SCIENTIFIC REPORT

for the

EUROPEAN SCIENCE FOUNDATION

SIZEMIC NETWORK: First International Workshop on

"Trophic Dynamics in Ecosystems:
feeding interactions, species identity, and body size"
4th-7th April 2008, Clare College Cambridge, UK

Organisers: Richard Law (University of York) and Julia Blanchard (Cefas)
Supported by the European Science Foundation (ESF), and the Centre for Environment, Fisheries & Aquaculture Science (CEFAS) and the University of York

1. Summary

The first SIZEMIC workshop aimed to generate dialogue about the merits and shortcomings of the research methods currently in use for understanding trophic interactions in ecosystems. The aim of the workshop was also to set the scene for subsequent SIZEMIC activities, which will be focused on collaborative research and meetings. We had an open call for participants to apply (and received much more interest than expected!) attracting an impressive group of scientists with research interests in traditional food webs, size-spectra, aquatic ecosystems, terrestrial ecosystems, from both academic and applied realms, and spanning early to senior career stages.

The workshop began with a full day of stimulating talks from invited internationally recognised ecologists. A combination of plenary and breakaway group discussions took place over the following day and a half. The aim of the discussions was to generate topics for research that might form the basis of working groups over the lifetime of the SIZEMIC (2007-2011). The topics were: 1. "From data to webs – does it really matter how we aggregate for understanding the big picture?", 2. "Interaction strengths at the individual or species level?", 3. "Where does species identity (or size) matter the most?", 4. "Time for a paradigm shift in biodiversity?", and 5. "Is there more to life than species and body size?".

Stimulating discussions gave rise to the formation of new topics and several groups submitted proposals for working groups. The meeting sparked off a considerable amount of enthusiasm and interest – thus giving rise to the SIZEMIC network. Output of the meeting included two supported working groups that have been chosen and activities are currently underway. Speakers presentations, information on working groups and photos from the conference have been posted on the website (www.sizemic.org/presentations.html).

2. Description - Scientific Content

TROPHIC DYNAMICS IN ECOSYSTEMS: FEEDING INTERACTIONS, SPECIES IDENTITY, AND BODY SIZE

The first SIZEMIC workshop aimed to generate dialogue about the merits and shortcomings of the research methods currently in use for understanding trophic interactions in ecosystems. Currently, there are two main paradigms for thinking about trophic dynamics of large numbers of interacting species: (1) webs with nodes of known species of fixed body size joined by feeding links; (2) size spectra of organisms of unknown species that grow and die through eating one another. Experiments and size-based models of few interacting species show, however, that body size, individual growth and species identity **all** contribute to the complex webs that determine the structure and function of ecosystems. The intention was to spark off new and exciting research directions that integrate and break down current research boundaries.

The aim of the workshop was also to set the scene for subsequent SIZEMIC activities, which will be focused on collaborative research and meetings. We had an open call for participants to apply (and received much more interest than expected!) attracting an impressive group of scientists with research interests in traditional food webs, size-spectra, aquatic ecosystems, terrestrial ecosystems, from both academic and applied realms, and spanning early to senior career stages.

KEYNOTE TALKS

The workshop began with a “Welcome and Introduction” by
Richard Law, University of York and a full day of stimulating talks from invited internationally recognised ecologists including: Joel Cohen (Rockefeller and Columbia Universities, USA), Ulrich Brose (Darmstadt University of Technology, Germany), Simon Jennings (Cefas, UK), Lennart Persson (Umeå University, Sweden), Peter de Ruiter (Wageningen University, NL), Pablo Marquet (CASEB/IEB/ Universidad Católica de Chile, Chile) and Ken Andersen (DIFRES,UK).

The content of each talk is provided below and the presentations can be viewed from the SIZEMIC website: http://www.sizemic.org/presentations.html. These talks linked to the topics that would form the basis of in depth plenary and group discussions during the rest of the workshop.

“Does one size fit all?”
Joel Cohen, Rockefeller and Columbia Universities

Understanding ecosystem dynamics will require data structures that integrate diverse approaches to describing ecosystems. The food web directed graph has been used since 1880; it has a node for each group of organisms and an arrow for each feeding link from resource to consumer. In recent decades, this data structure has been extended by adding to each node the average individual body mass and numerical abundance of the associated organisms; and by adding to each edge estimates of the fluxes of energy and materials. Further extensions to individuals and to the environment are desirable and feasible. I give two examples here, and others in the talk. The average body mass could be replaced by the frequency distribution of body mass or other physiological stage, and bivariate frequency distributions could report the frequency of eating by the body size or physiological stage of both the resource individual and the consumer individual. If chemical compositions (or at least measurements of C, N and P) were added to the vector of each node's attributes and if a nodal population growth model took explicit account of chemical concentrations of nutrients and toxins, then population biology and food web dynamic ecology

could integrate with biogeochemistry (ecological stoichiometry). But it is easier to imagine a data structure (a skeleton of thought) than it is to flesh it out with reliable data (the muscles on the bones). This meeting can help bridge the gap between what can be studied theoretically and what can be achieved empirically.

"Size and species-based analyses of food webs"
Simon Jennings, Centre for Environment, Fisheries and Aquaculture Science

Size-based analyses of food webs, where body size rather than species identity is the principle descriptor of an individual's role in the food web, provide insights into food web structure and function that complement and extend those from species based analyses. This talk describes the application of cross-species and phylogenetic comparative analysis to study relationships between species' body size and trophic level in aquatic food webs, and how these relationships compare with those that classify all individuals by body size irrespective of species identity. The results show that weak cross-species relationships between species' body size and trophic level can belie powerful size-based structuring, and that size-based analyses can be used to estimate food web properties such as predator-prey size ratios, transfer efficiency, maximum food chain length and relationships between predator and prey species diversity. These estimates can contribute to the development, parameterisation and validation of food web models.

"Should interaction strengths be at the individual or species level?"
Peter de Ruiter, Wageningen University Research Centre

…or at the functional group level? In my talk I will approach interaction strength from a conceptual and an empirical perspective. First, interactions are obviously dealing with a 'set of two' (individuals/populations/species/functional groups), but the strengths of the interactions, and especially how interaction strengths influence community structure and stability depends on the organisation of interaction strengths in the community as a whole. From there I will present examples of interactions strengths in real food webs in order to show patterns that are important to stability; herewith I will also introduce the concept of maximum loop weight as a way to understand and 'quantify' food web stability. Finally I will discuss how these findings may relate to the ecological implications of body-size.

"Size-dependent foraging affects predator-prey interaction strengths and food-web stability"
Ulrich Brose, Darmstadt University of Technology

Metabolic theory predicts that per capita metabolism and consumption rates follow three-quarter power-laws with individual body mass. Foraging theory predicts that these overall consumption rates are unevenly distributed amongst the multiple feeding links of predators, and attack rates follow a hump-shaped relationship with the predator-prey body-mass ratios. These theories are illustrated by experimental data on the rates of metabolism, consumption and attack of ground-dwelling beetles and spiders at the per capita (metabolic theory) and per link (foraging theory) levels. A combination of both theories suggests that (i) per capita biomass fluxes first increase and then decrease with predator mass, (ii) small predators have higher per capita biomass fluxes when attacking small prey, whereas large predators have higher biomass fluxes while consuming large prey, and (iii) total biomass fluxes decrease with predator mass. Interestingly, these relationships indicate variation in predator-prey interaction strengths in natural food webs may be highly constrained by the species' body masses (i.e., size-dependent foraging). Prior models used interaction strength as an unconstrained variable affecting population stability and documented that anything is possible. In contrast, model analyses based on size-dependent foraging yield body-mass dependent interaction strengths and suggest that what is probable is

only a restricted subset of what is possible. In particular, they demonstrate that omnivory stabilizes population dynamics, which has profound implications for our understanding of complex food-webs.

“Time for a paradigm shift in biodiversity? The role of size-structure in ecosystem function”

Pablo Marquet Centre for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecologia Pontificia Universidad Católica de Chile and Institute of Ecology and Biodiversity (IEB)

In ecology, unlike physical science, most problems are not usually resolved but go out of fashion. Paradigms in ecology bounce back, linger and are usually reborn in disguise to coexist. This in part reflects the complex nature of our study systems but also the difficulty in anchoring ecological enquiry to simple and fundamental principles and state variables. The emphasis in abundance and diversity is giving way to an emphasis in energy, size and biomass as potential state variables for understanding ecological systems. In this talk I will present a framework that emphasize the importance of size for ecosystem structure and functioning and will outline some vexing questions that need to be addressed if we are to think of a paradigm shift in biodiversity. This shift I propose, entails ways of finding the unity underlying diversity.

“Growing predators and growing prey – Effects on dynamics and community structure”

Lennart Persson, Umeå University

Theoretical and empirical evidence suggests that the fact that individuals grow substantially in size over their life time has strong impact on both the dynamics and structure of ecological systems. Food-dependent growth of predators may induce cycles that cascades through the food web via overcompensatory increase in predator per capita fecundity. Food dependent growth of predators may also demote coexistence in intraguild predation systems. In consumer-resource resource systems, ontogenetic size dependent differences in different process rates may induce cycles. Food-dependent development in consumers will also induce alternative stable states in communities including a high sensitivity to catastrophic collapses in predators. In my talk I will review the theoretical basis for these strong effects of ontogenetic development on community dynamics and structure and the growing empirical evidence.

"Modelling size spectra: beginnings, present state and future prospects"

Ken Andersen, Danish Fisheries Research, Technical University of Denmark

An overview of the state-of-art of current efforts in mathematical modelling of size spectra, focussing on marine systems, which are strongly structured by predator-prey interactions governed by the rule "smaller fish are eaten by larger fish". Currently there is an outburst of different size-based models which can roughly be classified as either trophic models or continuum ecosystem models. The basic principles of the models are essentially the same, namely descriptions of individual encounter with predators and prey and individual bioenergetics. The models predicts size spectrum slope, total abundance productivity rates etc. The next logical step from the pure size-based models is to add a food web structure or to add an extra trait. I will show an example of how this can be done, but also of which new problems it raises.

GROUP DISCUSSION & TOPICS

A combination of plenary and break-away group discussions took place over the following day and a half. The aim of the discussions was to generate topics for research

that could form the basis of working groups over the lifetime of the SIZEMIC (2007-2011).

These were loosely based around the following topic areas, which participants were requested to choose from in terms of their research interests.

TOPIC 1- From data to webs – does it really matter how we aggregate for understanding the big picture?
There are a bewildering number of ways in which we can lump species or individuals into groups to describe food web interactions and macroecological patterns. Does using species or taxonomic averages result in the same emergent patterns as when variation due to individual body size or life history stage is accounted for?

TOPIC 2 - Interaction strengths at the individual or species level?
Moving from observed patterns to model design. In describing model foodwebs, some might say that interaction strengths are meaningless. Trophic interactions change as organisms grow within a species. One cannot assume all individuals within a species are identical. Should the focus be at the individual level or at the species level? Does scaling from the individual to the population at this stage mask critical foodweb interactions?

TOPIC 3- Where does species identity (or size) matter the most?
In terrestrial systems species identity matters and body size is unimportant. In aquatic systems the reverse is true. Terrestrial and aquatic systems have entirely different kinds of trophic dynamics and need to be treated separately.

Topic 4 - Time for a paradigm shift in biodiversity?
Species identity does not matter: a kilogram of tuna is the same as a kilogram of jellyfish! What matters for the functioning of an ecosystem is diversity of size structure. The traditional theory relating biodiversity and stability does not apply in size spectra. By promoting the diversity of size structure, species diversity will look after itself.

Topic 5 - Is there more to life than species and body size?
What about life-histories? In many cases the ontogenetic changes on trophic interactions that occur are more discrete than continuous growth processes. What extent do life history processes like growth play a role in the ecological dynamics of the food web? The ecological parameters of food webs and size spectra are evolutionary variables and the trophic structure of an ecosystem will not be understood without understanding the processes that takes place within it.

PROPOSALS FOR WORKING GROUPS

Participants were given guidelines to follow if, through their group discussions, they identified research topics they would like to pursue under the structure of working groups.

We defined a working group as a small group of researchers comprising at least four people, based in at least two different institutions in different ESF countries. The purpose of a working group is to do collaborative research within the general remit of SIZEMIC and is loosely based on the NCEAS-model for working groups (http://www.nceas.ucsb.edu/research/wg).

We wanted particularly to foster groups of people from different backgrounds, where synergisms may spark off new and exciting research activities and where early-stage researchers form an active part of the group. We encouraged people to propose working groups only if they were committed to carrying through the ideas they wanted to pursue.

During the meeting some groups split into smaller groups and sparked off new topics for discussion including: spatial processes, stoichiometry, trophic niche-space and applications of probability moments to food webs. These open-ended discussions had the effect that SIZEMIC was in a position to respond to the agenda developed by the research community, rather than imposing the structure on the community.

Titles of submitted proposals were: "Moments in the life of food webs", "Characterizing food web diversity", "Size, Space and Structure: How does the size and mobility of organisms influence stability, connectivity, and scaling of food webs?", "Human impacts on food webs – are there patterns across ecosystems?", "Measuring the Dimensionality of Trophic Niche-Space", and "On the Generality of Elton's Rule: Comparing Aquatic and Terrestrial Ecosystems across Environmental Conditions" **.**

At the end of the meeting several groups submitted proposals that were evaluated and ranked by the Steering Committee of SIZEMIC during the 2nd Steering Committee meeting that took place immediately following the workshop (from 13:30 7/04/2008 – 11:30/04/2008).

3. Main Results & Future Direction

The 1st workshop enabled researchers to find common interest and research goals across various ecosystem types (terrestrial, freshwater, and marine) and realms of ecology (applied, theoretical, empirical) and has enabled SIZEMIC to begin its life as an active research network. Already researchers are exchanging ideas, publications and sparking off synergisms!

One of the main results of the SIZEMIC workshop is the support of Working Groups. During the SC meeting it was agreed that two would be supported (and were chosen based on their scientific quality and relevance to SIZEMIC):

- **"Human impacts on food webs – are there patterns across ecosystems? *An integration of species and size based approaches"* (summary)**

  Group Leader: Frank van Veen, NERC Centre for Population Biology, UK
  f.vanveen@imperial.ac.uk

- **"Testing the Generality of Elton's Rule: Comparing Aquatic and Terrestrial Ecosystems Across Environmental Conditions" (summary)**

  Group leader: Julia Reiss, Queen Mary University of London, UK
  j.reiss@qmul.ac.uk

Further details on these groups can be found on the websites: www.sizemic.org/workinggroups.html and www.esf.org/sizemic.

It was also agreed that funds were available to support one more Working Group and an OPEN CALL for proposals will be posted shortly, with a deadline of October 31.

Other near-future activities will include Travel grants for research exchanges (aimed for early-stage researchers) and plans for the next international science meeting to take place in Sweden (to be organised by one of this year's participants, Dr Andrea Belagrano and Prof Bo Ebenman).

APPENDIX 1 – Final Programme

Trophic Dynamics in Ecosystems: feeding interactions, species identity, and body size 4th-7th April 2008, Clare College Cambridge, UK

EUROPEAN SCIENCE FOUNDATION
SIZEMIC NETWORK: First International Workshop

Programme for Participants
(All rooms in Old Court, except bedrooms in Memorial Court)

Friday, 4th April
14:00 onwards En-suite bedrooms available Memorial Court
19:00-21:00 Drinks reception, buffet and registration JCR
Bar thereafter Buttery

Saturday, 5th April
07:45 Self-service breakfast - full English Buttery
08:30 Registration Godwin Room

09:00 Programme starts (plenary only) Latimer Room

09:00 "Welcome and Introduction"
Richard Law, University of York

09:30 "Does one size fit all?"
Joel Cohen, Rockefeller and Columbia Universities

10:20 Refreshments Great Hall

10:50 (Topic 1) *"Size and species-based analyses of food webs"*
Simon Jennings, Centre for Environment, Fisheries and Aquaculture Science

11:40 (Topic 2) *"Should interaction strengths be at the individual or species level?"*
Peter de Ruiter, Wageningen University Research Centre

12:30 Buffet lunch Great Hall

13.30 (Topic 3) *"Size-dependent foraging affects predator-prey interaction strengths and food-web stability"*
Ulrich Brose, Darmstadt University of Technology

14:20 (Topic 4) *"Time for a paradigm shift in biodiversity? The role of size-structure in ecosystem function"*
Pablo Marquet Centre for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecologia Pontificia Universidad Católica de Chile and Institute of Ecology
and Biodiversity (IEB)

15:10 Refreshments Great Hall

15:40 (Topic 5) *“Growing predators and growing prey – Effects on dynamics and community structure”*
Lennart Persson, Umeå University

16:30 *"Modelling size spectra: beginnings, present state and future prospects"*
Ken Andersen, Danish Fisheries Research, Technical University of Denmark

17:20-17:50 Plenary discussion

19:00-21:00 3-course waiter-service dinner Great Hall

Sunday, 6th April
07:45 Self-service breakfast - full English Buttery

09:00 Plenary Latimer
“Working Groups” Richard Law

09:30 Group discussions
Topic 1 – data to webs Latimer
Topic 2 – interaction strengths Godwin
Topic 3 – species identity F07
Topic 4 – biodiversity F08
Topic 5 – more to life B1
10.30 Refreshments Great Hall

11:00 Group discussions (all five rooms) Latimer, Godwin, F07, F08 & B1
12:30 Buffet lunch Great Hall

13:30 Group discussions (all five rooms) Latimer, Godwin, F07, F08 & B1
15:30 Refreshments Great Hall

16:00 Group discussions (all five rooms) Latimer, Godwin, F07, F08 & B1
17:00 End for punting
17:15 Punts depart Mill Lane/Silver Street
18:15 Punting ends
19:00-21:30 4-course waiter-service dinner Great Hall

Monday, 7th April
07.45 Breakfast Buttery
09:00 Plenary Latimer, Godwin, F07, F08 & B1
09:30 Group discussions (all five rooms) Latimer, Godwin, F07, F08 & B1
09.30 latest Bedrooms to be vacated
10.30 Refreshments Great Hall
11:00 Group discussions (all five rooms) Latimer, Godwin, F07, F08 & B1
11:30 Concluding session (plenary only) Latimer Room
12:30 Buffet lunch (packed lunch option) Great Hall
13:30 onwards Departure