys				
	Gelterswoog	Rotenwoogtal	Kolbenwoog / Kolbental	Erlentalweiher	Walk-mühltal
C. hastulatum	●●●●●-----	----------	●●●●●●●---	●●●●●●●●▪▪	●●●●●-----
S. arctica	----------	●●●●●-----	●●●●●-----	----------	----------
L. dubia	----------	----------	●●●●●▪▪▪--	●●●●●●●●▪▪	-------●--
O. ceorulescens	----------	●●●●●●●●●●	---------- ?	●●●●●●●-●●	----------

● population; ▪ single individuals; - no record

Figure 6. Changes of the dragonfly fauna in the monitoring area: decrease of the mooreland species between 1998 and 2007 (each sigh represents one year).

First Example: Anisoptera of Mediterranean origin in the Palatinate

Table 3 shows the change in the dragonfly fauna (Anisoptera) in the last four and a half decades in two different but neighbouring regions of the Palatinate (= part of the federal state of Rhineland-Palatinate). Whereas in the mid 1960ies the dragonfly fauna in the lower situated and warmer "Vorderpfalz" was already a mixture of Mediterranean and Eurosiberian elements, in the cooler and higher Westpfalz it was still dominated by Eurosiberian species (see Itzerott 1965). For the author this was a normal and typical situation and the fauna was indicating very well the different climatic frame conditions.

About 30 years later the Westpfalz faced a big change: the species numbers increased and the Mediterranean species reached nearly the same percentage as in the "warmer" Vorderpfalz; at the same time temperatures increased about one to two degrees in the formerly "cooler" Westpfalz (Ott 1996, 2001a)!

Again fourteen years later in 2009 the situation did not differ that drastically anymore, but some changes still have been observed (Trockur et al. in prep.; Ott unpubl. data). Besides some turnovers a slight increase of species numbers in total could be registered. In the Vorderpfalz three new species were found in the meantime: *Leucorrhinia rubicunda* (Linnaeus 1758), *L. caudalis* (Charpentier 1840) and *Stylurus flavipes* (Charpentier 1825). The latter two species are also autochthonous. In the Westpfalz *Epitheca bimaculata* (Charpentier 1825), *Somatochlora flavomaculata* (Vander Linden 1825) and *Libellula fulva* O.F. Müller, 1764 were new.

Interestingly all new species are Eurosiberian elements, but this does not mean the start of a return to a former situation: looking at the details it is more a stabilisation of the situation. As shown before – see e.g. fig. 6 – especially the Eurosiberian elements became much rarer and were found in fewer sites. In the central Palatinate forest, a part of the Westpfalz, some Mediterranean species now are definitely or probably indigenous, like *Crocothemis erythraea* or *Ashna affinis* (Ott 2010b).

Table 3. Changes in the Anisoptera fauna of two regions in the Palatinate: V = Vorderpfalz, W = Westpfalz, Med E = Mediterranean Elements, Eurosib. E = Eurosiberean Elements (1965: Itzerott 1965, 1995; Ott 1996, 2009; Trockur et al. 2010, Ott unpubl. data).

year	area	dragonflies		
		no. species	**Med. E (%)**	**Eurosib. E (%)**
1965	V	29	55	45
	W	16	31	69
1995	V	33	52	48
	W	30	47	53
2009	V	34	47	53
	W	34	44	56

In this context it must be considered, that this analysis is only done for the Anisoptera but not for the Zygoptera (as Itzerott 1965 published only on the Anisoptera and no data for Zygoptera are available in this detail). Within the Zygoptera quite some expansions of Mediterranean elements in the central Palatinate were registered in recent years, like for *Lestes barbarus* (Fabricius 1798), *Ischnura pumilio* and *Coenagrion scitulum* (Ott 2006b, 2008b; Lingenfelder 2008).

Second Example: the odonatofauna in the SLL+-region

Recently the dragonfly fauna of the so called SLL+-region – consisting of the two German federal states Saarland and Rhineland-Palatinate, as well as Luxembourg, the French department Lorraine and the Belgian Wallonia – was investigated and analysed for an atlas project (Trockur et al. in prep). In this area, covering 65,401 sqkm, also the southern species increased in abundance and enlarged their ranges. When comparing the situation before and after 1990, many southern species increased in the numbers of grid cells where they were found (e.g. *Crocothemis erythraea* + 109, *Erythromma viridulum* (Charpentier, 1840) + 107, *Aeshna mixta* Latreille, 1805 + 73, *Anax imperator* + 72). Also species like *Anax parthenope, Sympetrum meridionale* and *Sympetrum fonscolombii* became more abundant and very recently another damselfly - *Coenagrion scitulum* - showed a remarkable expansion (Lingenfelder 2008), being new for many parts of the area.

If this trend continues, without any doubt more species with a Mediterranean origin will appear in the near future, like *Boyeria irene* (already present near Lake Constance - see Schmidt 2005 or in the French Departement Haute-Marne – see Ternois 2008), *Anax ephippiger* (Burmeister, 1839) (already appearing several times as a guest – see Schorr 1989) and even the African *Trithemis annulata* (Palisot de Beauvois, 1805), which is expanding in southern France and now was also found in Lombardy (Boudot et al. 2009).

On the other hand Eurosiberean elements decreased (e.g. *Lestes sponsa* (Hansemann, 1823) - 39, *Coenagrion hastulatum* - 31). Especially *Coenagrion hastulatum* is facing a strong decrease in the Palatinate (see fig. 7); obviously the species is very sensi-

tive to lowered water tables. Some species even seem to be close to extinction, as their populations are very small, the quality of the biotopes is poor (moorelands already degraded) and the distances between the remaining biotopes are very long (high degree of fragmentation); this is in particular true for *Somatochlora arctica* (Ott 2006a), but also some other species face a similar – only slightly better – situation (*Aeshna juncea, Leucorrhinia dubia*, see Ott in press).

More examples: the odonatofauna in Bavaria and North Rhine-Westfalia

The same trends – increase of southern species, often accompanied by the decrease of mooreland species – were registered in several other federal German states or regions.

In a region of Bavaria (Nordwest-Oberfranken) investigations on the dragonfly fauna started in the 1970ies by the Bund Naturschutz (NGO in nature conservation). In the last years observations of a decrease in mooreland species increased. In 2006 all available old data were analysed and compared with data collected in this year (ÖBO 2007). If possible, the same waters as in former times were investigated to have a direct comparison. For this study a total of 41 water bodies were assessed.
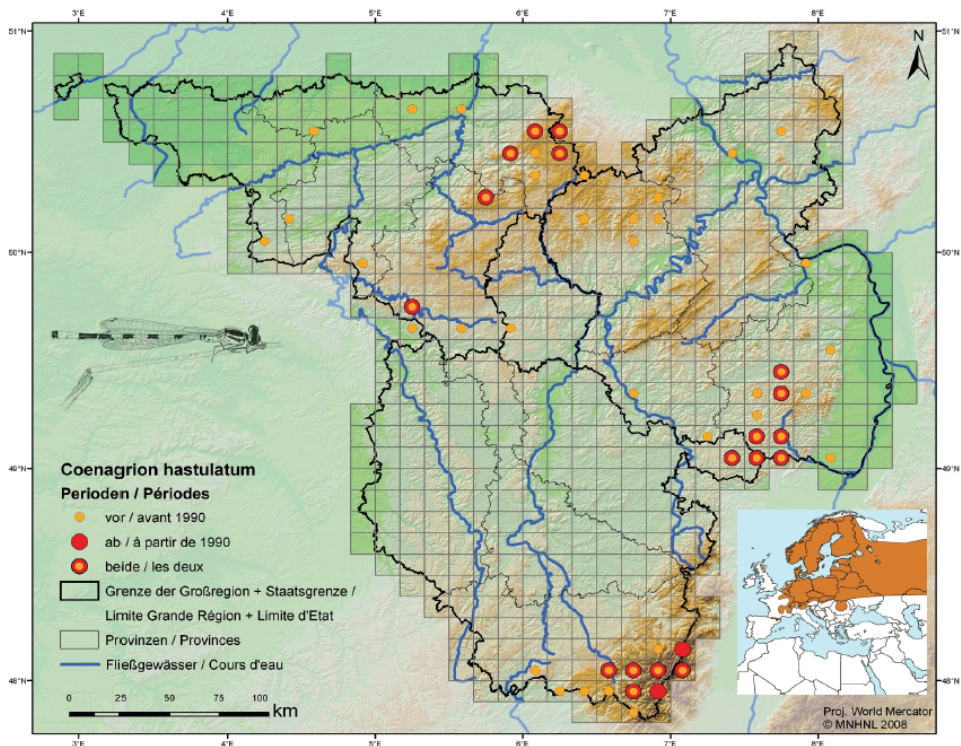
Figure 7. Distribution of the mooreland species *Coenagrion hastulatum* and *Somatochlora arctica* in the Sar-Lor-Lux-plus-region (Trockur et al. in prep.)

For the first time ever in this area *Crocothemis erythraea* was found now, which in two cases also appeared in typical mooreland waters, together with *Leucorrhinia dubia*. The latter species could not be registered anymore in half of the formerly populated waters, and *Aeshna juncea* disappeared even from 60 % of the waters colonised in the 1980ies and 1990ies. Also *Coenagrion hastulatum* dissapeared from 50 % of the formerly populated waters; in particular from the waters below 350 a.s.l. *Leucorrhinia rubicunda* (Charpentier 1825) was not found anymore, *Leucorrhinia pectoralis* also vanished from all its former waters and for *Somatochlora arctica* only one observation was made. So all mooreland species showed a strong decrease, whereas on the other hand *Crocothemis erythraea* now was found in three mooreland waters; the authors see the climatic changes as the reason for this change in the dragonfly fauna, as until today the main effects occurred mainly in the climatically favourable lowlands.

For the federal state of North Rhine-Westfalia the increase and spread of thermophilous dragonflies in recent decades is shown by Conze et al. (2010) through an analysis of about 150,000 data sets which were collected by a working group. Also in this case *Crocothemis erythraea* was the "leading" species.

Aspects of nature conservation

Biodiversity increase and consequences for the Red Lists

In the past decades biodiversity on all levels faced a more or less strong decrease, which is documented in the red lists of species and biotopes. If new species now arrive in an area, biodiversity – if we look only at the number of species – increases. To maintain a high biodiversity is one of the goals of nature conservation in general, and consequently the present situation should be regarded as positive and desired, also if we look at the fact that many southern species were on the last red list while now in the updated version many of them could be taken off (Ott and Piper 1998; Ott et al. in prep.).

But we still do not know, whether in the medium or long term, at least on a regional scale, biodiversity will rather decrease. As shown by the examples in Bavaria, the Palatinate or the SLL+region, in particular species of mooreland biotopes, which are more sensitive or stenoecious, seem to suffer from the present climatic situations (increased temperatures, falling water tables, drying out of waters, invasion of other species, e.g. with aggressive larvae). Beside the mooreland species also the alpine species are at risk: when looking at scenarios of future development for many regions, these species may not survive the next decades, as e.g. in Germany many regions will see some kind of "mediterranisation" of the climate (lack of water in the summer and higher temperatures). In particular the small water bodies in higher altitudes may easily dry out for a longer period, which most probably will lead to the extinction of many alpine dragonfly species.

After some increase in dragonfly biodiversity on the national level – as a consequence of the invasion of southern species – biodiversity will probably decrease, as we will lose the mooreland and alpine species.

Effects on the Natura 2000 web in the Palatinate forest

This decrease of biodiversity will probably also take place at the landscape level: due to the lack of water in extreme warm years many waters lost their habitat suitability (see fig. 8) and thus the species indicating the typical communities of the Natura-2000-biotopes (according to Ssymank 1998). This is shown in tab. 4: whereas two decades ago the typical species were still present (see Niehuis 1984), in recent investigations they only could be found in significant fewer numbers or even could not be found anymore at all (Ott 2007b, in press).

The species *Aeshna juncea, Leucorrhina dubia, Coenagrion hastulatum* only survived in very few and small populations, they could be classified as loser; for *Somatochlora arctica* only one single population is left in the whole German part of the Biosphere reserve Pfälzerwald-Vosges du Nord (Ott 2006a, 2010b, see also fig. 7).

Interestingly, several populations of these endangered species are not found in reserves or protected biotopes – dragonflies should be integrated more in reserve planning, what was recently also suggested by Heino et al. (2009), who showed that many protected areas were not delineated based on the requirements of freshwater organisms.

In principal the recolonisation of the waters from the French part of the reserve, the Vosges du Nord, is always possible, as there the situation seems to be still better

Table 4. Dragonfly fauna in some waters of the Natura 2000 web in the biosphere reserve Palatinate Forest (A = 1980-1995; B = 2005-2007, water table: + = intact, - = lowered, **O** = present/population, **O¹** = present/single individuals; * = a little outside of the reserve; species shaded = disturbance indicators).

waters	Jagdhaus-weiher		Vogelwoog *		Pfälzerwoog		Rösselsweiher		Kranzwoog	
time span	A	B	A	B	A	B	A	B	A	B
water table	+	-	+	-	+	-	+	+	+	-
species										
P. nymphula	O	O	O	O	O	O¹	O	O¹	O	O
C. hastulatum	O		O		O		O		O	
A. juncea	O		O		O		O		O	
S. arctica	O									
L. dubia					O		O		O	O¹
L. pectoralis										
S. danae	O	O	O		O	O	O	O	O	
L depressa		O	O	O	O	O				O
O. cancellatum		O	O	O	O	O		O		O
G. pulchellus		O	O			O		O		

Figure 8. The nature reserve Pfälzerwoog; in August 2006 the water fell nearly completely dry. Foto: J. Ott

for mooreland species (Duchamps and Morelle, pers. comm.). But on the other hand the waters in the Palatinate now have another abiotic quality and other communities are now established (see the example of the monitoring-project Kolbenwoog), consequently the dystrophic waters lost or will loose their characteristics. Without doubt this also will have consequences for the ecosystem services of these waters (water retention, landscape aesthetics etc.) and other – already existing impacts (fragmentation, lowering of the groundwater table) – will have additional effects.

Changes on the national level: some recent trends in Germany

Changes in the phenology

In general insect species react on the increase of temperature with a change in their phenology: increasingly observations are made very early or very late in the season. This process started in the 1990ies, since then with an increasing number of such observations.. Here some recent data for Germany are summarized.

E.g., in mid December 1994 *Sympetrum striolatum* was still on the wing in Switzerland and in early November 1999 *Lestes sponsa* (Hansemann 1823) in Baden-Württemberg (Jödicke 2000). In 1994 and 1997 *Somatochlora metallica* was on the wing

until October (Reder 1997) while in 2000 *Gomphus flavipes* was registered in the Rhine Valley still in mid October (Reder 2001).

Extremely early and warm springs – like in 2007, one of the warmest years since climatic data are registered in Germany – did have an additional effect on the phenology: in Baden-Württemberg more than 30 species emerged earlier than ever registered before (Hunger 2007). Some for only a few days, but many species emerged even one (e.g. *L. barbarus, E. najas* (Hansemann 1823), *L. caudalis* (Carpentier 1840)), two (e.g. *C. hastulatum* and *pulchellum* (Vander Linden 1825), *C. aenea* (Linnaeus 1758)) or even three weeks (*L. dubia*) earlier then ever observed before.

Sometimes very late emergences are registered recently for *Gomphus vulgatissimus.* Niehuis and Heilig (2004) found a fresh individual on the 29th of July 2004 in southern Palatinate, where the flight period in general lasts only until late June and Westermann (2002) found an eclosing male on the 9th of August 2002 in Baden-Württemberg.

For the Lausitzregion in eastern Germany Donath (2009) compared the data of the first emergence: he could present several records of extreme early emergence from 2009 and by comparing this situation with the year 1977 he could also show a general trend of an earlier emergence of about one week. Some species like *Coenagrion pulchellum, Orthetum cancellatum, Leucorrhinia dubia* and *Lestes dryas,* Kirby 1890 emerged even two weeks earlier in 2009 – with the warmest April at least since 1891.

Besides a prolonged phenology of the adults also an impact on the eclosion period was registered which is indicated by very late and "not normal" eclosion: at the end of September 1999 a teneral male of *Gomphus vulgatissimus* was seen in Lower Saxony (Fliedner and Fliedner 2000). In Baden-Württemberg 33 individuals of *Lestes sponsa* emerged during the first week of September 2005 (Koch 2005).

In the mid or long term this might lead to a desynchronisation in the phenology. It is well known that thermal impacts on waters – e.g. by power plants – lead to earlier eclosion, even in winter. Consequently, also the general increase of the temperature will most probably have the same effect.

More generations: from semi- to univoltine, from uni- to bivoltine

A wide range of species now has a second generation: in Germany species which formerly were univoltine now became bivoltine, or migrating species had a second generation. In the mid 1990ies this was only registered for a few species and areas, like for *S. fonscolombii* in Bremen, Lower Saxony and northern Hesse (e.g. Pix 1994), or *Ischnura elegans* and *I. pumilio* in North Rhine-Westfalia (Inden-Lohmar 1997). In the consecutive years this phenomenon became much more widespread and was seen in an increasing number of species, as well as all over Germany. E.g. it was shown for *E. cyathigerum*, *E. najas*, *I. elegans* and *S. fonscolombii* in Baden-Württemberg (Schiel 2006; Koch 2002), and for *I. elegans* and *pumilio*, *E. najas* and *S. fonscolombii* in Bavaria (e.g. Burbach 2000). In Rhineland-Palatinate *I.pumilio* and *E. cyathigerum* in some years do have a second generation (Ott 2008b, unpubl. data).

Especially in hot summers, like the one in 2003, this effect is apparent and even the Mediterranean *Crocothemis erythraea* might have a second generation in Germany (Horn 2003). In some years (1999, 2000, 2006) this was also shown for *Anax imperator* in southern Germany in four localities, the species generally is known to be bivoltine only for the Mediterranean (Westermann and Weihrauch 2007).

Species formerly not known to have a univoltine cyclus in Central Europe, like *Gomphus pulchellus* and *Leucorrhinia caudalis*, show it now in southern Germany (Schirrmacher et al. 2007) or partly, like *Leucorrhinia pectoralis* and *Brachytron pratense,* in north-eastern Germany (Brauner 2006).

Moving to higher altitudes

Anax imperator is in general a lowland species, but recently also can be found in altitudes of more than 1000 m a.s.l. (Hunger et al. 2006) and even on 915 m a.s.l. an indigenous population was registered (Westermann 2003c). But also damselflies move to higher altitudes, *Lestes viridis* (Vander Linden 1825) in general found in the lowland is found breeding in 900 m a.s.l. (Westermann 2003a). Also *Lestes barbarus* was found in the Black Forest regularly up to 700 m a.s.l. where it is also breeding in some cases (Hunger et al. 2006; Salcher 2006), in the Palatinate it populated the higher centre expanding from the lowlands and is now found breeding in altitudes of ca. 400 m a.s.l. (Ott 2006b). Again in the Black Forest at an altitude of 1010 m a.s.l. another damselfly – *Erythromma najas* – was found indigenous, which represents the highest reproduction site in Germany so far (Westermann and Westermann 2003) and in 2005 the highest elevation of an autochthonous population in central Europe was registered for *Gomphus pulchellus* (Selys 1840) (Westermann 2006). This western Mediterranean species started its east and northward expansion already in the last decades (Rudolph 1980) and now – besides the continuation of this expansion – also moves to higher elevations.

Changes on the European level – some recent trends

Even if the expansion of damsel- and dragonflies on the European level are not demonstrated for all countries in a totally comparable way – as in many countries data collection is done in a different way and intensity – the general pattern however is very obvious.

To compare this trend the situation in the early/mid 1980ies is taken from Askew (1988) who for the first time presented maps on the European distribution. For the situation in 2009 data and information were taken from different publications and national atlas projects (e.g. Nielsen 1998; NVL 2002; Karjulainen 2002; Nelson and Thompson 2004; Grand and Boudot 2006; Parr 2003, 2004, 2005, 2006, 2007, 2008, 2009; Bouwman et al. 2008; Dolny et al. 2008; Bernard et al. 2009), as well as websites of the national odonatological societies.

Table 5. Damselfly and dragonfly species of Mediterranean origin in 2009: showing clear northern range expansions in Europe compared to Askew (1988).

Species name	Range expansion in
Ischnura pumilio	New for Sweden in 1992, remarkable increase from 2007 onwards
Coenagrion scitulum	France, Germany, Belgium, Luxemburg, also in the East, e.g. in the Czech Republic
Erythromma lindenii	North-eastern France, parts of Belgium, northern and eastern Germany, new to UK
Erythromma viridulum	North-eastern France and Netherlands (now very common and present on all Wadden islands), northern Germany and also in Poland: here it expanded in the last 3 decades up to 300 km; in 1999 new to the UK, here spreading quickly in the south-east, obviously in "waves"; new to Denmark, between 2001 and 2009 already found in 53 localities, in 2004 new to Sweden and in constant expansion in the south
Lestes barbarus	Central parts of Europe, becoming more abundant, new to the UK
Aeshna affinis	Northern France and Germany, Netherlands. New to the UK (possible sighting in 1993, then e.g. in 2004 and 4 times in 2006), Denmark (2 records for 2006) and Finland (1 male in 2008)
Aeshna mixta	UK up to the central parts, in Poland significant increase and area of native occurrence has expanded 350 km northwards; new to Ireland, Sweden and Finland; in Finland first recorded in 2002, now a rare breeder in the south, in Sweden also larvae were found and in particular in 2007-2009 a high number of observations
Anax imperator	Obviously in many countries increasing, e.g. Germany and Poland, here rare about 100 years ago, but now widespread, also in higher elevations; UK up to the central parts and new to Scotland, also new to Ireland, Denmark and Sweden; in Denmark first recoded at the end of the nineties, but in the last 10 years recorded in more than 200 localities; in Sweden spreading very quickly northwards (> 700 km), after being recorded in 2002 for the first time
Anax parthenope	Northern France, Belgium, Netherlands, northern Germany and Poland, new to UK (first recorded 1996, Gloucestershire; has bred in Cornwall, record year in 2003 and increasing numbers between 2005 and 2007: in more than 60 sites) and also Ireland
Boyeria irene	North-eastern parts of France, new to Germany
Gomphus pulchellus	Northern and eastern parts of Germany, also to Austria
Oxygastra curtisii	Rediscovered in Germany after more than 50 years
Crocothemis erythraea	All central Europe, new for the UK in 1995
Sympetrum meridionale	All central Europe, up to northern Germany and Poland
Sympetrum fonscolombii	New to Denmark, between 2003 and 2009 found in 9 localities, new to Sweden, found in 1997, 2003 and 2007
Species name	**Increasing tendency of migrations/invasions, e.g. observed in**
Anax ephippiger	Germany, in some years even reproducing; other central European countries (e.g. Poland)
Sympetrum fonscolombii	UK, Ireland, northern France, Belgium, Netherlands, Germany, Poland, partly indigenous populations (second generation)

Especially when looking at the northern European countries, expansions from the south are obvious, or at the "other end of the continent": at the southern countries, where recently African species expand to the north as well (see below).

In Sweden for example beside the above mentioned new species others – which were already present in low numbers – currently expand in a remarkable way, like *Calopteryx splendens* (Harris 1782), *Libellula depressa* (Linnaeus 1758) and *Sympetrum striolatum* (Charpentier 1840). The same trend is seen in the UK, where species formerly mainly restricted to the south – e.g. *Libellula depressa* and *Orthetrum cancellatum* – expanded northwards. *Libellula depressa* reached Scotland where it was first recorded in 2003 and again twice in 2007 (Parr 2004, 2007).

In Poland *S. meridionale* (Selys 1841), *S. fonscolombii* (Selys 1840) and *striolatum* are now „normal" elements of the fauna, formerly they were rare and species like *Crocothemis erythraea* and *Orthetrum albistylum* are moving northwards (Bernard et al. 2009).

New for Lithuania in 2003 became *Aeshna affinis* Vander Linden, 1820 (Bernard 2005), which is very likely to be also indigenous. For Latvia in 2008 *Anax parthenope* was registered for the first time and in 2008 and 2009 it was found in five localities (Kalnins 2009), where in one case it also eclosed. In Belarus several species are now new to the national fauna and/or expanded, like *Sympecma fusca* (Vander Linden 1820), *Lestes viridis, Erythromma viridulum, Orthetrum brunneum* and *O. albistylum* (Selys 1848) (Buczynski and Moroz 2008).

On the other hand in the Mediterranean countries we can observe a recently started process: the expansion of African species as shown in table 6 (again compared with Askew 1988; the present situation according to the websites mentioned above and Boudot et al. 2009).

The Violet Dropwing (*Trithemis annulata,* see fig. 9), a typical species all over Africa and the Middle East, formerly occurred only up to southern Spain and central Italy (Askew 1988). But now it can be found even in southern France, having crossed entire Spain and also the Pyrenees and in Italy it now reached the area of Ferrara (Boudot et al. 2009). Another *Trithemis* species – the afro-tropical Orang-winged Dropwing (*Trithemis kirbyi* Selys 1891) – was not known for Europe at all, but then was discovered for the first time on the isle of Sardinia in 2003 (Holusa 2008). After being discovered in 2007 also in southern Spain near Malaga by D. Chelmick, in 2008 for the first time larvae of this species were found proofing its first autochthony in Europe (Cano-Villegas and Conesa-Garcia 2009).

The third example of an African respectively Asian species expanding its range to the north is the Black Pennant (*Selysiothemis nigra* Vander Linen 1825), which in Italy is actually found up to the area of Trieste/Venice (Boudot et al. 2009) in the eastern part and up to Parma (M. Salvarani pers. comm.) in the western part.

Figure 9. A male of the Orange-winged Dropwing (*Trithemis kirbyi*): new in Europe. Foto: J. Ott.

Table 6. African species recently expanding in Europe

Species name	Range expansion in
Trithemis annulata	Spain (entire country crossed), Italy (up to Lombardy) and France (only in the south)
Trithemis kirbyi	New to Spain (also indigenous, in the area of Malaga) and Italy (Sardinia)
Selysiothemis nigra	Now present in northern Italy (near Parma in the west and Venice in the east), northern Spain (close to the French border) and Slovenia

Biological effects - Climatic change: a filter for different ecological strategies and species

The biological effects of the rise in temperature for Odonata could be summarized as follows (updated from Ott 2001a; see also Hickling et al. 2005; Corbet et al. 2006; Dingemanse and Kalkman 2008; Hassel and Thompson 2008):

– more prominent tendency for expansion
– more northerly breeding, also breeding in higher altitudes
– changes in the composition of the fauna
– eclosion earlier in the season, overall alteration in the phenology
– second generation, changes in voltism
– more rapid larval development

The tendency for expansion is in particular notable in warm years like 2003: see in this context e.g. Parr (2004, 2007, 2009) where many species were seen far away from known breeding sites (*Erythromma viridulum*: ca. 100 km, *Brachytron pratense*

Table 7. Winners and losers of climatic change (Ott 2001a, updated).

winner	loser
species with preferences for higher temperature	species with preferences for lower temperature
"lowland species"	"mountain species"
common and widespread species	locally distributed / rare species
species of eutrophic waters	species of oligotrophic waters
euryoecious / ubiquitous species	stenoecious species
good flyers	bad flyers
fast / short larval development	slow / long larval development
r - strategists	K - strategists
species with aggressive and / or temperature-tolerant larvae	species with "sensitive" and / or temperature-intolerant larvae
<u>examples:</u> *Ischnura elegans, I. pumilio, Lestes barbarus, Libellula depressa, Crocothemis erythraea, Anax imperator*	<u>examples:</u> *Coenagrion hastulatum, Somatochlora arctica, S. alpestris, Aeshna subarctica, Leucorrhinia albifrons*

(O.F. Müller 1764): ca. 100 km, *Cordulia aenea*: > 100 km, *Orthetrum coerulescens*: 20–30, even up to ca. 45 km).

Finally climatic changes can be regarded as a filter: they favour the species which are able to adapt to the new situations (higher temperatures, drying out of waters etc.) and eliminate the species which cannot cope with the new environmental conditions. There are winners and losers of the situation.

The future is … hot?! What do scenarios tell us and what does this mean for dragonflies?

Even if in some countries (e.g. Germany) or even in the entire EC the emissions are stable or reduced (see EEA 2009a), worldwide emissions of carbon dioxide and other greenhouse gases will still be increasing (IPCC 2007a).

Assuming that these gases are the reasons for the climatic changes (on which there is a general agreement within the scientific community), the changes of the abiotic conditions (e.g. temperature increase, changes in the precipitation) will go on, as well as the effects on the biotopes and communities.

The different scenarios – like the ones which are used by the IPCC (IPCC 2007a) or the ones in the ALARM-project (Settele et al. 2010a, 2010b) – expect that there will be an additional increase of temperature of at least 2 degrees within the next decades, some scenarios expect an even higher increase.

This means that all the shown conditions for dragonflies in Europe, e.g. higher temperatures in the waters, lack of the precipitation in summer, falling water tables,

higher air temperatures, more sunshine etc. will continue and become even more intense in the future.

As the range expansions to the north demonstrated here (see tab. 6) were the results of only an increase of about 1° Celsius in Central Europe in the last decades, in the future the changes of the waters and their communities – higher proportion of thermophilic and southern species etc. – could be expected to be even stronger and faster, finally these species will dominate the dragonfly fauna.

However, also some Mediterranean species in the medium term may loose large parts of their distributional area in the south, as in particular in the Mediterranean many waters will dry out and so lose their biotope quality in general for aquatic species (see August and Geiger 2008; Ott 2010a).

The effects of climatic changes in the Mediterranean will however be much stronger on other taxa, like the Trichoptera and Plecotera, as these taxa have many endemics (Hering et al. 2009; Tierno de Figueroa et al. 2010).

On the European level there might be little concern for most of the southern generalist dragonfly species level, while on the other hand the species of moorelands, higher altitudes and colder biotopes will continuously be eliminated, as in particular these biotopes will suffer in the next decades (Ott 2001a, in press). In higher areas biodiversity will increase as a result of the "invasion" of lowland species – see Oertli et al. (2008) and Oertli (2010) – but this will without any doubt have a negative effect on the more sensitive species of the mountains, which can not move any higher, as there are no more waters. In general mountains like the Alps or the Pyrenees will face strong impacts and changes of their water regimes (e.g. for the Alps: EEA 2009b) and in particular species with a small range and those which live in rare climates (e.g. interglacial relicts) will be reduced disproportionally (Ohlemüller et al. 2008).

Consequently these cold stenothermal species will be eliminated, which is also true for other sensitive species of the lower mountains or even the lowlands. In the Black Forest (see Hunger et al. 2006) *Aeshna caerulea* – a species restricted to peat bogs above 830 m a.s.l. – is more or less extinct, as the climatic circumstances became increasingly unfavorable for the species.

The same is true for *Aeshna subarctica* in northern Germany: their larvae are specialists of peat bogs, and monitoring studies in the federal states of Brandenburg and Mecklenburg-Vorpommern show their dramatic decrease (Peters 2008; Bönsel 2001). The reasons seem to be the eutrophication of the waters in general and the extreme summer heat in the waters, which has negative impacts on the larvae, as these have preferences for lower temperatures.

Furthermore there will also be many cumulative and synergistic effects, which hitherto have hardly been studied.

These factors are for example:

*   acidification of the waters ("acid rain", impacts on the aquatic communities)
*   eutrophication through immissions (leading to oxygen consumption, algal blooms and succession)

* (ground-)water extraction (lowering of water table, impacts on ground water depending ecosystems)
* higher concentrations of pollutants / toxic substances (mainly in the running waters) and also alien invasive species (alien crayfish, grass carps etc.) will play an increasingly important role.

For example the level – and thus also the lowering – of the groundwater determines the relative susceptibility of regions to changes in temperature and precipitation, ergo the extraction will be an additional and cumulative threat (see Maxell and Kollet 2008).

This might be the case for the example "monitoring Kolbental" which was shown here: if at the end the extraction has a negative effect on the groundwater level, the whole area with its biotopes will be impacted even more.

Another example is the increase of the water temperature of rivers: the mean water temperature in the river Rhine increased by 3 degrees during the last 100 years, 2 degrees as a result of cooling water discharge and another one as an effect of climatic changes (BUND 2009). But not only the mean water temperature increased, also the days with water temperatures above 23° and 25° C, and the probability of extreme high water temperatures, passing a critical – or tipping – point of 28 degrees, where many species (e.g. fish, molluscs) die and then cause "toxic waves" of ammonium etc., leading to other impacts.

These problems are reviewed and summarized for European rivers by WWF (2009), where it is shown, that the known and expected changes in the river temperatures do already have many ecological consequences – and will have even more in the future – as the communities of the waters are adapted to a certain temperature regime. Effects are posed on the abiotic conditions – e.g. lack or higher consumption rate of oxygen (Sand-Jensen and Pedersen 2005) – as well as on the composition of the communities (e.g. the mollusc fauna will be reduced: Mouthon and Daufresne 2006; the fish communities altered: Daufresne and Boet 2007). Finally complete food webs are changed (Emmerson et al. 2005).

It is also relevant that not only the general temperature increase will have an effect on the flora and fauna, but also the extreme situations (e.g. heat waves), which are expected to happen much more often (Daufresne et al. 2007).

This leads to another aspect: as shown before, temperature increase functions like a general filter (see tab. 7), but the increasing number of extreme events will function as a second filter.

Extreme climatic conditions – which used to be rare and localised – become more and more abundant and also new situations will occur, which until today did not happen at all (see Meehl et al. 2000 and Wigley 2009). This will lead to many impacts, also on the communities' level (see the above mentioned examples of the rivers, or Thibault and Brown 2008) and synergism of global warming and other stresses (e.g. habitat destruction) can disrupt the communities (Root et al. 2003).

Still it is unclear, whether the undoubtful increasing of the competition when new species arrive in a water body, also leads to an exclusion of the former fauna. This

might be in particular the case, when new biotope types are colonised: e.g. *Crocothemis erythraea* enters now acid waters (Ott 2010b), whereas the species formerly preferred secondary waters like sand- and gravel pits (Ott 1996) and now may use another niche (see here: Broennimann et al. 2007).

Emmerson et al. (2005) pointed out, that already small changes in the number of species in a food web can have consequences both for community structure and ecosystem processes, consequently community stability and ecosystem functioning is altered. In particular when a top predator arrives, what is shown by Byström et al. (2007): the extinction of the char was caused by the pike (trough predation and competition) which expanded to the north and effects on the whole food web were registered. Consequently, also effects on the dragonfly fauna of northern countries can be expected, even if there are still many open questions in community ecology (see Booth et al. 2009: what will be the effects of the changes in phenology on the different trophic levels?). Biotic interactions and feedback processes lead to highly complex, nonlinear and sometimes abrupt responses. To identify and quantify these processes remains a huge challenge (see Walther 2010).

Conclusions

In Europe, dragonflies have a moderate number of species, their ecology is mostly well known, and they are easy to identify, thus they are perfect indicators. This is in particular true – as shown here – for the effects of climatic changes on different levels (single waters, landscape or national / European level).

Contrary to other taxa they depend only on waters, which are more or less omnipresent, and their expansion is only due to their dispersal and migration behaviour. Butterflies depend also on plants, and if these do not expand their range, also the butterflies are unable to do so; grasshoppers are transported sometimes by vehicles and so their expansion is some kind of artificial. This makes dragonflies some kind of unique as climate change indicators.

Here it is shown that in the recent decades there were massive range expansions of damsel- and dragonflies in Europe, leading to changes in the communities. Climatic changes are the reason for these expansions, leading to a higher biodiversity in many areas, but they are also the reason that now some species are threatened or will be threatened in the future. This is in particular true for mooreland species and species of higher altitudes, in the future maybe also for species of springs or species of smaller running waters (mainly in the Mediterranean).

Climate change can be seen as a threat for the dragonfly fauna in addition to the impacts which already had been identified. Many synergistic and cumulative effects do occur and will do so even more in the future (e.g. lack of precipitation and an increase of water demand and consumption). Alien invasive species (e.g. fish, crayfish) might also play an increasingly import role.

The effects – most of them negative – for the waters and (dragonfly) communities have a consequence also for future strategies in nature conservation, as e.g. one of the

most important concepts to protect biodiversity in Europe – the Natura-2000-network might not work anymore, as these biotopes are increasingly detiorated and lose their function.

To follow these processes and to identify the effects of global change phenomena, it is of crucial importance to establish and maintain European wide data collections and monitoring schemes.

Acknowledgements

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Denmark: http://home1.stofanet.dk/erland_refling/danish_dragonflies.htm
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Sweden: http://www.artportalen.se/bugs/default.asp