COUNTRY: UNITED KINGDOM

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Project Title:
Marine Productivity: physical controls on ecosystem dynamics (National Environment Research Council thematic programme)

Project Description:
The programme's aim is to investigate the population dynamics of zooplankton (the tiny animals that drift with the currents in the sea) and particularly the way physical factors such as temperature, water movements etc. influence those dynamics. The programme aims to develop coupled modelling and observational systems for the pelagic (open water) ecosystem.

Marine Productivity provides a major UK contribution to the international Global Ocean Ecosystem Dynamics project (GLOBEC). Effort is directed at testing hypotheses addressing the questions:

- How are basin-scale structures in zooplankton species maintained?
- How do zooplankton species respond to basin-scale forcing? and
- What are the impacts of basin-scale physical changes on secondary production in shelf seas?

Similar studies on the physical factors controlling the distributions of key zooplankton species (and their implications for higher trophic levels) are being planned by Canada and the US for the Labrador Sea and adjacent shelf areas, as part of their national GLOBEC programmes.

An exciting possibility is that this suite of complementary research for the North Atlantic will enable us to understand and predict marine ecosystem behaviour over the complete range of relevant ecological scales, covering not only species' physiologies, life cycles and trophic interactions, but also the climatic factors operating at the regional and global level.

Key questions, issues and hypotheses:
The main aim of the Marine Productivity thematic programme is to develop coupled modelling and observation systems for the pelagic ecosystem, with emphasis on physical factors affecting zooplankton dynamics. Effort is directed at testing hypotheses addressing the following questions:

- How are basin-scale structures in zooplankton species maintained?
- How do zooplankton species respond to basin-scale forcing?
- What are the impacts of basin-scale physical changes on secondary production in shelf seas?

Targets:

- To identify the dominant spatial and temporal scales of physical parameters and zooplankton population dynamics, by observation, modelling and retrospective analysis.
- To parameterise the critical processes governing zooplankton dynamics by observations and experiments.
- To construct and validate spatially explicit models of zooplankton and their food and predators, capable of resolving short term changes in population structure.
- To provide data for model validation by developing and applying new interdisciplinary techniques to a wide spectrum of biological and physical parameters.
- To develop a database and information system for historic and new data and models

Website:
http://www.nerc.ac.uk/funding/thematics/marprod/

Participating Institutions:
Aberdeen University
British Antarctic Survey (BAS)
Department of Agriculture & Rural Development, Northern Ireland (DARDNI)
Dunstaffnage Marine Laboratory (DML)
Fisheries Research Services, Aberdeen (FRS)
Heriot-Watt University
Plymouth Marine Laboratory (PML)
Port Erin Marine Laboratory
Proudman Oceanographic Laboratory (POL)
Queens University Belfast
Scottish Association for Marine Science (SAMS)
Sir Alister Hardy Foundation for Ocean Science (SAHFOS)
Southampton Oceanography Centre (SOC)
Stirling University
University of Exeter
University of Leeds
University of Liverpool
University of Southampton
University of St. Andrews
University of Strathclyde
University of the Highlands and Islands (UHI)
University of Wales, Swansea

Duration:
5 yr

Budget:
£1.5m for Phase 1 (from Jan 2000); £5.0m for Phase 2 (from Oct 2001)

Funding Agency:
Natural Environmental Research Council (NERC)

Phase 1 Projects – Focus on shelf seas

Initially, effort has concentrated on assembling and analysing relevant historical databases; testing existing biological models in a variety of physical settings; and developing the technology needed to provide new field data for hypothesis testing.

The Irish Sea provided the main geographic focus, on the basis that it is:

- an area where small-scale physical and biological processes are particularly important for zooplankton life cycles;
- semi-enclosed, with definable boundaries (simplifying modelling);
- historically well-described; and
- currently the site of detailed fishery studies

Complementary laboratory experiments, comparisons between models, and remote-sensing analyses will allow Marine Productivity projects to help interpret new datasets collected in 2000-01 by other researchers and agencies (e.g. European Union, Department of Agriculture and Rural Development [Northern Ireland], Centre for Ecosystem Fisheries and Aquaculture Sciences, and the Port Erin Marine Laboratory [University of Liverpool] funded work).

The programme has already generated new insights into the role of microzooplankton in energy flows within shelf seas, and the effects of food quality (nitrogen-poor versus nitrogen-rich foods) on copepod growth rates. In addition, it has been possible to convert historical zooplankton abundance data (since 1948) into numbers per cubic metre, confirming the validity of systematic trends and

climatic correlations. This has been achieved by analysing flowmeter data from deployments of instrumented Continuous Plankton Recorders since 1995.

For the North Sea, "data-mining" studies have shown that resident species show different longterm trends to Atlantic species, and that annual variability in advection is more important than stratification effects in determining the observed fluctuations of the copepod *Calanus finmarchicus* for this area.

Other Phase 1 projects include an innovative population modelling approach, which combines knowledge of spatial distributions with information about the developmental stage and physiological status of zooplankton. This algorithm has been successfully tested with *Calanus* data for the northern North Sea and Norwegian Sea, and (under Phase 2) the model domain is now being extended to the whole North Atlantic.

In all, 15 Phase 1 projects received support (which were detailed in GLOBEC Special Contribution No.4), involving 57 researchers (Principal Investigators, Co-Investigators, collaborators, research staff and research students) at 17 institutions. Overall support for Phase 1 was approximately £1.5M between 2000 and 2002.

Phase 2 – Focus on open ocean

Phases 1 and 2 of the Marine Productivity programme are connected by the movements of zooplankton from the open ocean to shelf seas. The main, field-based phase of the Marine Productivity programme is directed at the open North Atlantic, and involves four research cruises. The research effort is integrated under the following broad questions:

- How are ocean basin-scale patterns of zooplankton abundance maintained?
- How do zooplankton species respond to basin-scale physical forcing?
- What are the impacts of basin-scale physical changes on secondary production in shelf seas?

These questions emphasise large-scale patterns, dynamics and influences, to test the assumption that climatically-driven physical processes, operating on the regional scale, are the main factors determining the distribution and abundance of marine zooplankton.

Since it is clearly impracticable to study all zooplankton on a basin-wide scale, a limited number of key species have been selected for detailed study of their life cycle dynamics and demography. These species include *Calanus finmarchicus*, since:

- it is the favoured food for many commercially-important fish;
- it occurs in high numbers over large areas (depth-integrated densities of 60,000 per m^2, comprising 70-80% of zooplankton biomass in the northern North Atlantic);
- it is the only marine organism identified by Department for the Environment, Transport and the Regions (DETR) / Department for the Environment Farming and Rural Affairs (DEFRA) as a candidate indicator for climate change; and
- two EU-supported projects: ICOS (The Investigation of *C. finmarchicus* migrations between Oceanic and Shelf seas off northwest Europe) and TASC (Trans-Atlantic Study of *C. finmarchicus*) have begun studying factors affecting the distribution and abundance of *C. finmarchicus* in the waters between Scotland, Norway and Iceland.

The Marine Productivity programme will extend this coverage to the Irminger Sea, to the south east of Greenland. It will also investigate other important components of the ecosystem, including the euphausiid shrimps *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* (predators on *Calanus*); and *Oithona* copepods (potential prey for *Calanus* adults, and/or predators on their eggs). In addition to high-resolution measurements and modelling of hydrodynamics in the North East Atlantic, molecular techniques will be used for taxonomic analyses of *Calanus* larval stages; biochemical and isotopic studies will be used to elucidate feeding pathways; and genetic studies will test whether physical regimes can isolate (or unify) populations.

During spring and summer, when phytoplankton food is relatively plentiful, the growth and reproduction of *C. finmarchicus* in the upper ocean can be rapid. However, a different survival strategy is needed for other times of year, and the pre-adult stage (5th copepodite) spends around six months in diapause, i.e. overwintering at depths of 1-3km. The Marine Productivity Programme is investigating the seasonal factors affecting *C. finmarchicus* survival by undertaking fieldwork in early

winter (November - December 2001 and 2002), spring (April-May 2002) and summer (July-August 2002). These surveys and process studies should make it possible to quantify the importance of biological factors (changes in food timing, quality or quantity; changes in predation) and physical factors (changes in overwinter conditions and deep transport; changes in surface advection and on-off shelf transport) on the species' interannual variability and longterm population trends.

Eleven Phase 2 projects received support, involving 72 researchers at 18 institutions (including laboratories in Iceland, Norway, Canada and USA). Total investment is approximately £4.6M between 2001 and 2005.

Phase 2 projects:

1) Recruitment and mortality of *Calanus* eggs and nauplii

Andrew Hirst (BAS, Cambridge, aghi@bas.ac.uk), Steve Hay (FRS Aberdeen) and Roger Harris (PML)

Mortality in marine copepods can be more important than fecundity and growth in determining spatio-temporal patterns of abundance, biomass and secondary productivity. As the mortality of egg and nauplii is most variable, least understood, and yet by far the greatest, we place most emphasis on these stages. We will measure early mortality and its variability in *Calanus*, assess underlying causes, with the aim of understanding the consequences of changing physical and biological forces in the natural environment. We will perform detailed experimental work in the laboratory, make appropriate measures in the North Atlantic, and work at the L4 station off Plymouth, and Stonehaven off Aberdeen. The study will target fecundity and hatch success as recruitment terms, and the effects of food, starvation, and temperature on early nauplii development, growth and survival/mortality in *C. finmarchicus* and *C. helgolandicus*. Rates of cannibalistic predation and their control will be investigated, as well as determining which predators are most important at the North Atlantic stations.

2) Data-driven, basin-scale, modelling of the abundance and demography of *Calanus finmarchicus* in the North Atlantic

William Gurney (University of Strathclyde, bill@stams.strath.ac.uk), Simon Wood (St Andrews), Michael Heath (FRS Aberdeen); Michael Fasham, Yanli Jia and Kelvin Richards (SOC)

This study is designed to elucidate the relationship between oceanic circulation and the abundance of *Calanus finmarchicus* over its whole North Atlantic range. Capitalising and extending on our successful spin-up project (GR02/2749) we shall use automatic optimisation to fit a series of process-based demographic models to existing and projected abundance data. Formal statistical methods will be used to evaluate the relative goodness of fit generated by models embodying competing hypotheses, thus allowing us to distinguish between them.

3) Zooplankton demography and trophic interactions in the sub-arctic North Atlantic, and their coupling to physical oceanography: 40 years on from the NAO minimum

Michael Heath (heathmr@marlab.ac.uk); Kelvin Richards, Raymond Pollard, Denise Smythe-Wright & David Hydes (SOC); Colin Moffat & Steve Hay (FRS Aberdeen); Gary Smerdon (PML); Chris Reid (SAHFOS); Andrew Brierley & Phillip Hammond (St Andrews); Paul Thompson & Peter Boyle (Aberdeen)

This project will conduct a campaign of seagoing measurements in the Irminger Sea and adjacent areas to discover the relationships between oceanic circulation, the life cycle dynamics and demography of three key crustacean zooplankton (*Calanus finmarchicus*, *Thysanoessa longicaudata* and *Meganyctiphanes norvegica*) and the structure and productivity of the pelagic food web. The impact of climate variability on these relationships will be examined by means of a comparative analysis of the data collected during the campaign with comparable measurements made in 1963 during the NORWESTLANT surveys, and with data from the Continuous Plankton Recorder surveys.

4) The role of *Oithona spp.* in the marine productivity of the North Atlantic basin

Richard Lampitt (SOC, RSL@nerc.ac.uk) and Roger Harris (PML)

Oithona spp. is the most abundant copepod in many marine ecosystems including the North Atlantic. However, because of its small size, its ecology is not well known and its role in the ecosystem undetermined. In addition, there are strong indications of important predation by Calanus on *Oithona nauplii* with the potential for the nauplii to be an important prey during periods before the spring bloom. The objectives of this proposal are: (i) to increase our knowledge in the ecology of *Oithona* by assessing its diet, productivity, total biomass and production; and (ii) to investigate the link between

Oithona and *Calanus* with special emphasis on the possible consequences of a climatic shift on the size structure of the zooplankton population.

5) Nutritional regulation of egg production of *Calanus finmarchicus* in the North Atlantic

Thomas Anderson (SOC, tra@soc.soton.ac.uk); Michael Bell (Stirling); David Pond and John Williams (SOC)

The proposed work is a combination of two projects: (1) An examination of the role of food quality (C, N , fatty acids) in influencing egg production of *Calanus finmarchicus*, using ship-board experiments in which copepods are fed in situ food. Experiments will be undertaken on Marine Productivity cruises in spring and autumn. The work is proposed as a tied studentship. (2) Complementary ship-board experiments in which copepods are fed labelled tracers in food to examine the extent to which *Calanus* can synthesise de novo so-called "essential" fatty acids. Analysis of results will be underpinned by the quantitative stoichiometry theory proposed by Anderson and Pond (2000: Limnology and Oceaography 45, 1162-7).

6) Determining ciliate parameters for intra and inter-basin scale models: abundance, biomass, cell size structure, biodiversity and production

David Montagnes (Port Erin/Liverpool (dmontag@liv.ac.uk) and Michael Heath (FRS Aberdeen)

We consider microzooplankton in two main roles: as competitors with, and as food for, mesozooplankton. We will parameterise the abundance, size structure, biomass, biodiversity and production of ciliates. These parameters will be examined at inter and intra basin-scale levels to test hypotheses concerning ciliate production and its fate. The project will also provide a service to other components of the Marine Productivity programme by producing useful data for model parameterisation.

7) Automated identification of *Calanus* to species level at any developmental stage

Gary Smerdon, (Plymouth Marine Laboratory grs@pml.ac.uk)

Identification of *Calanus* individuals to species level is problematic and normally impossible with early developmental stages (nauplii and early copepodites). This programme will develop an automated system for identification based on a modified method of Lindeque *et al*. (1999). The system requires a robotic workstation with integral thermal cycler, and will provide underpinning identification (>20 000 individuals) for the Broad Scale Survey project (Heath *et al*.) and for the Hirst *et al.* project.

8) Trophic interactions of copepods - application of natural abundance of stable isotopes

Kevin Flynn (University of Wales: Swansea, k.j.flynn@swansea.ac.uk) and Nicholas Owens (PML)

Natural abundance isotope ratio (NAIR) signatures will be determined for components of the zooplankton food chain collected during Phase 2 Marine Productivity cruises in the North Atlantic. This will enable the detection of shifts in trophic level and diet for individual species over geographic and temporal transects, and the detection of differences in diet between different species inhabiting the same water column. We shall also attempt to determine corrective algorithms for the determination of NAIR signatures in preserved zooplankton enabling a future interpretation of CPR records. The approach is core to the MarProd hypotheses concerning the trophic activity of zooplankton and the only method covering meaningful periods of time between cruises.

9) Effects of current systems in the North Atlantic Ocean and Norwegian Sea on the genetic structure of *Calanus finmarchicus* populations

Graham Savidge, Queen's University Belfast (g.savidge@qub.ac.uk); Christine Maggs and Jim Provan (QUB)

Samples of *Calanus finmarchicus* will be collected during spring and summer from approximately 18 stations located across the North Atlantic and from the Norwegian Sea. Microsatellite primers for *C. finmarchicus* will be developed and used to analyse levels and patterns of diversity within and between samples. The data obtained will be used to establish the presence of sub-populations of the species together with associated gene flow and will be interpreted in relation to the current structure of the area using historical data and, if possible, data to be generated elsewhere in the MarProd programme. Complementary data will be obtained from a limited number of winter samples and from a time series of samples from the eastern American seaboard

10) Environmental, nutritional and endocrine regulation of diapause in the calanoid copepod, *Calanus finmarchicus*

David Pond (Southampton Oceanography Centre, dwpo@soc.soton.ac.uk); Gary Smerdon (PML), Laurence Dinan (Exeter)

Diapause is a key feature of the life-cycle of many marine copepods and is thought to be regulated by a number of interacting factors that range from broad scale environmental cues, through to the action of specific hormonal messengers acting at the cellular level. The proposed studentship aims to study the interaction between the environment, nutrition, the levels of specific endocrine hormones and their receptors in marine calanoid copepods. In particular, this research aims to develop a predictive capability of the behaviour and life- cycle of *C. finmarchicus* in the North Atlantic, thereby providing crucial information for researchers developing population dynamic models for this key species.

11) Use of satellite remote sensing to determine phytoplankton abundance and production

Stephen Groom (s.groom@pml.ac.uk), Ian Joint & Jim Aiken (PML)

Satellite remote sensing will be used to provide support for the North Atlantic study in the Marine Productivity programme, in particular for seagoing activities.

GLOBEC-related UK Research Activities (excluding Marine Productivity):

Participating Institutions:

British Antarctic Survey (BAS)
Centre for Environment, Fisheries & Aquaculture (CEFAS)
Department of Agriculture & Rural Development, Northern Ireland (DARDNI)
Fisheries Research Services, Aberdeen (FRS)
Marine Biological Association, Plymouth (MBA)
Scottish Association for Marine Science (SAMS)
Sir Alister Hardy Foundation for Ocean Science (SAHFOS)
Southampton Oceanography Centre (SOC)

Main Studies

1) Southern Ocean ecosystem dynamics

Dr E Murphy (British Antarctic Survey; e.murphy@bas.ac.uk)

The programme will generate a Southern Ocean view of ecosystem operation through analyses of a relatively simple and tractable marine food web with krill as a key component. Two component projects: Variability of Southern Ocean Ecosystems (VSOE) and Spatial Structure in the Southern Ocean Ecosystem (SSSOE).

Funding: NERC (core strategic)

2) Development of biologically-based multi-species models

Dr M Bravington (Centre for Environment, Fisheries & Aquaculture Science; m.bravington@cefas.co.uk)

The objective is to develop simple 'forward-looking' multi-species models [for fisheries] which provide an insight into how management actions are likely to affect biologically interacting species, and result in changes in overall yield. This will improve assessments of the impact of management measures (such as fishing effort control and technical conservation) on fish stocks.

Funding: MAFF (Ministry of Agriculture, Food and Fisheries)
Budget: £76k pa (2000/01)
Duration: 1998 - 2003

3) Development of improved assessment models and evaluation of management procedures for multi-species systems

Centre for Environment, Fisheries & Aquaculture Science

The main objectives are: i) to undertake case-specfic evaluations of management/assessment procedures for the North Sea flatfish fisheries and suggest possible improvements; ii) to simulate and compare alternative management procedures for specific stocks This work will provide support to decision makers on fishery management options through the development of complex models and modelling procedures.

Funding: MAFF
Budget: £239k pa (2000/01)
Duration: 1999 - 2004

4) Development of models of plaice population dynamics incorporating biological processes for use in risk assessment

Centre for Environment, Fisheries & Aquaculture Science, Lowestoft; Port Erin Marine Laboratory; and Imperial College London. In collaboration with Netherlands Institute for Sea Research.

This project is constructing population models for plaice in the Irish and North Seas which explicitly incorporate processes such as maturation, spawning, egg and larval drift and growth and mortality on the nursery grounds. Fieldwork is focused on the Irish Sea, with sampling in 2001 and 2002 (building on the extensive data collections made in 2000). The aim is to develop models initially for the Irish Sea, and then examine their applicability to the North Sea.

Funding: MAFF
Budget: £310k pa (2001/02)
Duration: 2000 - 2005

5) Effects of environment on recruitment and incorporation into fisheries management

Centre for Environment, Fisheries & Aquaculture Science, Lowestoft

This project involves the identification of large-scale environmental forcing on fisheries recruitment. Work has focussed on cod and plaice stocks, with the impact of sea temperature as a major theme. The project is currently examining methods of incorporating real-time observations on sea temperature into predictive models useful for fisheries management. Future work is likely to focus on the mechanisms by which temperature impacts recruitment.

Funding: MAFF
Budget: £122k pa (2000/01)
Duration: 1999 - 2002

6) Biological oceanography

Dr R Gowen (DARDNI Belfast; richard.gowen@dardni.gov.uk)

Long-term studies of nutrients and plankton dynamics are being undertaken at two sites in the western Irish Sea (near-coastal site and in the stratified region). Moored instruments at these stations support CTDs, fluorometers, water samplers (nutrients and phytoplankton) and sub-surface light sensors. Ship board sampling is carried out at least monthly for collection of zooplankton samples.

7) Marine fisheries

Dr R Gowen (DARDNI Belfast; richard.gowen@dardni.gov.uk)

Annual surveys are carried out to investigate the distribution and abundance of zooplankton, fish larvae and juveniles in the western Irish Sea (three 5-7 day cruises between April - June, using Gulf VII high speed plankton sampler with coarse and fine nets). Samples also collected for growth studies of larval fish and their relation to environmental conditions.

8) Marine ecosystems

Dr M Heath (FRS Marine Laboratory, Aberdeen; heathmr@marlab.ac.uk)

This programme includes studies of fish population biology (recruitment, population structure, stock identity; environmental time series); multispecies interactions (effects of fishing on marine ecosystems; resource partitioning; marine foodweb energy flow); and habitats and species (ecology of zooplankton and early life stages of fish; environmental effects on pelagic productivity and fish recruitment; simulation modelling of ecological processes and population dynamics). Geographic focus on northern North Sea and northeastern Atlantic.

9) Fisheries management

Dr R Cook (FRS Marine Laboratory, Aberdeen)

This programme includes acoustic surveys for pelagic fish, and the assessment, modelling and management of pelagic fish stocks (emphasis on herring and mackerel). Also stock assessments for demersal and inshore fisheries.

10) The aquatic environment

Dr C Moffat (FRS Marine Laboratory, Aberdeen)

This programme includes studies of ocean climate variability, decadal climate change, and interactions between physical processes and fish stocks. Also data management and quality assurance, environmental protection, ecotoxicology, and marine biotoxins.

11) Bio-physical transport modelling of the early life-stages of mackerel

Dr S H Coombs (Marine Biological Association; shc@mba.ac.uk)

Co-ordination and participation in EU project (SEAMAR: Shelf- Edge Advection, Mortality and Recruitment) on the planktonic stages of mackerel along the shelf and shelf-edge west from Portugal, through Biscay, to the west of Ireland and Scotland. Uses a circulation and transport model to track the advection of eggs, larvae and post-larvae under different meteorological forcing scenarios. Incorporates growth and mortality modules linked to temperature and food availability to predict survival.

Funding: EU, NERC
Budget: £80k pa
Duration: 1999 -2001

12) Continuous Plankton Recorder (CPR) survey of the N W European shelf and the North Atlantic

Dr P C Reid (SAHFOS, Plymouth; pcre@nerc.ac.uk)

The CPR survey provides cost-effective monitoring of large-scale changes in near-surface plankton, using merchant ships to tow sampling gear. All zooplankton larger than 2mm are identified, and subsamples taken for analysis of small zooplankton and phytoplankton. Current research topics include: long term changes in the plankton community structure in response to abiotic events; vertical migration of various species; geographical distribution of *Calanus*; biodiversity along the European shelf edge; and development of environmental instrumentation of CPRs.

Funding: MAFF, DETR, NERC (core strategic) & others
Budget: c £700k pa
Duration: Ongoing (since 1946)

13) Zooplankton dynamics

Dr G Tarling (SAMS, Dunstaffnage; gant@dml.ac.uk)

Studies of the interactions between physical factors, physiological ecology and behaviour of meso- and macrozooplankton. Behavioural and physical data is synthesised into models that predict vertical migration regimes and effect of currents and shears on dispersal patterns. Models are being developed for Clyde Sea area and the Irish Sea.

Funding: NERC, UHI, MAFF and EU
Budget: c £100k pa
Duration: ongoing

14) Ocean processes

Dr R Pollard (Southampton Oceanography Centre, rtp@soc.soton.ac.uk)

Multidisciplinary research directed at defining and modelling upper ocean processes; export and fluxes to the deep-sea floor; and the biology of pelagic and benthic deep-sea fauna. Hydrobiological goals include the development of bioacoustic techniques, and the linking of ocean physics and chemistry to biological distributions and biogeochemical fluxes. Biological modelling goals include the development and validation of simple, realistic models of marine ecosystem dynamics, and the development of 3D models of the ocean carbon cycle for studies of future climate. Most work focuses on the N E Atlantic, also interest in the Indian Ocean (Arabian Sea, Gulf of Oman) and elsewhere.

Funding: NERC (core strategic)
Budget: £642k pa (2000/01)
Duration: 1994 – 2002

15) Upper ocean processes and biogeochemistry

Prof P Holligan (Southampton Oceanography Centre; pmh1@soc.soton.ac.uk)

Multidisciplinary research directed at physical mixing in the surface ocean (ocean eddies and fronts, tidal and shelf break fronts, remote sensing of surface ocean, dynamics of marine boundary layer); system modelling (phytoplankton and global nutrient cycles, thermocline dynamics); plankton productivity and ecology (microbiology, phytoplankton and zooplankton ecophysiology); and trace metal and nutrient biogeochemistry.

Funding: HEFCE, NERC and others
Duration: Ongoing