TESTABLE MODELS OF AQUATIC SYSTEMS: A NERC SPECIAL TOPIC FOR INTEGRATING EXPERIMENTS AND MODELLING

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Introduction

A major part of the support for fundamental research on aquatic ecosystems continues to be provided by the Natural Environment Research Council (NERC). In recent years, the Council has implemented a more proactive approach to supplement the system of standard research grant applications by individual scientists. Here, funds are released for "thematic" studies in a selected special topic or programme. This allows a co-ordinated research effort to be made on subjects of general interest and topical importance. "Testable Models of Aquatic Ecosystems" was a Special Topic of the NERC, initiated in 1995, the aim of which was to promote ecological modelling by making new links between experimental aquatic biologists and state-of-the-art modellers. We believe that the exciting progress achieved by the programme will be of general interest to readers of *Freshwater Forum.*

The foundation of this Special Topic was the recognition that sound management policies for any ecological system depend upon an ability to predict the likely range of outcomes resulting from both natural and anthropogenic environmental change. Although all such predictions are essentially extrapolations from past experience, their accuracy can be improved dramatically when they are made on the basis of a detailed understanding of the internal dynamics of the system. Mathematical models are a particularly powerful way of developing hypotheses about the causal mechanisms that underlie the dynamics of natural systems. The programme was devised to catalyse the complex tasks of formulating and testing such models by enabling continuous close collaboration between experimental and field biologists and modellers. In this way, models could be produced, checked, refined and, importantly, falsified by new experimental results.

The Topic covered both marine and freshwater systems. Although dynamically distinct and often treated as separate disciplines, marine and freshwater ecosystems are characterised by similar physical environments and biological processes at the individual, population and community levels. Knowledge and understanding that is encapsulated into models for one system may prove to be directly relevant to the other.

Awardees and topics

NERC allocated £890k to the support of the "Testable Models" Special Topic. This was used to fund eleven awards, including three studentships, and supported three annual workshops. Most of the projects started in January 1995 and continued for three years, although one project was a 1-year "scoping study" and one PhD did not start until October 1997 (see Table 1).

The programme may be subdivided into three general areas of focus: "organisms to populations", with four projects; "populations to communities", also with four projects; "spatial models", with three mutually interlinked projects.

Organisms to populations

The four projects in this section each sought to study aspects of the responses of individual organisms to the effects of environmental variability, and to build models of populations incorporating the aggregate of individual behaviours.

(1) Nutrient interactions between a diatom and two harmful dinoflagellates. This approach is exemplified in experiments on nutrient interactions between a diatom and two harmful marine flagellates (Project 1, Table 1), which were then used to develop models describing the rates of population increase for each of the species represented. However, the first models failed to simulate the results from multi-species cultures. Re-analysis of the results has led, for the first time, to the development of a usable and reliable (i.e. tested) model describing the effects of simultaneous nitrogen and silicon deficiencies on the marine diatom used in the experiments. Using this model, it is possible to simulate the outcome of the multi-species experiments. Experiments on predation by copepods on the three algae (which included toxic species) failed to demonstrate a clear advantage of being toxic. Subsequent consideration of the growth dynamics of toxic algae using mechanistic models suggests that there is little or no significant cost to being toxic, while any advantage in being toxic would have to operate at the level of discouraging predators rather than killing them.

(2) Predator-prey interactions. This pilot study on testable mathematical models of predator-prey interactions (Project 2, Table 1) applied formal mathematical descriptions, using fuzzy logic (which introduces elements of unpredictability into logical processes), to behavioural responses of the marine brown shrimp (prey) during attacks by juvenile cod (predator). Simple rules were established which defined the escape and exclusion envelopes of a shrimp in response to an attack. Unpredictability is an important component of the escape response of brown shrimp that reduces the ability of predators to learn escape-patterns. Fuzzy modelling techniques offer scope for more

Table 1. Projects supported by the NERC Special Topic (* Numbers 9, 10 and 11 are linked awards).

	Identification number and title	Principal investigators	Institutions
1	Modelling nutrient interactions between a diatom and two harmful dinoflagellates under conditions simulating spring and summer.	K. J. Flynn, W. S. C. Gurney.	University of Wales, Swansea; University of Strathclyde.
2	Testable mathematical models of predator–prey interactions: an interdisciplinary approach.	D. M. Neil, J. Anderson, M. T. Burrows.	University of Glasgow: CCMS Oban.
3	Population consequences of individual spawning decisions in fish.	J. D. Reynolds, W. J. Sutherland.	University of East Anglia.
4	The effect of horizontal and vertical patchiness on the timing of biological productivity in stratified marine systems, with special regard to solar radiation (2 PhD students).	J. McGlade, J. Aiken, A. Taylor.	University of Warwick; CCMS PML.
5	An investigation of permanence and community assembly using protozoa in laboratory microcosms	P. H. Warren, R. Law.	University of Sheffield; University of York.
6	Investigating the assembly of phytoplankton communities with PROTECH (1 PhD student).	P. Tett, C.S. Reynolds.	Napier University: IFE.
7	Annual development of communities in sandy bays.	R. D. M. Nash, R. N Gibson, M. T. Burrows.	Port Erin Marine Laboratory (PEML), University of Liverpool; CCMS Oban;
8	Quantifying and testing qualitative models of rocky shore communities: the relative importance of deterministic processes, stochastic events and spatial heterogeneity.	S. J. Hawkins, R. G. Hartnoll, T. A. Norton, M. T. Burrows, R. N. Hughes.	University of Southampton; PEML, University of Liverpool; University of Wales, Bangor.
9	Foraging and predation risk: exploiting patchy environments.*	D. G. Raffaelli.	University of Aberdeen.
10	Testable models of competition for space.*	W. S. C. Gurney.	University of Strathclyde.
11	Mobility, patchiness and species interactions: models of a well characterised stream community.*	A. G. Hildrew.	Queen Mary & Westfield College.

representative models of natural predator-prey interactions, as this unpredictability can be taken into account.

(3) Population consequences of spawning decisions in fish. Traditionally, the fields of animal behaviour and population dynamics have been separate despite the fact that animal behaviour clearly can influence individual, and hence population, success. A simulation model (Project 3, Table 1) linking behaviour to population dynamics of fishes, which can be tailored readily to other systems, was developed and field-tested for the European bitterling *Rhodeus sericeus.* This fish lays its eggs in the siphons of freshwater mussels (Unionidae) and so the spawning site can be clearly defined and characterised. The study showed that production of juvenile bitterling was correlated with abundance of mussles although predation by perch *Perca fluviatilis* also had an influence. Experiments showed that bitterling tended not to lay eggs in mussels that were already carrying bitterling emryos, so reducing embryo mortality. The work produced the most comprehensive test, at the population level, of a model including behaviour and population dynamics. The model can be used to predict the consequences, for the fish population, of environmental change or habitat loss due to hydrological changes or changes in the mussel population, and could also be adapted for other fish species or animals of conservation interest.

Populations to communities

The four projects in this section each developed models on the assembly, permanence and resilience of communities, with special reference to the effects of seasonal changes on the patterns of community development, and to the ways in which communities are affected by stochastic events and spatial heterogeneity.

(1) Investigating permanence and community assembly using protozoa. For the first time, the long-term persistence properties of all combinations of species from a species pool was systematically examined to estimate the number of sets capable of long-term coexistence, using microcosms containing protozoa (Project 5, Table 1). The susceptibility of each coexisting set to invasion, and long-term end-states following invasion, were determined and used to construct a transition diagram of the assembly pathways for the experimental species pool. This provided a unique opportunity to identify characteristics of the assembly map that have been speculated upon in the ecological literature (e.g. assembly cycles). These data were used to test, for the first time, two predictions from permanence theory (a new, qualitative approach to measuring stability in dynamical systems), and the results provided qualified support for the theory. The predictions from a qualitative Markov model based on the assembly map, which predicts the frequency of occurrence of each species in a multiple-habitat system, were derived and

examined. Species distributions were shown to depend on the assembly process, rather than on the more commonly examined species extinction and colonisation rates.

(2) Investigating the assembly of phytoplankton communities with PROTECH. The late-starting Project 6 (Table 1), on the assembly of phytoplankton communities, began with several existing models that have been developed in recent years to simulate the dynamics of nuisance blooms. Since some of these, at least, are capable of delivering authentic outputs, it was felt that they could be directed to elucidate the ecological principles underpinning selection of adaptive traits, succession, competitive exclusion, the effect of inoculum bias, and the extent to which diversity is maintained by disturbance and stress. The essential groundwork of validating the model assumptions, verifying the model provisions and testing the sensitivity of the models, has been completed, and the performances of species, individually and collectively, in defined environments are currently being tested. The studentship continues until September 2000.

(3) Annual development of communities in sandy bays. Diverse communities of fish and epibenthic crustaceans develop in sandy bays through a succession of ordered recruitment events. Individual-based models were developed, taking into account the processes of settlement, mortality (including predation), and size-dependent depth preference and density-dependent growth rate. The models take into account spatial and temporal variation resulting from migration of mobile species and spatial distribution of predators (Project 7, Table 1). The final model successfully synthesised known and novel ecological phenomena controlling growth and survival of plaice *Pleuronectes platessa* in a way that would have been impossible with a single-process model. Since the plaice is a commercially important species, the model should be a valuable aid to the prediction of variation in production of juvenile plaice among different sites and years.

(4) Effect of deterministic processes, stochastic events and spatial heterogeneity on rocky shore communities. Rocky shores show a great complexity of pattern and process but very few paradigms about the underlying causes. Models were developed on algal zonation, algal-limpet patch dynamics and dogwhelk foraging. In Project 8 (Table 1), models based on foraging by individual limpets and its influence on algal patch dynamics were developed using a cellular automaton approach. These showed the importance of limpet homing frequency on patch dynamics. A complex spatial model based on the location of individual limpets was able to generate the algal patchiness observed on the shore. Spatial patterns of predation by dogwhelks on barnacles were modelled. Tests of different hypotheses showed that field patterns could only be matched by taking mortality risks for the dogwhelk into account.

Spatial models

Spatial variability is an important factor that affects the outcome of predation and competition, and this was addressed by three linked projects (9, 10 and 11 in Table 1) in which the modelling work was carried out under Project 10.

(1) Foraging and predation risk: exploiting patchy environments. Tidal movements of young fish and crustaceans onto and away from the shore generate an intense, pulsed trophic signal in coastal food webs. Four hypotheses were modelled to explain the cause of dense bands of the shrimp *Neomysis integer* which move behind advancing tides (Project 9, Table 1). Foraging and resource gradient models were rejected as unlikely because there was little evidence that *Neomysis* was able to discriminate between areas with different resource levels and because *in situ* gradients of food disagreed with the model requirements. A random diffusion model was unable to predict the distributions found in the field. However, a hydrodynamic refuge model reproduced the clumped distribution of *Neomysis* in the field and was supported by experimental evidence. This model implies that *Neomysis* actively selects water depths where water-flow is low and this prevents removal of the animals from the estuary by water currents.

(2) Mobility patchiness and species interactions in a well-characterised stream community. Studies on communities of insect larvae in Broadstone Stream have continued for over twenty years. There are two main predators, a caddisfly *Plectocnemia conspersa* and an alderfly *Sialis fuliginosa.* An inter-generation model was devised for the two predators and two species of their prey (stoneflies, *Leuctra* and *Nemurella),* the first time this has been achieved for a stream system (Project 11, Table 1). The results showed that there was little apparent interaction between the prey: the two stoneflies did not avoid one another to minimise "attack" by predators in high densities of prey. The model predicts that prey density was close to the environmental carrying capacity and that the predators have little impact on prey density. This prediction, which runs counter to the expectations of stream ecologists, is currently being tested directly by a large-scale field experiment, in which *Sialis* is removed from a section of the stream.

Benefits of the programme on "Testable Models" Special Topic

Although the findings are presented above in resume form, it is apparent that each of the projects has achieved a considerable measure of success in attaining its objectives and contributing an advance in knowledge and understanding that will lead to publication in the scientific literature; indeed, several papers have been published already. Our task here is simply to comment upon the execution of the Special Topic in its entirety and to consider the benefits that the "Testable Models" programme may have brought.

One evident achievement has been to establish the value of models to the development of ecological thought. It is clear, for instance, that non-modellers or reluctant modellers among the awardees have gained confidence in their use and versatility, and now seek their further development. It is interesting to note also that several of the projects (notably 7 and 9) used their models to falsify and reject interpretative hypotheses. This is an important application of model philosophy to scientific method.

In several cases (Projects 1, 3, 8, 11), models have been developed which simulate, with a high probability and an acceptable precision, the processes under consideration. These models did not always correspond to biological preconceptions. Hildrew (Project 11) showed that adult insects dispersed rather shorter distances from their home streams than was thought to be true, which carries implications for the dynamics of population recruitment and survivorship. There were also surprises in the extent to which predator performance, and thus predator exclusion, impacts on the behaviour of the prey populations. In the development of sandy bay communities (Project 7), the importance of ontogeny in governing the seasonally changing species interactions was powerfully demonstrated. This is an important factor that cannot be excluded from the understanding of food-web effects.

A final benefit of modelling which became apparent was that gaps in information or understanding are highlighted by the rigorous approach of modelling. Thus, even in a well-studied stream, much information needed by the modellers had to be specially collected (Project 11).

Conclusions

Researchers habitually proclaim the benefits of their work to others in the same field. Measured against its own ambitious objectives, the Testable Models Special Topic has been highly successful in promoting the development and application of models, most particularly through the interplay between experimental ecologists and formal modellers. The scheme has crossed other interdisciplinary boundaries and facilitated active discussion and collaboration among freshwater and marine scientists. The progress it has achieved will be of interest to freshwater and marine biologists everywhere. However, perhaps most importantly, it has successfully proselytised the modelling cause within the participating population of scientists within the Special Topic and, hopefully, it eventually will do likewise throughout the wider community of aquatic biologists.