Report from workshop to NorACIA February 2007

Project leader: Ronny Aanes (Norwegian Polar Institute, NPI)
Time: 11-12 January 2007
Venue: NPI at the Polar Environmental Centre, Tromsø

Workshop arranged under NorACIA theme 3: Effects on ecosystems and biodiversity

Workshop working title: "*Ecological effects of variations and changes in climate in northern ecosystems: current knowledge and future challenges*".

Participants:
Ronny Aanes (NPI)
Tim Coulson (Imperial College/Cambridge University, UK)
Per Fauchald (Norwegian Institute of Nature Research, NINA)
Rolf A. Ims (University of Tromsø, UiT)
Anne Loison (CNRS, Lyon, France)
Audun Stien (UiT/NINA)
Bernt-Erik Sæther (Norwegian University of Science and Technology, NTNU)
Torkild Tveraa (NINA)
Nigel G. Yoccoz (UiT)

Programme

11 January

12:30 – 13:30
Lunch

14:00 – 14:20
Ronny Aanes
Ecological effects of climate change: from knowledge based on correlations and simple models to scenarios and reality

14:30 – 14:50
Tim Coulson
Demography, dynamics and climate: challenges

15:00 – 15:20
Anne Loison
Will climate impact all ungulates in the same way? Some evolutionary insights based on an interspecific comparison of maternal care

15:30 – 15:50
Torkild Tveraa
Population regulation and limitation in reindeer

16:00 – 16:20
Per Fauchald
Life history responses to environmental change: An experimental approach

16:30 – 16:50
Adun Stien
o' Voles an' Reindeer

17:00 – 17:20
Nigel Yoccoz
Integration of small-scale, intensive studies of demographic mechanisms and large-scale, extensive studies of dynamical patterns: some random ideas (or idées fixes…)

20:00 Dinner

12 January

09:00 – 09:20
Rolf A. Ims
Some challenges and opportunities in research on ecosystem level effects of climate change in northern Norway:
Are we able to suggest strategies for "building resilience"?

09:30 – 09:50
Bernt-Erik Sæther
Disentangling the effects of climate

10:00 – 11:30
General discussion
Chair: Rolf A. Ims

11:30 – 1200
Lunch

12:00 – 14:00
General discussion continues

14:00 The end

Abstract
The participants presented data and results based on their own research in northern and alpine environments with species ranging from moths to moose. Generally, the presentations included the effects of variations in weather/climate on spatial and temporal variation in the dynamics of different species and trophic levels. The effects of life-history evaluated through experimental and comparative studies were also presented in context of patterns in population dynamics related to variations in weather and climate. Finally, different methodological approaches were presented revealing pros and cons depending on type of data and question(s) asked.

There are several important take-home messages from the workshop concerning the environmental impact on populations and/or components of northern ecosystems: (1) we must identify climatic drivers (i.e. the main environmental variable(s) that guide the population dynamics), (2) data on demography largely improves the ability to make predictive models based on time series, (3) a proper modeling of the effects of environmental variation on the observed population dynamics must account for key-processes in the dynamics, like density dependence and age-structure, (4) it is unlikely that we would be able to construct predictive models telling the faith of a given species in e.g. 10-50 years ahead (e.g. population size) (5) it may be a pit-fall to generalize results from one population to another due to spatial variation in the effects of environmental variation, (6) a better understanding of how life history strategies are changed in response to climatic conditions is needed to predict future responses, (7) researchers and managers must be prepared for "surprises", i.e., observing a future different from what could be expected from a-priori knowledge due to the complexity involved in biotic-abiotic interactions, and the uncertainty in climate scenarios.

Background
Population dynamics refers to the variation of population density in time and space. The observed dynamics of a given population results from deterministic and stochastic factors, often with a complex interplay between them (Lande et al. 2003). Deterministic factors refer to a change in population size from one time step to another being a function of density. Stochastic factors include three forms; i) *Demographic stochasticity* is chance events of individual mortality and reproduction, and can often be ignored in large populations, ii) *environmental stochasticity* is fluctuations in the probability of mortality and reproduction between time steps affecting all individuals similarly, and iii) *sampling error* in population size or density. The latter does not affect the dynamics but the measure of it. A major part of the environmental stochasticity in current studies refers to variation in weather (meteorological observations less than 30 years) and climate (30 years and more). Hereafter we use the word *climate* for both terms.

The future Arctic/sub-Arctic climate will on average be warmer, more variable and contain more frequent extreme climatic events (IPCC 2001). Also, climate change is expected to be more intense at northern latitudes compared to the global average (IPCC 2001, Mann et al. 1998). For a long time a major challenge in ecology has been to quantify the effects of climate on a given species, population or components of a given ecosystem, spanning back to e.g. Elton (1924) and Andrewartha and Birch (1954). It is well known that variations in climate affect individual performance and thus population dynamics (e.g. Walther et al. 2002, Stenseth et al. 2002). Biological responses to climate

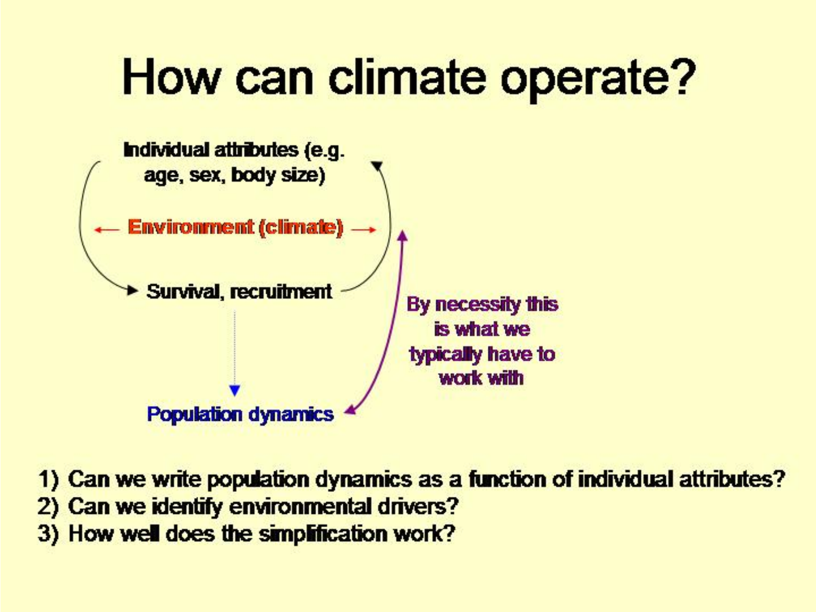
change are widespread and may have different expressions. For instance, it has been shown that a warmer globe gives earlier flowering in plants (Post and Stenseth 1999) and egg-laying in birds (McCleery and Perrins 1998), increased (Winkel and Hudde 1997, Sæther et al. 2000) and decreased (MacInnes et al. 1990, Veit et al. 1997) reproductive success in birds, range expansion in birds (Thomas and Lennon 1999) and herbivores (Andersen et al. 2004), changed assemblage of fish species (Holbrook et al. 1997), massive die-offs in marine ecosystems (Stenseth et al. 2002), and increased risk of extinctions in amphibians (Pounds et al. 1999) and butterflies (Parmesan 1996).
These examples show some of the complexity when studying the ecological effects of variation in weather and climate, with contrasting responses between and within trophic levels and species. Our objective with the workshop was to present current knowledge from northern ecosystems, and to discuss the main future challenges.

Type of data determines what we can understand

Commonly we study a time series of observations when trying to understand ecological effects of climate. Let's outline a couple of examples for medium-sized to large herbivores that reproduce annually in a seasonal environment. This is typical for such species in northern ecosystems: The type of data may vary in length, detail and accuracy. Worldwide the probably most common biological time series consists of an estimated number of individuals in a given population over a given period of time. This series may be annual total counts or an estimate based on a given estimation technique (e.g. capture-mark-recapture). A quantification of sampling error is advantageous because it gives the uncertainty in the estimate, else one often have to assume no sampling error (which may give wrong estimates of the effects of environmental variation as some may be due to sampling error rather than the stochastic environment). The latter should be avoided if possible, but the magnitude of the problem may depend on species and area (e.g. topography and visibility of animals). Likewise, the study area should provide relevant climatic variables from weather stations, mirroring the true environmental variation a given population experiences throughout the year. Also this is not often available, and one has to rely on the nearest weather station from e.g. a meteorological institute (which may be tens of kilometers away). An often used alternative is to use a global climate index like the North Atlantic Oscillation/Arctic Oscillation as a proxy for the environmental variation in the area. However, due to spatial variation in the correlations between the indexes and weather in a given region, the local relationships between the global index and local weather must be known.

At the other hand, some have the luxury with time series consisting of very good population estimates with a low uncertainty, known demography (i.e. known individual attributes like e.g. sex, age, body size, time of death etc.).

This is what we actually study:



However, we rarely have all the information in the figure.

Having the above in mind we describe 3 data series, 2 of which can be considered "typical available data", and 1 rare but luxury type of data. We briefly go through what information we can get out of them in the context of effects of environmental variation on the population dynamics. We use hypothetical examples from what could be medium-sized to large herbivores in northern ecosystems.

1. *Climate-herbivores*

Data: Time-series of number of animals and observations of weather during the same period.

In this case we can quantify how much of the observed annual variation in number of individuals are due to deterministic factors (density dependence) and stochastic factors (climate in this case). Usually we are left with some unexplained variance within the noise term. We can explain very little about the mechanisms, i.e. *how* climate affect the dynamics (e.g. through effects on certain segments of the population).

The added value of several climatic variables:

Usually ecologists use measures of temperature and precipitation from weather stations close to the area where the population of interest is located. If temporal measurements are available we could find whether the climatic driver(s) are seasonally dependent or not. If so, we may approach a mechanistic understanding if e.g. much snow during winter is associated with few animals the following summer, i.e. a negative correlation between winter snow and populations size. Then it is likely that the snow operated through mortality and/or reduced fecundity of females. If summer temperature is positively correlated to number of animals counted the next summer, it is likely that biomass production has a positive effect on survival and/or fecundity in the population. This does not give a true mechanistic understanding, but nevertheless makes us able to outline hypotheses about what is going on.

2. *Climate-herbivores-resources*

Data: Time-series of number of animals, observations of weather during the same period and information of resources available (i.e. food).

Here we have expanded our data set by including one more trophical level, the food of herbivores. This increase our ability to understand the population fluctuations in a more mechanistic way as we now can investigate the relationship between climate and herbivores, climate and resources (plants in this case), and the interaction between herbivores and their food resources.

3. *Climate-herbivore-resources-demography*

Data: Time-series of number of animals, observations of weather during the same period, information of resources available (i.e. food), and demographic data from the population.

Here we have expanded the data set to include virtually the complete ensemble in what may affect the population dynamics of an herbivore. In an important contribution Coulson and colleagues (2001) showed the importance of known individual attributes to provide a mechanistic understanding of the observed population dynamics in their study of Soay sheep. Their study demonstrated that different sex and age classes may respond in contrasting fashion to changes in density or climate. By utilizing long-term monitoring and demographic data from known individuals they showed that the observed population fluctuations are a complex mixture of sex, age, density and environmental variation.
An important conclusion from this study is that identical climate can give contrasting population dynamics because individuals of different sex and/or age respond differently to density and climate.

Spatial variation

Studying one population, or alternatively one area, may be of limited value due to spatial variation in both climate and population characteristics. The new climatic scenarios proposed by IPCC (2007) shows that we can expect large differences in changes in climate on both large and small scales. For instance, in northern Norway it is expected that coastal areas will be warmer and wetter during the next 100 yrs, whereas continental areas (like the interior of Finnmark, Northern Norway) may get less precipitation in the future. Although such spatial variation exists today it is suggested that it may be more pronounced in the future, and is therefore an important point to account for when trying to predict ecological effects of climate change. Accordingly, Tveraa et al. (2007) showed different responses in dynamics and demography to climate and harvesting strategies depending upon whether semi-domesticated reindeer inhabited coastal areas or inland/continental areas. Also, the characteristics (e.g. strength and form of density dependence) of a given species may differ from one population to another resulting in different responses to a given environmental variation (e.g. Sæther et al. 2006).

Populations and ecosystems

As biological time-series long enough to explore population dynamics emerged the studies usually involved only one trophic level (the population in question). Such studies may give valuable insight of e.g. the dynamic structure of a given population, but may be of little value when attempting to predict the future. This is due to that one has to hold all other factors constant, which is unlikely in reality. Recently, more studies have become available using more than one trophic level, e.g. using remote sensing such data as the Normalized Difference Vegetation Index (NDVI) (e.g. Tveraa et al. 2007), or some other index of resource availability (e.g. Aanes et al. 2002). However, there is an urgent need for studies with a wider ecosystem approach, designed for a specific purpose (e.g. the effects of environmental variation). Such studies are time-demanding and costly but should be prioritized to due its value in science and for management purposes.

Predictions may fail

Due to the inherent complexity in biotic and abiotic systems we are likely to get some surprises regarding ecological effects of climate change. We expect such surprises in the future because we do rarely get sufficient information of all parameters affecting a given population. Likewise, future climate scenarios are uncertain. That is, although the general pattern may be "warmer and wilder" exceptions is likely to occur, and hence affect the population dynamics in a different way than predicted.

Conclusion

The major objective is to find the most important climatic driver(s) of a given population. That is, what climatic parameter(s) explain the most of the variation in population densities? This gives a lot of information on what changes could be expected given different climatic scenarios. As climate changes one should be aware of the possibility that the main climatic driver(s) may also change.

The workshop emphasized the importance of including demography in monitoring protocols to understand how populations may respond to climate change. Within this context, and for planning conservation and harvesting strategies, counting number of animals may be of limited value (see e.g. Gaillard et al. 2000). Monitoring protocols should thus more often include demography as these type of data increases our understanding of the mechanisms underlying population fluctuations, and hence the ability to build sound predictive models.

When starting or maintaining a biological time-series one should care about the design such that the series contain the information needed to answer the questions underlying the reason for monitoring a given population. Why do we monitor this population? What information do we want the data to give us within a given time frame? How good are we to monitor this population – i.e. can we estimate the sampling error? The latter is important because if we do not know how good our data is, they may be of little value (see also Yoccoz et al 2001).

Due to possible spatial variation between populations and/or the environment extrapolating knowledge from one population could be a serious pitfall. This is because specific dynamical properties of different populations as well as that a given environmental factor may operate in different ways in different areas.

Too few studies, or monitoring protocols, focus on ecosystems, or vital components of ecosystems. We are aware of that such studies are challenging and costly. However, if the objective is to look at the effects of environmental variation/climate change in a given ecosystem monitoring one or two species may make it difficult to predict changes due to the inherent complexity in all ecosystem types.

Even the best available data show that it is hard to make predictions for more than just a few time steps ahead of a given population. This relates both to the complexity mentioned above but also to the uncertainty in climate scenarios. Thus, both scientists and managers should be temperate in their expectations of the possibility to predict ecological consequences of climate change in the long term. Nevertheless, we believe that interdisciplinary research on this subject in the coming years will provide information on what we are able to predict and not.

References

Aanes, R., Sæther, B.-E., Smith, F.M., et al. (2002) *Ecology Letters* 5: 445-454.

Andersen, R., Herfindal, I., Sæther, B.-E., et al. (2004) *Oikos* 107: 210-214.

Andrewartha, H.G. and Birch, L.C. (1954) The Distribution and Abundance of Animals. The University of Chicago Press, Chicago, Illinois.

Coulson, T., Catchpole, E.A., Albon, S.D., et al. (2001) *Science* 292: 1528-1531.

Elton, C.S. (1924) *British Journal of Experimental Biology* 2: 119-163.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz et al. 2000. Ann Rev Ecol Syst 31:367-393.

Holbrook, S.J., Schmitt, R.J. and Stephens J.S. (1997) *Ecological Application* 7: 1299-1310.

IPCC (2001) Climate Change. The IPCC Third Assessment Report. Volumes I (Science), II (Impacts and Adaptation) and III (Mitigation Strategies). Cambridge University Press, Cambridge.

IPCC (2007) Climate Change 2007: The Physical Science Basis.

Lande, R., Engen, S. and Sæther, B.-E. (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.

MacInnes, C.D., Dunn, E.H., Rusch, D.H., et al. (1990) *Canadian Field Naturalist* 104: 295-297.

Mann, M.E., Bradley, R.S. and Hughes, M.K. (1998) *Nature* 392: 779-787.

McCleery, R.H. and Perrins, C.M. (1998) *Nature* 391: 30-31.

Parmesan, C. (1996) *Nature* 382: 765-766.

Post, E. and Stenseth, N.-C. (1999) *Ecology* 80: 1322-1339.

Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. (1999) *Nature* 398: 611-615.

Sæther, B.-E., Engen, S., Tufto, J., et al. (2000) *Science* 287: 854-856.

Sæther, B.-E., Grøtan, V., Tryjanowski, P. et al. (2006) *Journal of Animal Ecology* 75: 80-90.

Stenseth, N.C., Mysterud, A., Ottersen, G., et al. (2002) *Science* 297: 1292-1296.

Thomas, C.D. and Lennon, J.J. (1999) *Nature* 399: 213.

Tveraa, T., P. Fauchald, N. G. Yoccoz, R. et al. 2007. Oikos in press.

Veit, R.R., McGowan, J.A., Ainley, D.G., et al. (1997) *Global Change Biology* 3: 23-28.

Walther, G.-T., Post, E., Convey, P., et al. (2002) *Nature* 416: 389-395.

Winkel, W. and Hudde, H. (1997) *Journal of Avian Biology* 28: 187-190.

Yoccoz, N.G., Nichols, J.D. and Boulinier, T. (2001) *Trends in Ecology and Evolution* 16: 446-453.