

# MICHAEL JOHN ROBERT FASHAM 29 May 1942 – 7 June 2008

Journal:	Biographical Memoirs of Fellows of the Royal Society
Manuscript ID:	RSBM-2015-0014.R1
Article Type:	Memoir
Date Submitted by the Author:	n/a
Complete List of Authors:	Anderson, Thomas; National Oceanography Centre, Marine Systems Modelling Bryden, Harry; National Oceanography Centre, Ocean and Earth Science
Subject Areas:	20th Century < Biographical history < HISTORY OF SCIENCE, Computer modelling and simulation < COMPUTER SCIENCE/ INFORMATION TECHNOLOGY, biological < Oceanography < EARTH SCIENCES, biogeochemistry < Cross-disciplinary subjects < BIOLOGY
Keywords:	marine ecosystems, ecological modelling, ocean biogeochemistry



### MICHAEL JOHN ROBERT FASHAM

## 29 May 1942 – 7 June 2008

## ELECTED FRS 2000

# BY THOMAS R. ANDERSON<sup>1</sup> AND HARRY L. BRYDEN<sup>1</sup> FRS

<sup>1</sup>National Oceanography Centre, Southampton SO14 3ZH, United Kingdom

Professor Michael Fasham played a pioneering role in the development of marine ecosystem models for the study of nutrient and carbon cycling in the ocean. He is particularly celebrated for his famous Fasham-Ducklow-McKelvie model which was the first of its kind to separate new and regenerated forms of nutrient, as well as including microbial recycling pathways. Fasham's models provided key understanding of the links between primary production, carbon cycling and export (of organic matter from the surface to deep ocean) based on both deep and insightful parameterisation inspired by his many collaborations with leading experimental and field biologists of the day, and by his expert use of data for model calibration and validation. He had the ability to see the big picture, linking observation and models to achieve a unified understanding of system dynamics. As well as the direct contributions of his own science, Fasham played a pivotal role in steering the international scientific agenda, notably his leadership of the Joint Global Ocean Flux Study (JGOFS) which had the aim of understanding ocean carbon cycling and sinks via coordination of extensive field programs, synthesis and modelling. He will be remembered by those who knew him for his openness, enthusiasm and modesty, a man who was fun to know and to work with and who loved the thrill of scientific adventure and discovery.

## FAMILY BACKGROUND AND EDUCATION

Michael (Mike) John Robert Fasham was born in Edgware, Middlesex on 29 May 1942. His father Ronald Henry Alfred Fasham was posted to 467 Squadron during the War, flying Lancaster bombers and completing an operational tour of 35 flights over Germany and France. Ronald had met Mike's mother, Hazel Grace Day, through their joint love of cycling and the two married in November 1940. Mike and his mother at first lived with her parents in Kingsbury during the war but they later rented a flat in nearby Neasden and eventually moved to Kenton in 1953. Sisters Diane and Jacqueline were born in 1947 and 1958.

Mike attended Wykeham Primary School and was apparently a troublesome boy although his mother, having missed out on the best educational opportunities herself, soon sorted him out. It was during his last two years at Wykeham that Mike was inspired by his teacher, Mr. Bodger, to become a scientist and he duly passed his 11 plus scholarship exam in 1953. He then moved on to Kilburn Grammar School in Brondesbury where he focused on science subjects including physics and chemistry, but not biology (the school's biology laboratory had been destroyed by a bomb in 1944 and was not rebuilt until 1958). Aside from his studies, Mike blossomed on the sports field playing rugby for the school's first XV and running in the Middlesex Schools 100 yard final (although he came last!). His parents bought him a Raleigh bike when he was 13 and he spent time cycling with friends throughout the UK, as well as a trip to the Rhine and Moselle valleys when he was 15.

Passing A levels in maths, applied maths, physics and chemistry, Mike enrolled for a degree in physics at Birmingham University in 1960. He took geology as an extra subject as he had been fascinated by the scientific results coming out of the International Geophysical Year (1957-58) that included topics such as geomagnetism, cosmic rays, meteorology and seismology. Mike particularly enjoyed the geology lectures and by now he had set his sights on a career in geophysics. Core physics nevertheless continued to capture his imagination and by the final year he was immersed in subjects such as relativity, quantum mechanics and particle physics. Exam time arrived on his 21<sup>st</sup> birthday, leaving Mike little energy to down the obligatory eight pints of beer that evening! The award of a 2.1 degree duly followed in 1963.

A choice now presented itself: continue in academia with postgraduate study or get a job in industry and earn some money. After vacillating for a while, Mike joined the fortunehunting gang. He took up a position with the United Steel Company and, along with two other apprentices, started work in the Operational Research department situated in Cybor House, Broomhill, in January 1964. He was allocated to a project to determine the optimum number of cranes that would minimise delays in the steel melting shop of the Appleby-Frodingham works in Scunthorpe. The work involved using a Ferranti Pegasus computer, a vacuum-tube based machine with a 4k drum store and an internal store of 40 words. This early experience of using computers and writing programs would be invaluable for Mike's future career. He also developed an interest in statistics at this time, again a skill that would prove useful in future. After four months work, Mike concluded that the optimum number of cranes was five, exactly the number that were already in place! The problem solving was

#### Under Review for Bio Mems. R. Soc.

enjoyable and Mike soon found himself thinking about returning to an academic research environment to do a postgraduate degree. United Steel would probably have sponsored him to take a Masters course in Operational Research but the enduring appeal of geophysics was to win the day. Mike knew that the Geology Department at Birmingham ran an MSc in applied geophysics. Resigning his position at United Steel, he enrolled for a PhD, but taking the MSc course in the first year in order to obtain a firm grounding in geophysics.

The MSc work consisted of a broad range of lectures on solid earth geophysics, as well as extra training in statistics. There was also a field project involving a geophysical survey of the Bovey Tracey basin, situated on the eastern edge of Dartmoor. Mike had responsibility for the gravity survey which entailed driving around with a Worden gravimeter looking for Ordnance Survey benchmarks so that an accurate height could be obtained for each gravity measurement. Interpretation of the results was rather complex but, thanks to his recently acquired programming skills, Mike was able to show that the basin depth was considerably deeper than had been previously thought (1). His PhD, supervised by Prof. D.H. Griffiths, entailed researching the geological structure of the Scotia Sea in the Southern Ocean. Mike analysed a number of magnetic transects that had been made on British Antarctic Survey supply trips between the Falklands, South Georgia, Graham Land and the South Sandwich Islands, characterising the different anomalies and using multivariate statistical methods to search for geographical patterns. The analysis showed long linear spatial correlations of positive and negative anomalies which, in his final year, Mike was able to explain using the sea floor spreading theory developed by F. J. Vine FRS and D. H. Matthews FRS at Cambridge University. As it happened, Mike's statistical methodology of analysing these data sets was soon rendered obsolete with the advent of navigation via satellite data and he did not therefore write the results up for publication. He was awarded his PhD in 1968. Mike's one long-lasting regret is that, throughout his career, he never actually managed to visit Antarctica.

During the years he was back in Birmingham, Mike had shared a number of houses and flats with a variety of friends, some of whom dated back to his undergraduate days. They all worked hard but also somehow managed to find the time and money to enjoy themselves immensely. Partying one evening in August 1967 Mike looked across the room and saw his future wife, Jocelyn (Jos) Hart, who was studying for an MSc in comparative neurosensory physiology and behaviour. A whirlwind romance ensued and the two of them were engaged just three weeks later, much to the amazement of their friends. After a further three months

they married, the only drawback being that the bride and groom, having merged their overdrafts, could not afford a honeymoon and so spent the time instead in their flat in Ealing, deciding on whether they had enough money for an Indian takeaway. As always, Mike continued to play rugby and after reaching the dizzy heights of playing for a (minor) Wasps team, as well as the Moseley 2<sup>nd</sup> team, his later games at Guildford and Godalming RFC were thankfully less athletic, but always enjoyable.

At this time, Mike was thinking about what he might do after getting his PhD. Many of his colleagues in the geophysics department had been undertaking geophysical surveys in the Antarctic using teams of dogs but, for whatever reason, Prof. Griffiths was not supportive of this avenue and Mike once again left the academic fold, albeit temporarily. Nigel Ridley-Thomas, who had been on Mike's MSc course, had been appointed head of geophysical surveys at Wimpey Laboratories and offered him a position to develop geophysical computer software. The money was good but Mike soon became disillusioned and unhappy with the new role. The working atmosphere was necessarily very commercial and he missed the freedom of academic life. Furthermore, he and Jos had moved to a flat on Richmond Hill in early 1968 and, although the area was nice, it was beneath the flight path to Heathrow. Mike soon discovered that he had a low tolerance to noise, lying in bed in the morning counting planes passing overhead at 3-minute intervals. One weekend, after visiting friends who lived in the peaceful Kentish countryside, Mike realised that they had to leave London. Picking up the Sunday's Observer, he saw an advert for a job in the computer department of the National Institute of Oceanography (NIO) at Wormley (near Godalming, Surrey). In September 1968 Mike and Jos moved into a lovely rented cottage close to Milford station and in the following year they purchased a town house in Hill Road, Godalming. At 26 years of age, Mike had a degree in physics, a PhD in Geophysics and a wealth of experience with both computers and statistical techniques. There was no inkling as yet, however, that his greatest achievements would be in the realm of biological oceanography.

## OCEANOGRAPHY: DEBUT AND TRANSITION TO BIOLOGY

Mike started work in the computer group at NIO in September 1968. Computers were new to oceanography at this time and Jim Crease, leader of the group, had successfully persuaded NIO to purchase two mainframe IBM 1800 computers. The first of these was installed aboard the NERC (Natural Environment Research Council) research ship, RRS Discovery, for work

Page 5 of 36

at sea while the other was located back in the laboratory for post-cruise processing and analysis of data. The IBM was so large (about two metres in height) that a hole had to be cut in the side of the ship to allow it to be installed on board! Mike's job was to be responsible for the shipboard system, involving development of functionality in two main areas, navigation and data processing (2). Precise navigation involved logging satellite fixes taken using a Magnavox 702 satellite receiver which, in combination with the dead reckoning position of the ship (based on the ship's heading from gyro and the two component electromagnetic log), allowed precise calculation of the ship's position. The necessary calculations were handled for the first time by the IBM 1800 on Mike's second cruise, Discovery 29, to the Rockall region and the Azores in August to October 1969. The quality of the received satellite signal depended on ship's heading and so, in order to acquire the satellite fix most accurately. Mike would often make his way to the Bridge in the middle of the night to convince the Mate to alter ship's heading! Computerised data logging of oceanographic measurements on board ship was also highly advantageous. As well as navigation, measurements included Swallow float velocities, CTD (Conductivity, Temperature, Depth) station profiles of temperature and salinity versus depth, meteorological observations and bathymetry. Cruises usually lasted at least several weeks or more and a large boon for the scientists was the production of plots and charts from the computer-held data which both enhanced effective decision making regarding the scientific programme, as well as indicating potential instrument malfunction. Mike's programming skills were at a premium given the need for efficient use of the disk space available: the IBM 1800 had a core storage capacity of 32k with three additional interchangeable disks each with the "immense" (Mike's own description) capacity of 500k. We take computers for granted today but not only did Mike have to deal with the limited disk space, there was also the ancillary equipment which included paper tape punch and readers, disk ancillary store, typewriters, plotters, etc.

The shipboard computer group consisted of three, Jim Crease, Mike Fasham and Brian Hinde. There were many Discovery cruises and between them they tried to cover them all. Mike participated on seven cruises during the period from 1968 to 1973 and, as he often said, it was fortunate that he did not suffer from seasickness. Two IBM engineers were also seconded to the group for a year and everyone worked long hours. In order to relax at the end of the day, Mike and Jim would often play a rubber of bridge with the engineers and then go back for some late night computing for further cognitive entertainment.

#### Under Review for Bio Mems. R. Soc.

All scientists at the NIO were encouraged by the Director, Sir George Deacon FRS, to have a personal research interest to be pursued in addition to assigned duties. Harking back to his university days, Mike's first thought was to pursue a geophysical topic but found himself heading in another direction when word got round NIO about his statistical skills and Margaret Thorrington-Smith, of the Biology Department, asked him to help her analyse phytoplankton data from the Indian Ocean Expedition of 1964. Dendograms were constructed to organise species into phytohydrographic regions (Thorrington-Smith, 1974). Soon afterwards, Mike met Martin Angel, another of the marine biologists and a specialist in ostracods (a group of crustacean zooplankton). Martin had taken part in the 1965 SOND cruise (the name denoting the months September to December during which the cruise took place) to an area southeast of Fuenteventura in the Canary Islands, looking at the biodiversity, vertical distribution and migratory behaviour of animals (zooplankton) in the upper 1000 m of the water column. Faced with an enormous data set describing many species, depth zones and the changing light environment (diel cycle and depth). Martin wanted to go beyond the usual descriptive analysis and the two of them wrote a paper (3) involving extensive analysis of the data using techniques such as factor analysis and cluster analysis. Formally joining the Biology department at the NIO in 1973, Mike spent the following years working with the biologists using statistical methods in the study of the biogeography of zooplankton in the northeast Atlantic (4, 5, 6, 10).

Mike was always one to chip in to the teamwork and hard graft that was required in seagoing scientific expeditions. As well as his own direct contribution, going to sea also gave him a full appreciation of the difficulties involved in making a coordinated suite of physical and biological observations and the errors and uncertainties thereof. Mike wanted to be involved in the biological sampling programme, although continuing also with computing duties using the IBM 1800. Travelling to the equatorial Atlantic on board cruise Discovery 61 in the spring of 1974, he used fluorometers to measure the distribution and patterns of chlorophyll in the ocean. Many cruises were to follow with Mike continuing the fluorometry work, allowing him to directly study the patchy distribution of plankton in the sea and its relationship to light, nutrients and the physical structures in the upper ocean (7).

Cricket was a passion of Mike's and he was a regular for many years with the NIO team. Mike's forté was his style. He fancied himself as the David Gower of the side but, more often than not, ended up wafting his bat at the ball as it went by. On one occasion, there was a cricket match at sea, during cruise Discovery 92 to the Porcupine Sea Bight in 1978. Mike's

#### Under Review for Bio Mems. R. Soc.

birthday happened to take place during the cruise, as did that of his colleague, Howard Roe, and the two of them were presented with a cricket bat crafted from planks by the ship's carpenter inscribed "To Fasham and Roe, Discovery Cricketers of the Year 1978". The match took place on the after deck of the ship and, needless to say, it was not long before the ball disappeared over the side. To Mike's great delight, years later, he and his son Matthew (coopted as a demon bowler) played together for the IOS cricket team, but on dry land where the balls merely disappeared into the undergrowth.

Mike's ascent and mastery of his new discipline, biological oceanography, took place at remarkable speed. His multifaceted knowledge of physics, biology, statistics and mathematics gave him holistic insight into the interrelationships between light, nutrients, physical mixing and the underlying observed patterns of plankton patchiness in space and time. His seagoing continued unabated and, in 1979, he had the honour of acting as Principal Scientist on cruise Challenger 5/79, the cruise program involving a study of the developing phase of the phytoplankton spring bloom in the shelf seas to the southwest of the United Kingdom. But it was in the theoretical understanding of plankton dynamics that Mike excelled most to the extent that he was already becoming a leading authority in his field. As such, he was invited to write a major review article concerning the theoretical basis of plankton patchiness (8). Much of the content focused on statistical analysis of plankton distributions but Mike was also becoming increasingly interested in the potential of describing plankton dynamics using simultaneous differential equations. In particular, he noted the ideas of John Steele FRS, a mathematical biologist based in Aberdeen, who used variants of the famous predator-prey model of Alfred Lotka and Vito Volterra to investigate plankton dynamics. Mike first met Steele at a NATO Advance Science Institute (ASI) meeting on plankton patchiness in Sicily in November 1977 and subsequently wrote a paper in the follow-up book (edited by Steele), Spatial Pattern in Plankton Communities (9). Shortly afterwards, Mike joined SCOR (Scientific Committee on Ocean Research) Working Group (WG) 59 whose remit was to review the state of the art in biological oceanographic modelling and implications for the design of research programmes. Meetings took place in 1977 at the IOS (Institute of Oceanographic Sciences) Wormley (renamed from NIO) and in 1979 and at the Bellair Research Institute in Barbados. Membership of the WG was limited to a small number of distinguished luminaries including Ken Mann, Trevor Platt FRS, John Field, Bob Ulanowicz and Fred Wulff. Mike wrote three major sections in the proceedings, Mathematical Models in Biological Oceanography (Platt et al., 1981). Mike was now at the

very heart of the debate about the choice between holistic methods for studying marine ecosystems versus the reductionist approach based on differential equations. A further meeting of the WG led to the setting up of a NATO ASI in Bombannes, France, in May 1982. Mike had the distinction of being the sole editor of the resulting proceedings, *Flows of Energy and Materials in Marine Ecosystems: Theory and Practice* (11) spanning some 30 articles spread over 733 pages. The stage was set for the move to reductionist methods in marine ecosystem modelling along with close integration with the field/observational community and Mike was in pole position to lead the way.

## JGOFS

Global warming hit the headlines in the 1980s. At the Villach Conference in 1985, leading experts declared that warming is inevitable due to build up of greenhouse gases in the atmosphere. Climate science entered mainstream politics, discussions over international agreements on CO<sub>2</sub> emissions commenced and later, in 1988, the IPCC would be established. Research to accurately quantify the sources and sinks of carbon in the global biosphere was imperative and, to address the ocean component, the Joint Global Ocean Flux Study (JGOFS) was launched in 1987. The objectives were to understand, on a global scale, the time-varying fluxes of carbon in the ocean and atmospheric exchange of CO<sub>2</sub>, and to develop capability to predict their response to anthropogenic perturbation. A large proposal was approved for funding by NERC in 1988 as the initial UK contribution to JGOFS and, shortly afterwards, an associated SCOR Committee for JGOFS was set up under the leadership of Bernt Zeitzshcel. Mike was delighted to accept an invitation to act as a UK representative, along with Harry Elderfield FRS. The JGOFS field programme got underway in 1989 with the North Atlantic Bloom Experiment (NABE) in which British, American and German ships rendezvoused in the mid-Atlantic to study the spatial and temporal development of the spring phytoplankton bloom (16, 22, 23, 25). This was truly Big Science and, indeed, the JGOFS programme was to last fifteen years with participants from more than thirty nations. Mike had the honour of acting as Principal Scientist on Discovery 182, the British cruise contributing to NABE, overseeing an integrated programme of measurements including dissolved inorganic carbon, pCO<sub>2</sub>, chlorophyll, primary and bacterial production, nutrients and physics. Later that year he was elected as vice chair of the JGOFS Scientific Committee. Mike was now at the very heart of the international effort and his first job was to oversee the writing of the JGOFS Science Plan that was published in 1990 (15).

Page 9 of 36

Throughout this intense period of activity, Mike was continuing to make remarkable progress in his own personal research. The role of microorganisms in marine ecosystems was becoming recognised at this time, the so-called "microbial loop". Back in March 1984, Mike attended a symposium on "Flow analysis of nutrients in the marine euphotic zone" held in Quebec and, in the proceedings, he published a flow analysis model of a generic marine ecosystem (i.e., not applied to any particular site in the ocean) which included the dissolved organic matter to bacteria to protozoa pathway (12). Results indicated the importance of the microbial loop contribution to total community respiration but, in order for further progress, improved parameterisation was needed based on field data for specific ocean ecosystems. The following October, Mike travelled to San Miniato (Italy) to attend a workshop on photosynthetic picoplankton in the ocean. It was at this meeting that he met Hugh Ducklow, a marine microbiologist based at Horn Point Laboratory (University of Maryland). The two of them struck up a collaboration that, during the following years, would revolutionise the stateof-the-art of marine ecosystem models. Hugh gave a presentation showing data on bacteria and phytoplankton data from a field study of Warm Core Rings off the northeast US coast (Ducklow, 1986). Mike now had the opportunity to accurately parameterise his model, benefiting greatly from both the Warm Core Ring data and Hugh's expertise on microbial ecology. The two of them attended a SCOR workshop in Santa Cruz in December 1986, "Network analysis in marine ecology" and, the following year, set about parameterising the model, with Alain Vezina of the University of Quebec joining them. It was a mighty task given the "staggering number of assumptions" but nevertheless reached a successful conclusion with publication in the workshop proceedings in 1989 (13).

Flow analysis necessarily assumes steady state, a rather severe restriction given the dynamic nature of most marine ecosystems. Mike therefore again turned his thoughts to the reductionist approach. Steele had paved the way in the 1970s using a simple nutrient-phytoplankton-zooplankton (NPZ) ecosystem situated within the upper (mixed) layer of a two-layer "slab" ocean model (Steele, 1974). The idea was developed further by Geoff Evans and John Parslow to make the depth of the upper layer seasonally varying, again incorporating an NPZ ecosystem (Evans and Parslow, 1985). Mike and Hugh Ducklow met once more, this time at the joint AGU/ASLO Ocean Sciences meeting in New Orleans, 1988. Mike had set up a time-dependent version of their flow analysis model and could not get it to run successfully. Over coffee and beignets at Café du Monde, the two of them reviewed the parameterisations and found that the rules for consumption of DOM needed adjustment to

ensure that only the small labile pool was accessed by bacteria. There and then, the model was set in motion once more and it ran successfully! The two of them launched a project that would lead to the famed Fasham-Ducklow-McKelvie (FDM90) model (Scott McKelvie, based at NIO, helped with sensitivity analysis in the latter stages of the work) that would revolutionise the face of marine ecosystem modelling (14). Using the slab model of Evans and Parslow as the physical basis, the complexity of the model ecosystem was increased beyond NPZ to include microbial pathways and to divide nutrient between new (nitrate) and regenerated (ammonium) forms. Detritus was also added as a state variable, facilitating the prediction of export of sinking particles from the surface layer to the deep ocean.

The FDM90 model was set up to simulate Bermuda Hydrostation "S", an ocean station in the Sargasso Sea which provided a long time series of data for nutrients, plankton and physical properties of the water column. Mike painstakingly went about formulating and parameterising the model. Attention to detail was his hallmark and, to keep track, detailed records were kept in notebooks. In all, 201 runs of the model are dutifully listed exploring his various ideas and parameterisations. Results were sometimes printed out and sellotaped below his jottings (Fig. 1). The model successfully reproduced the annual cycles of nutrients, phytoplankton, primary production and export for Station S, providing an understanding of the associated cycling of nitrogen and carbon in the ocean. The main legacy of the model is, however, that it provided the basic structure for representing the recycling of nutrients by the marine ecosystem in time-dependent models by including separate state variables for nitrate and ammonium and an associated microbial loop via DOM and bacteria. As such, it provided the foundation for the many models that followed and even today, 25 years on, the paper is heavily cited. Of all Mike's achievements, he is best remembered for the FDM90 model.

For holidays, after so much travelling with work, Mike rejected any destination involving airports and so instead he, Jos and Matthew frequently spent time meandering at 4 m.p.h. along the many tranquil canals of the UK. His penchant for keeping records once again came to the fore as he would note the various species of birds, wild flowers, butterflies and other wildlife, underlining them in Jos's reference books. His fine eye for detail and thoroughness in approach also served him well with his interests in philately and genealogy. Mike successfully traced his family lineage back to the 17<sup>th</sup> century, at which time the Fashams were farmers in East Kent. In the 1830s, however, Daniel Stephen Fasham relinquished the farming tradition and went to sea, becoming a master mariner in Ramsgate, and maybe it was from him that Mike inherited his sea legs.

Page 11 of 36

The International Geosphere-Biosphere Programme (IGBP) had been launched in 1987 to coordinate international research on the effects of climate change on physical, chemical and biological processes that regulate the Earth system. Mike attended the fifth meeting of the IGBP Executive Committee held in Moscow, March 1990, where it was agreed that JGOFS would become a constituent programme of IGBP. As a result of his links with IGBP, Mike later sat on the GLOBEC (Global Ocean Ecosystem Dynamics) Numerical Modelling Working Group and the GAIM (Global Analysis, Interpretation and Modelling) Scientific Committee. Over and above his committee duties. Mike pressed ahead with his personal research. At the heart of JGOFS lay the development of global models predicting the cycling and export of carbon from the surface to deep ocean, underpinned by intensive sampling in the field. By the late 1980s, computers were beginning to have sufficient power to run threedimensional models that could simulate the time-varying physical circulation at basin and global scales. The Princeton group, led by Jorge Sarmiento, was at the forefront of working on these ocean general circulation models (OGCMs). In the earliest simulations, the role of biology in nutrient cycling was parameterised implicitly by restoring nutrients to observed surface distributions by exporting excess nutrient to depth using simple power laws (Najjar et al., 1992). Mike had met Jorge at the afore-mentioned ASLO meeting in New Orleans, 1988, initiating a new venture: incorporation of the FDM90 model (while still under development) into the Princeton OGCM. A number of visits were made to Princeton, leading to stimulating and exciting discussions among a number of participants including Jorge, Mike, Hugh Ducklow, Robbie Toggweiler, Geoff Evans and Trevor Platt and ultimately publication of the work in 1993 (24). It was the first study of its kind, with an explicit ecosystem model embedded in a multiple (twenty-five) layer GCM (the ecosystem was restricted to the upper three layers which spanned 123 m), and run for a North Atlantic domain with seasonal forcing. Given its pioneering nature and relatively crude model grid, the resulting simulation was a remarkable success, although reported only modestly by the scientists involved, e.g., the "overall pattern of the model predicted annual mean chlorophyll agrees quite well with the CZCS [satellite colour] data" (24).

In 1991 Colin Summerhayes, then director of the Institute of Oceanographic Sciences, advised Mike to reduce his commitments in order to achieve individual merit promotion. Although Mike enjoyed the committee work, he therefore reluctantly resigned from the JGOFS Steering Committee, although remained a member of the JGOFS Global Modelling and Synthesis Task Team. Indeed, he attended a number of North Atlantic Planning Group

meetings in the coming years and would take over the chairmanship of the Group in 1995. Mike was also a member of the Numerical Modelling Working Group of International GLOBEC around this time (serving from 1993-1997). Meetings were always a good way of stimulating thought and discussion for Mike and in 1990 a NATO science panel made provision for funding a series of Advanced Science Institute workshops on climate change and the carbon cycle. Mike took the opportunity to attend an ASI on the Global Carbon Cycle held in Cioccio, Tuscany, in September 1991, publishing "Modelling the marine biota" in the proceedings (17). Practical examples were provided, with the usual careful parameterisation, by applying the FDM90 model to time series locations in the ocean at Bermuda Station S and Station India (60°N 20°W) in the North Atlantic. It was another classic publication, a treatise in the state-of-the-art of marine ecosystem modelling. The following year, Mike visited the delightful Chateau de Bonas in the Gascogne region of France to attend a workshop which he had organised along with Geoff Evans of Fisheries and Oceans Canada. The two of them edited the proceedings "Towards a model of ocean biogeochemical processes" (18) and Mike contributed to three of the papers (19, 20, 21). The title of the volume was a long-term aspiration of Mike's, namely the development of an ecosystem model with a single unique parameter set that could be robustly used in global OGCMs to study the biogeochemical cycling of carbon and nitrogen and their response to changing climate. He set the ball rolling and the issue remains a topic of debate today. At the very forefront of his field, Mike achieved merit promotion in 1993.

## SOUTHAMPTON

Alongside his work with Sarmiento in the United States, Mike's vision was to pursue the development of global ocean biogeochemical GCMs in the UK and two opportunities presented themselves. First, moves were afoot to relocate the Institute of Oceanographic Sciences at Wormley to Southampton. The James Rennell Centre for Ocean Circulation (JRC) was set up in Chilworth in 1990 under the direction of Raymond Pollard, housing physicists and ocean modellers transferred from IOS and an injection of new recruits. Mike was asked if he would like to transfer to the JRC and the opportunity to be part of a larger group of modellers was too good to miss. Physical OGCMs were already running at IOS, notably the Fine Resolution Antarctic Model (FRAM) and the development of global models was underway (Coward et al., 1994). Second, global simulations using physical OGCMs were also taking place at the UK Met Office. Under its auspices, the Hadley Centre for

#### Under Review for Bio Mems. R. Soc.

Climate Prediction and Research was formed in 1990. What was needed was to incorporate state of the art marine ecosystem models into these physical codes. It was a mighty task and Mike started building his own group of biological modellers. Tom Anderson had already been taken on to work on ecosystem model development and John Hemmings would soon join the group.

For various reasons beyond Mike's control, incorporating biology into the IOS physical GCMs was slow to take off the ground and it was with the Hadley Centre that the most rapid progress was made, at least early on. Mike had met with Howard Cattle and Chris Gordon and a collaborative venture was initiated in which work was subcontracted to Mike's group to develop an NPZD model (NPZ plus detritus) and incorporate it into the Hadley OGCM. Expertise was needed to embed the biology in the physical code and to undertake the simulations and Ian Totterdell was taken on for this task. The new ecosystem model was aptly named HadOCC (the Hadley Centre Ocean Carbon Cycle model; Palmer and Totterdell, 2001). Subsequently, this ocean model was embedded within a fully coupled Earth system model that also included an atmosphere and terrestrial vegetation and the resulting HadCM3LC climate model was the first of its kind used for the prediction of the coupled global carbon-climate system (Cox et al., 2000). Mike later contributed to the development of the Diat-HadOCC model (the successor to HadOCC which included the phytoplankton group diatoms) which was used by the Hadley Centre as part of the HadGEM2-ES model for simulations which informed the IPCC 5th Assessment Report.

By now the whole of IOS, including everyone at Wormley, had moved to the purposebuilt Southampton Oceanography Centre located at the dockside (now renamed as the National Oceanography Centre Southampton, NOCS), a union of NERC staff with the oceanography department of the University of Southampton. A supercomputer was installed in-house and with it the development of the global GCM OCCAM (Ocean Circulation and Climate Advanced Modelling). Katya Popova joined the group in 1998 and a new ecosystem model was developed which included phytoplankton, zooplankton, detritus, nitrate, ammonium and chlorophyll as state variables, the latter to assist in model validation. Simulations were carried out to study the extent to which global variability in primary production and export production can be realistically predicted using advanced physical parameterisations of the upper mixed layer (42). In recent years global ocean biogeochemical modelling has gone from strength to strength in Southampton, particularly with the development of the MEDUSA (Model of Ecosystem Dynamics, nutrient Utilisation,

 Sequestration and Acidification) ecosystem model (Yool et al., 2011) and it is Mike who must take the credit for providing the foundations of this success.

The global ocean modelling was underpinned by regional modelling studies to provide understanding and insight and Mike's scientific endeavours continued apace, as always maximising opportunity on the back of new and fruitful collaborations. NATO had encouraged Russian scientists to attend the ASIs and it was at Chateau de Bonas that Mike met Vladimir Ryabchenko and Boris Kagan of the Shirshov Institute in St Petersburg, physicists keen to broaden their horizons into ecosystem modelling. Mike made the first of several visits to St Petersburg in 1994 and at once fell in love with the place describing it as "one of my greatest cultural experiences". Early work focused on investigating the dynamics of the FDM90 model, especially oscillatory and chaotic solutions (27, 30, 31). Further work involved embedding FDM90 into a 3D model of the North Indian Ocean (32, 43) with funding from EC INTAS (International Association for the promotion of cooperation with scientists from the former Soviet Union) and the Royal Society. Tom Anderson took part in this work and travelled also to St Petersburg. The warmth and friendliness of the people were "overwhelming" and could not have been further from the stereotypes of the cold-war era. Departure day was usually celebrated "na pososhok" (one for the road) with a few beers and vodkas. Boarding our flight home one time, I (TRA) remember Mike and I feeling decidedly sheepish after a few stern words from a stewardess who was less than happy with our somewhat extrovert disposition! One of the people we met in St Petersburg was Katya Popova whom Mike was very impressed with. Katya later obtained a Boris Yeltsin scholarship to spend a year working with Mike in 1996 (36). As mentioned above, she has since taken on a job in Southampton working with ocean GCMs and now leads the Ocean Biogeochemical Modelling group at the NOCS.

Mike's experiences with the FDM90 model had taught him that the most timeconsuming aspect was varying parameter values to get the best fit to observations. During the Chateau de Bonas meeting, Geoff Evans had mentioned that he was developing software to tackle this problem using nonlinear optimisation. Another collaboration beckoned and Mike used the optimisation method to fit ecosystem models to data from JGOFS cruises to the northeast Atlantic in 1989 and 1990 (26, 34). The work embodied Mike's philosophy that models should be firmly grounded in data in order to ensure robust and accurate prediction. Indeed, this was the foundation of JGOFS, namely the provision of data via intense sampling (including the time series stations) in order to understand processes and to parameterise

models which could then be incorporated into GCMs to predict the response of the ocean carbon cycle to changing climate. The real world is complex and so, providing there were underpinning data, Mike favoured building up complexity in models. Data were obtained not only from the field, but from laboratory studies also, and Mike was particularly impressed with the work of Kevin Flynn, a physiologist carrying out laboratory experiments with phytoplankton. He found out that, as a post-doc, Kevin had moonlighted as a writer of computer games and so, unlike many biologists, computers and modelling were not alien to him. The two of them subsequently worked on mechanistic models of the interactions of ammonium and nitrate for phytoplankton growth (28, 29), nutrient acquisition and growth of migrating phytoplankton (38) and a mechanistic model of internal cell biochemistry (including iron) of phytoplankton (41). The latter was applied to modelling field data for the effect of iron addition in the Southern Ocean as part of the SOIREE experiment.

It was by no means only the phytoplankton that interested Mike. During one of the early sessions working with Flynn, he paused from typing in the equations of the NPZ model and, tapping the screen at the "Z" box, remarked "this is where the real problem rests, not with the phytoplankton, but with the zooplankton: we need to get this right". His interest in zooplankton descriptions, meshing also with that of Anderson, led to his revisiting the core structure of his classic FDM90 model to modify the zooplankton equation (44). This, one of Mike's final publications, bears witness to the character of the man, that he was never one for resting on his laurels, nor for sitting back when good science could occupy his mind.

JGOFS was never far from Mike's heart and in 1997 John Field, who was then chair of the Steering Committee, rang and invited Mike to take over the chairmanship. A new synthesis phase was starting for JGOFS, now that most seagoing activities had concluded. Mike readily accepted, looking forward to at least three years in the job. A new committee structure was set in place at the following Steering Committee meeting in Cape Town, April 1988, that was successful in stimulating analysis of the vast data sets that had accumulated during the JGOFS years (33). Mike himself wrote synthesis articles summing up the success of JGOFS and providing a vision for the future (35, 37). One of his final achievements was to edit a 297 page book "Ocean Biogeochemistry - The role of the ocean carbon cycle in global change" (39), inspired by the JGOFS programme. He wrote the final summing up chapter "JGOFS: a retrospective view" (40) and his concluding sentence was "One of our challenges over the coming years is to continue the dialogue between modellers and observationalists to ensure that, as computer power increases, ocean models include sufficient complexity to

increase our confidence, and that of society, in our predictions of the planet's future." Mike himself was a master of that effective dialogue and all those who had the pleasure of knowing and working with him will remember his openness and willingness to share ideas, his enthusiasm and positivity, his modesty, wit and, by no means least, lively banter over a pint of beer (especially so if England were winning at rugby!).

#### RETIREMENT

Mike formally retired in 2002, reaching the age of 60, although he continued working. He was elected Fellow of the Royal Society in 2000 and two years later was awarded the Challenger Society Silver Medal. In 2001 he was awarded honorary professorship in the School of Ocean and Earth Sciences, University of Southampton. Posthumously, Mike was also awarded the ASLO (Association for the Sciences of Limnology and Oceanography) John Martin award in 2010, jointly with Hugh Ducklow and Scott McKelvie, in recognition of their paper of 1990 (14) for its high impact, sustained over many years. Prior to all of this, in October 1998, Mike was diagnosed with cancer which came as a huge shock. By early 2000 it had spread and Mike resigned the JGOFS chairmanship, handing over to Hugh Ducklow. Admirably, Mike pressed ahead as best he could with his science, maintaining regular visits to Southampton. He would occasionally arrive at NOC with novel haircuts "inspired" by his bouts of radiotherapy. Mike died on 7 June 2008 and is survived by his wife Jos and son Matthew. He had a stellar career with many publications although, as he himself remarked, quality is more important than quantity, something that is all too often forgotten today. His contribution to JGOFS, both organisational and in terms of his own personal science, was immense. It should also be remembered that Mike continued going to sea throughout his career, doing his bit when it came to the necessary hard graft of sea going operations. In all, he went on 26 cruises, three as Principal Scientist, the last being Discovery 227 to the eastern North Atlantic in 1997. He was an inspirational leader, always down-to-earth and ever willing to collaborate with others in the search for a greater understanding of the marine ecosystem and its role in the global carbon cycle. He is sorely missed by all who knew him.

LIST OF ACRONYMS		
AGU	American Geophysical Union	
ASI	Advanced Science Institute	
ASLO	Association for the Sciences of Limnology and Oceanography	
CTD	Conductivity, Temperature, Depth (profiler)	
CZCS	Coastal Zone Colour Scanner	
DOM	Dissolved organic matter	
EC INTAS	International Association for the promotion of cooperation with scientists	
from the former Soviet Union (European Community)		
FDM90	The model of Fasham et al. (1990)	
FRAM	Fine Resolution Antarctic Model	
GAIM	Global Analysis, Interpretation and Modelling	
GLOBEC	Global Ocean Ecosystem Dynamics	
HadCM3LC	The Hadley Centre climate-carbon cycle model, third configuration	
HadGEM2-ES	Hadley Centre Global Environment Model 2 – Earth System	
HadOCC	Hadley Centre Ocean Carbon Cycle model	
IGBP	International Geosphere-Biosphere Programme	
IOS	Institute of Oceanographic Sciences (Wormley)	
IPCC	Intergovernmental Panel on Climate Change	
JGOFS	Joint Global Ocean Flux Study	
JRC	James Rennell Centre for Ocean Circulation	
MEDUSA	Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and	
Acidification		
NABE	North Atlantic Bloom Experiment	
NATO	North Atlantic Treaty Organisation	
NERC	Natural Environment Research Council	
NIO	National Institute of Oceanography (Wormley)	
NOCS	National Oceanography Centre, Southampton	
NPZ(D)	Nutrient-phytoplankton-zooplankton(-detritus) ecosystem model	
OCCAM	Ocean Circulation and Climate Advanced Modelling	
OGCM	Ocean general circulation model	
SCOR	Scientific Committee on Ocean Research	
SOIREE	Southern Ocean Iron RElease Experiment	

## FIGURE LEGENDS

Frontispiece: Michael Fasham [circa. 1987]

Figure 1. The Fasham-Ducklow-McKelvie model (14): summed annual flows for run 30, taken from Mike's notebook. [1988] [referred to in second paragraph, p. 10; insert near there]

Figure 2. Mike at work. Note the JGOFS homepage displayed on the computer. [1997] [insert in "JGOFS" section, round about p. 11]

Figure 3. Mike and Jos enjoying a lively meal at home [circa 1995] [insert in "SOUTHAMPTON" section, somewhere near the beginning of that section].

Figure 4. Tom Anderson, Mike and Vladimir Ryabchenko in front of Catherine's Palace, St Petersburg [1996]. [insert in "SOUTHAMPTON" section, near main paragraph of p. 14 (which refers to St Petersburg)]

REFERENCES (those which include Mike as an author)

(1) Fasham, M.J.R. 1971. A gravity survey of the Bovey Tracey Basin, Devon. *Geol. Mag.*108, 119–130.

(2) Fasham, M. J. R. 1971. Sea-going computers. In *Deep oceans* (eds. M. R. Clarke & P. J. Herring), pp. 58–60. London: Arthur Barker Ltd.

(3) Angel, M. V. & Fasham, M.J.R. 1973. SOND cruise 1965: factor and cluster analyses of the plankton results, a general summary. *J. Mar. Biol. Ass. U.K.* **53**, 185–231.

(4) Fasham, M.J.R., Angel, M.V. & Roe, H.S.J. 1974. An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy Plankton Recorder. *J. exp. mar. Biol. Ecol.* **16**, 93–112.

(5) Angel, M. V. & Fasham, M.J.R. 1975. Analysis of the vertical and geographic distribution of the abundant species of planktonic ostracods in the north-east Atlantic. *J. Mar. Biol. Ass. U.K.* **55**, 709–737.

(6) Fasham, M. J. R. & Angel, M.V. 1975. The relationship of the zoogeographic distributions of the planktonic ostracods in the north-east Atlantic to the water masses. *J. Mar. Biol. Ass. U.K.* **55**, 739–757.

(7) Fasham, M. J. R. & Pugh, P.R. 1976. Observations on the horizontal coherence of chlorophyll *a* and temperature. *Deep-Sea Res.* **23**, 527–538.

(8) Fasham, M. J. R. 1978. The statistical and mathematical analysis of plankton patchiness. *Oceanogr. Mar. Biol. Ann. Rev.* **16**, 43–79.

(9) Fasham, M. J. R. 1978. The application of some stochastic processes to the study of plankton patchiness. In *Spatial pattern in plankton communities* (ed. J.H. Steele), pp., 131–156. New York: Plenum Press.

(10) Fasham, M.J.R. & Foxton, P. 1979. Zonal distribution of pelagic Decapoda (Crustacea) in the eastern North Atlantic and its relation to the physical oceanography. *J. exp. mar. Biol. Ecol.* **37**, 225–253.

(11) Fasham, M. J. R. (ed.) 1984. *Flows of energy and materials in marine ecosystems. Theory and practice.* New York: Plenum Press, 733 pp.

(12) Fasham, M. J. R. 1985. A flow analysis of material in the marine euphotic zone. In Ecosystem theory for biological oceanography (eds. R.E. Ulanowicz & T. Platt, T.) *Can. Bull. Fish. Aquat. Sci.* 213, 139–162.

(13) Ducklow, H., Fasham, M. J. R. & Vézina, A. 1989. Derivation and analysis of flow networks for open ocean plankton ecosystems. *In Network analysis in marine ecology* (eds. F. Wulff, J.G. Field & K.H. Mann). Coastal and Estuarine Studies 32, 159–205.

(14) Fasham, M.J.R., Ducklow, H.W. & McKelvie, S.M. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.* **48**, 591–639.

(15) Fasham, M. J. R. (ed.) 1990. Joint Global Ocean Flux Study. Science Plan. *JGOFS Report* **5**, 61 pp.

(16) Watson, A. J., Robinson, C., Robertson, J.E., Williams, P.J. le B. & Fasham, M.J.R.
1991. Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic. *Nature* 350, 50–53.

(17) Fasham, M.J.R., 1993. Modelling the marine biota. In *The global carbon cycle* (ed. M. Heimann), pp. 457–504. NATO ASI Series Vol. 115. Berlin: Springer-Verlag.

(18) Evans, G.T. & Fasham, M.J.R. (eds.) 1993. *Towards a model of ocean biogeochemical processes*. NATO ASI Series Vol. I10, 350 pp. Berlin: Springer-Verlag.

(19) Evans, G.T. & Fasham, M.J.R. 1993. Themes in modelling ocean biogeochemical processes. In *Towards a model of ocean biogeochemical processes* (eds. G.T. Evans and M.J.R. Fasham), pp. 1–20. Berlin: Springer-Verlag.

(20) Kirchman, D.L., Lancelot, C., Fasham, M.J.R., Legendre, L., Radach, G. & Scott, M.
1993. Dissolved organic matter in biogeochemical models of the ocean. In *Towards a model* of ocean biogeochemical processes (eds. G.T. Evans and M.J.R. Fasham), pp. 209–226.
Berlin: Springer-Verlag.

(21) Slater, R.D., Sarmiento, J.L. & Fasham, M.J.R. 1993. Some parameteric and structural simulations with a three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. In *Towards a model of ocean biogeochemical processes* (eds. G.T. Evans and M.J.R. Fasham), pp. 261–294. Berlin: Springer-Verlag.

(22) Lochte, K., Ducklow, H.W., Fasham, M.J.R. & Stienen, C. 1993. Plankton succession and carbon cycling at 47 N 20 W during the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Res. II* **40**, 91–114.

(23) Robinson, A. R., McGillicuddy, D.J., Calman, J., Ducklow, H.W., Fasham, M.J.R.,
Hoge, F.E., Leslie, W.G., McCarthy, J.J., Podewski, S., Porter, D.L., Saure, G. & Yoder, J.A.
1993. Mesoscale and upper ocean variabilities during the 1989 JGOFS bloom study. *Deep-Sea Res. II* 40, 9–35.

(24) Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R. & Evans, G.T. 1993. A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Global Biogeochem. Cycles* **7**, 417–450.

(25) Weeks, A. R., Fasham, M.J.R., Aiken, J., Harbour, D., Read, J.F. & Bellan, I. 1993. The spatial and temporal development of the spring bloom during the JGOFS North Atlantic Bloom Experiment, 198. *J. Mar. Biol. Ass. U.K.* **73**, 253–282.

(26) Fasham, M.J.R. & Evans, G.T. 1995. The use of optimization techniques to model marine ecosystem dynamics at the JGOFS station at 47°N 20°W. *Phil. Trans. R. Soc. Lond. B* 348, 203–209.

(27) Kagan, B.A., Popova, E.E., Ryabchenko, V.A. & Fasham, M.J.R. 1995. Short-term oscillations in the ecosystem of the ocean upper mixed layer: the existence domain. *Dokl. Akademii Nauk*, **345**, 544–548 (in Russian).

(28) Flynn, K. J., Fasham, M.J.R. & Hipkin, C.R. 1997. Modelling the interactions between ammonium and nitrate uptake in marine phytoplankton. *Phil. Trans. Roy. Soc. Lond. B* **352**, 1625–1645.

(29) Flynn, K. J. & Fasham, M.J.R. 1997. A short version of the ammonium-nitrate interaction model. *J. Plankton Res.* **19**, 1881–1897.

(30) Popova, E. E., Fasham, M.J.R., Osipov, A.V. & Ryabchenko, V.A. 1997. Chaotic behaviour of an ocean ecosystem model under seasonal external forcing. *J. Plankton Res.* **19**, 1495–1515.

(31) Ryabchenko, V. A., Fasham, M.J.R., Kagan, B.A. & Popova, E.E. 1997. What causes short-term oscillations in ecosystem models of the ocean mixed layer? *J. Mar. Syst.* **13**, 33–50.

(32) Ryabchenko, V. A., Gorchakov, V.A. & Fasham, M.J.R. 1998. Seasonal dynamics and biological productivity in the Arabian Sea euphotic zone as simulated by a three-dimensional ecosystem model. *Global Biogeochem. Cycles* **12**, 501–530.

(33) Fasham, M.J.R. 1998. JGOFS: the synthesis stage. US JGOFS News 9(2), 13.14.

(34) Fasham, M. J. R., Boyd, P.W. & Savidge, G. 1999. Modeling the relative contributions of autotrophs and heterotrophs to carbon flow at a Lagrangian JGOFS station in the northeast Atlantic: The importance of DOC. *Limnol. Oceanogr.* **44**, 80–94.

(35) Fasham, M.J.R. & Evans, G.T. 2000. Advances in ecosystem modelling within JGOFS. In *The changing ocean carbon cycle: a mid-term synthesis of the Joint Global Ocean Flux Study* (eds. H.W. Ducklow, J.G. Field & R. Hanson), pp. 417–446. Cambridge Univ. Press.

(36) Popova, E. E., Ryabchenko, V.A. & Fasham, M.J.R. 2000. Biological pump and vertical mixing in the Southern Ocean: Their impact on atmospheric CO<sub>2</sub>. *Global Biogeochem. Cycles* **14**, 477–498.

(37) Fasham, M.J.R., Baliño, B.M. & Bowles, M.C. 2001. A new vision of ocean biogeochemistry after a decade of the Joint Global Ocean Flux Study (JGOFS). *Ambio Special Rep.* **10**, 31 pp.

(38) Flynn, K. J. & Fasham, M.J.R. 2002. A modelling exploration of vertical migration by phytoplankton. *J. theor. Biol.* **218**, 471–484.

(39) Fasham, M. J. R. (ed.) 2003. *Ocean biogeochemistry*. *The role of the ocean carbon cycle in global change*. Berlin: Springer-Verlag, 297 pp.

(40) Fasham, M. J. R. 2003. JGOFS: a retrospective view. In *Ocean biogeochemistry*. *The role of the ocean carbon cycle in global change*. (ed. M. J. R. Fasham), pp. 269–277. Berlin: Springer-Verlag.

(41) Fasham, M.J.R., Flynn, K.J., Pondaven, P., Anderson, T.R. & Boyd, P.W. 2006. Development of a robust ecosystem model to predict the role of iron on biogeochemical cycles: a comparison of results for iron-replete and iron-limited areas, and the SOIREE ironenrichment experiment. *Deep-Sea Res. I* **53**, 333–366.

(42) Popova, E. E., Coward, A.C., Nurser, A.G., de Cuevas, B., Fasham, M.J.R. & Anderson,
T.R. 2006. Mechanisms controlling primary and new production in a global ecosystem model
– Part I: Validation of the biological simulation. *Ocean Sci.* 2, 249–266.

(43) Anderson, T.R., Ryabchenko, V.A., Fasham, M.J.R. & Gorchakov, V.A. 2007.
Denitrification in the Arabian Sea: A 3D ecosystem modeling study. *Deep-Sea Res. I* 54, 2082–2119.

(44) Mitra, A., Flynn, K.J. & Fasham, M.J.R. 2007. Accounting for grazing dynamics in nitrogen-phytoplankton-zooplankton models. *Limnol. Oceanogr.* **52**, 649–661.

ADDITIONAL REFERENCES (those which do not include Mike as an author)

Coward, A.C., Killworth, P.D. & Blundell, J.R. 1994. Tests of a two-grid world ocean model. *J. Geophys. Res.* **99**, 22725–22735.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408, 184–187.

Ducklow, H.W. 1986. Bacterial biomass in warm-core Gulf Stream ring 82-B: mesoscale distributions, termporal changes and production. *Deep-Sea Res.* **33**, 1789–1812.

Evans, G.T. & Parslow, J.S. 1985. A model of annual plankton cycles. *Biol. Oceanogr.* **3**, 327–347, 1985.

Najjar, R.G., Sarmiento, J.L. & Toggweiler, J.R. 1992. Downward transport and fate of organic matter in the ocean: Simulations with a general circulation model. *Global Biogeochem. Cycles* **6**, 45–76.

Palmer, J.R. & Totterdell, I.J. 2001. Production and export in a global ocean ecosystem model. *Deep-Sea Res. I* 48, 1169–1198.

Platt, T., Mann, K.H. & Ulanowicz, R.E. 1981. *Mathematical models in biological oceanography*. Paris: UNESCO Press, 57 pp.

Steele, J.H. 1974. The structure of marine ecosystems. Harvard Univ. Press, 128 pp.

Thorrington-Smith, M. 1974. The distribution of abundance, species diversity, and phytohydrographic regions in West Indian Ocean phytoplankton. *J. mar. biol. Ass. India* **16**, 371–380.

Yool, A., Popova, E.E. & Anderson, T.R. 2011. MEDUSA-1.0: a new intermediate complexity plankton ecosystem model for the global domain. *Geosci. Model. Dev.* **4**, 381–417.



233x298mm (300 x 300 DPI)

http://mc.manuscriptcentral.com/rsbm



175x135mm (300 x 300 DPI)



152x101mm (300 x 300 DPI)



97x95mm (300 x 300 DPI)





88x59mm (600 x 600 DPI)

http://mc.manuscriptcentral.com/rsbm

Fasham, M. J. R. 1970. The use of a shipborne computer for navigation. In *Electronic engineering in ocean technology*, pp. 259–270. London: Institute of Electronic and Radio Engineers.

Fasham, M.J.R. 1971. A gravity survey of the Bovey Tracey Basin, Devon. *Geol. Mag.* **108**, 119–130.

Fasham, M. J. R. 1971. Sea-going computers. In *Deep oceans* (eds. M. R. Clarke & P. J. Herring), pp. 58–60. London: Arthur Barker Ltd.

Stacey, A. P., Fasham, M.J.R., Black, D.I. & Scrutton, R.A. 1971. Design and application of digital filters for the Graf-Askania Gss2, No.11 sea gravity meter. *Mar. Geophys. Res.* **1**, 220–32.

Angel, M.V. & Fasham, M.J.R. 1971. Species assemblages and their depth distributions off the Canary Islands. In *The ocean world* (ed. M. Uda), pp. 269–270. Japan Society for the Promotion of Science.

Angel, M. V. & Fasham, M.J.R. 1973. SOND cruise 1965: factor and cluster analyses of the plankton results, a general summary. *J. Mar. Biol. Ass. U.K.* **53**, 185–231.

Angel, M. V. & Fasham, M.J.R. 1974. SOND cruise 1965: further factor-analyses of the plankton data. *J. Mar. Biol. Ass. U.K.* **54**, 879–894.

Fasham, M.J.R., Angel, M.V. & Roe, H.S.J. 1974. An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy Plankton Recorder. *J. exp. mar. Biol. Ecol.* **16**, 93–112.

Angel, M. V. & Fasham, M.J.R. 1975. Analysis of the vertical and geographic distribution of the abundant species of planktonic ostracods in the north-east Atlantic. *J. Mar. Biol. Ass. U.K.* **55**, 709–737.

Fasham, M. J. R. & Angel, M.V. 1975. The relationship of the zoogeographic distributions of the planktonic ostracods in the north-east Atlantic to the water masses. *J. Mar. Biol. Ass. U.K.* **55**, 739–757.

Kahn, D. A., Pugh, P.R., Fasham, M.J.R. & Harris, M.J. 1975. Underwater logarithmic irradiance meter for primary production and associated studies. In *Instrumentation in oceanography*, pp. 81–90. London: Institute of Electronic and Radio Engineers.

Fasham, M. J. R. 1976. Misalignment angle and calibration of a two-component electromagnetic log. *J. Navigation* **29**, 76–81.

Fasham, M. J. R. & Pugh, P.R. 1976. Observations on the horizontal coherence of chlorophyll *a* and temperature. *Deep-Sea Res.* **23**, 527–538.

Fasham, M. J. R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. *Ecology* **58**, 551–561.

Fasham, M. J. R. & Pugh, P.R. 1977. Horizontal patchiness of plankton caused by internal waves. *Deep-Sea Res.* 24, 323–323.

Fasham, M. J. R. 1978. The statistical and mathematical analysis of plankton patchiness. *Oceanogr. Mar. Biol. Ann. Rev.* **16**, 43–79.

Fasham, M. J. R. 1978. The application of some stochastic processes to the study of plankton patchiness. In *Spatial pattern in plankton communities* (ed. J.H. Steele), pp., 131–156. New York: Plenum Press.

Fasham, M.J.R. & Foxton, P. 1979. Zonal distribution of pelagic Decapoda (Crustacea) in the eastern North Atlantic and its relation to the physical oceanography. *J. exp. mar. Biol. Ecol.* **37**, 225–253.

Fasham, M. J. R., 1981. Analytic food web models. In *Mathematical models in biological oceanography* (eds. T. Platt, K.H. Mann, and R.E. Ulanowicz), pp. 54–65. Paris: UNESCO Press.

Fasham, M. J. R. 1981. Statistical mechanics. In *Mathematical models in biological oceanography* (eds. T. Platt, K.H. Mann, and R.E. Ulanowicz), pp. 79–85. Paris: UNESCO Press.

Fasham, M. J. R. 1981. Stochastic modelling and power spectral representation. In *Mathematical models in biological oceanography* (eds. T. Platt, K.H. Mann, and R.E. Ulanowicz), pp. 86–91. Paris: UNESCO Press.

Angel, M.V., Fasham, M.J.R. & Rice, A.L. 1981. Marine biology needed to assess the safety of a program of disposal of high level radioactive wastes in the ocean. In *Marine Environmental Pollution, vol. 2, Dumping and Mining* (ed. R.A. Geyer), pp. 297–312. Amsterdam: Elsevier.

Fasham, M. J. R., Holligan, P.M. and Pugh, P.R. 1983. The spatial and temporal development of the spring phytoplankton bloom in the Celtic Sea, April 1979. *Prog. Oceanogr.* **12**, 87–145.

Fasham, M. J. R. & Platt, T. 1983. Photosynthetic response of phytoplankton to light: a physiological model. *Proc. Roy. Soc. Lond. B* **219**, 355–370.

Fasham, M. J. R., Pugh, P.R., Griffiths, D. & Wheaton, J.E.G. 1983. A submersible fluorometer for the detection of chlorophyll. *Radio and Electronic Engineer* 53, 21–24.

Angel, M.V. & Fasham, M.J.R. 1983. Eddies and biological processes. In *Eddies in marine science* (ed. A.R. Robinson), pp. 492–524. Berlin: Springer Verlag.

Irwin, B., Platt, T., Lindley, P., Fasham, M.J.R. & Jones, K. 1983. Phytoplankton productivity in the vicinity of a front, S.W. of the Azores during May 1981. *Can. Data Rep. Fish. Aquat. Sci.* **400**, 101pp.

Fasham, M. J. R. (ed.) 1984. *Flows of energy and materials in marine ecosystems. Theory and practice.* New York: Plenum Press, 733 pp.

Legendre, L., Collos, Y., Elbrachter, M., Fasham, M.J.R., Gieskes, W.W.C. Herbland, A., Holligan, P.M., Margalef, R., Perry, M.J., Platt, T., Sakshaug, E. & Smith, D.F. 1984. Studies on marine autotrophs: recommendations for the 1980's. In *Flows of energy and material in marine ecosystems. Theory and practice* (ed. M.J.R. Fasham), pp. 629–639. New York: Plenum Press.

Fasham, M. J. R. 1985. A flow analysis of material in the marine euphotic zone. In Ecosystem theory for biological oceanography (eds. R.E. Ulanowicz & T. Platt, T.) *Can. Bull. Fish. Aquat. Sci.* 213, 139–162.

Fasham, M. J. R., Platt, T., Irwin, B. & Jones, K. 1985. Factors affecting the spatial pattern of the deep chlorophyll maximum in the region of the Azores Front. *Prog. Oceanogr.* **14**, 129–165.

Fasham, M. J. R. 1986. UK ocean fluxes modelling: a discussion. US GOFS Planning Report 4, 42–50.

Fasham, M. J. R. 1986. An ecosystem model of the carbon flow in the Celtic Sea. *Challenger Society Newsletter* **22**, 10–11.

Field, J.G., Wulff, F.V., Allen, P.M., Fasham, M.J.R., Flos, J., Frontier, S., Kay, J.J., Silvert, W. & Trainor, L., 1986. Ecosystem theory in relation to unexploited marine ecosystems. *Can. Bull. Fish. Aquat. Sci.* **213**, 241–247.

Roe, H.S.J., Domanski, PA. & Fasham, M.J.R. 1986. Great Meteor East: an interim report on biological sampling and general relationship to physical oceanography. Institute Oceanographic Sci. Rep. 225, 60 pp.

Simpson, W. R., Gwilliam, T.J.P., Lawford, V.A., Fasham, M.J.R. & Lewis, A.R. 1987. *In situ* deep water particle sampler and real-time sensor package with data from the Madeira Abyssal Plain. *Deep-Sea Res.* **34**, 1477–1497.

Heyraud, M., Domanski, P., Cherry, R.D. & Fasham, M.J.R. 1988. Natural tracers in dietary studies: data for <sup>210</sup>Po and <sup>210</sup>Pb in decapod shrimp and other pelagic organisms in the Northeast Atlantic Ocean. *Mar. Biol.* **97**, 507–519.

Ducklow, H., Fasham, M. J. R. & Vézina, A. 1989. Derivation and analysis of flow networks for open ocean plankton ecosystems. *In Network analysis in marine ecology* (eds. F. Wulff, J.G. Field & K.H. Mann). Coastal and Estuarine Studies 32, 159–205.

Sarmiento, J.L., Fasham, M.J.R. & Siegenthaler, U. 1989. Simulations of the carbon cycle in the oceans. U.S. Dept. of Energy 1989 Annual Technical Report, 67 pp.

Sarmiento, J. L., Fasham, M.J.R., Siegenthaler, U., Najjar, R.G. & Toggweiler, J.R. 1989. In *Models of Chemical Cycling in the Oceans: Progress Report II*. Ocean Tracers Laboratory Report 6, 46 pp. New Jersey: Princeton University.

Fasham, M.J.R., Ducklow, H.W. & McKelvie, S.M. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.* **48**, 591–639.

Fasham, M. J. R. (ed.) 1990. Joint Global Ocean Flux Study. Science Plan. *JGOFS Report* 5, 61 pp.

Denman, K., Fasham, M. & Zeitzschel, B. 1990. Joint Global Ocean Flux Study (JGOFS). *Oceanology International* 90, 101–108.

Weeks, A.R., Aiken, J., Bellan, I., Harbour, D. & Fasham, M.J.R., 1990. The seasonal development of the spring bloom in the North Atlantic in 1989. *Eos Transactions* **71**, 1411.

Ducklow, H. W. & Fasham, M.J.R. 1991. Bacteria in the greenhouse: modeling the role of oceanic plankton in the global carbon cycle. In *New concepts in environmental microbiology* (ed. R. Mitchell), pp. 1–31. New York: Wiley-Liss.

Fasham, M.J.R., Denman, K. & Brewer, P.G. 1991. Joint Global Ocean Flux Study: goals and objectives. In *Global environment change* (eds. R.W. Corell & P.A. Anderson), pp. 245–246. Berlin: Springer-Verlag.

Watson, A. J., Robinson, C., Robertson, J.E., Williams, P.J. le B. & Fasham, M.J.R. 1991. Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic. *Nature* **350**, 50–53.

Fasham, M.J.R., 1993. Modelling the marine biota. In *The global carbon cycle* (ed. M. Heimann), pp. 457–504. NATO ASI Series Vol. 115. Berlin: Springer-Verlag.

Evans, G.T. & Fasham, M.J.R. (eds.) 1993. *Towards a model of ocean biogeochemical processes*. NATO ASI Series Vol. 110, 350 pp. Berlin: Springer-Verlag.

Evans, G.T. & Fasham, M.J.R. 1993. Themes in modelling ocean biogeochemical processes. In *Towards a model of ocean biogeochemical processes* (eds. G.T. Evans and M.J.R. Fasham), pp. 1–20. Berlin: Springer-Verlag.

Kirchman, D.L., Lancelot, C., Fasham, M.J.R., Legendre, L., Radach, G. & Scott, M. 1993. Dissolved organic matter in biogeochemical models of the ocean. In *Towards a model of ocean biogeochemical processes* (eds. G.T. Evans and M.J.R. Fasham), pp. 209–226. Berlin: Springer-Verlag.

Slater, R.D., Sarmiento, J.L. & Fasham, M.J.R. 1993. Some parameteric and structural simulations with a three-dimensional ecosystem model of nitrogen cycling in the North

Atlantic euphotic zone. In *Towards a model of ocean biogeochemical processes* (eds. G.T. Evans and M.J.R. Fasham), pp. 261–294. Berlin: Springer-Verlag.

Fasham, M. J. R., Sarmiento, J.L., Slater, R.D., Ducklow, H.W. & Williams, R. 1993. Ecosystem behaviour at Bermuda Station "S" and Ocean Weather Station "India": A general circulation model and observational analysis. *Global Biogeochem. Cycles* **7**, 379–415.

Lochte, K., Ducklow, H.W., Fasham, M.J.R. & Stienen, C. 1993. Plankton succession and carbon cycling at 47N 20W during the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Res. II* **40**, 91–114.

Robinson, A. R., McGillicuddy, D.J., Calman, J., Ducklow, H.W., Fasham, M.J.R., Hoge, F.E., Leslie, W.G., McCarthy, J.J., Podewski, S., Porter, D.L., Saure, G. & Yoder, J.A. 1993. Mesoscale and upper ocean variabilities during the 1989 JGOFS bloom study. *Deep-Sea Res. II* **40**, 9–35.

Sarmiento, J.L., Fasham, M.J.R., Slater, R., Toggweiler, J.R. & Ducklow, H.W. 1993. The role of biology in the chemistry of  $CO_2$  in the ocean. In *Chemistry of the greenhouse effect* (ed. M. Farrell). New York: Lewis Publ.

Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R. & Evans, G.T. 1993. A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Global Biogeochem. Cycles* **7**, 417–450.

Platt, T., Sathyendranath, S., Joint, I. & Fasham, M.J.R. 1993. Photosynthesis characteristics of the phytoplankton in the Celtic Sea during late spring. *Fish. Oceanogr.* **2**, 191–201.

Weeks, A. R., Fasham, M.J.R., Aiken, J., Harbour, D., Read, J.F. & Bellan, I. 1993. The spatial and temporal development of the spring bloom during the JGOFS North Atlantic Bloom Experiment, 198. *J. Mar. Biol. Ass. U.K.* **73**, 253–282.

Fasham, M. J. R. 1995. Variations in the seasonal cycle of biological production in sub-arctic oceans – a model sensitivity analysis. *Deep-Sea Res. I* **42**, 1111–1149.

Fasham, M.J.R. & Evans, G.T. 1995. The use of optimization techniques to model marine ecosystem dynamics at the JGOFS station at 47°N 20°W. *Phil. Trans. R. Soc. Lond. B* **348**, 203–209.

Kagan, B.A., Popova, E.E., Ryabchenko, V.A. & Fasham, M.J.R. 1995. Short-term oscillations in the ecosystem of the ocean upper mixed layer: the existence domain. *Dokl. Akademii Nauk*, **345**, 544–548 (in Russian).

Kagan, B.A., Popova E.E., Ryabchenko V.A. & Fasham M.J.R. 1996. Short-period fluctuations in the ecosystem of the upper mixed layer of the ocean and regions of their existence. *Trans. Russian Acad. Sci.* **345A**, 166–171.

Smith, C. L., Richards, K.J. & Fasham, M.J.R. 1996. The impact of mesoscale eddies on plankton dynamics in the upper ocean. *Deep-Sea Res. I* **43**, 1807–1832.

Flynn, K. J., Fasham, M.J.R. & Hipkin, C.R. 1997. Modelling the interactions between ammonium and nitrate uptake in marine phytoplankton. *Phil. Trans. Roy. Soc. Lond. B* **352**, 1625–1645.

Flynn, K. J. & Fasham, M.J.R. 1997. A short version of the ammonium-nitrate interaction model. *J. Plankton Res.* **19**, 1881–1897.

Popova, E. E., Fasham, M.J.R., Osipov, A.V. & Ryabchenko, V.A. 1997. Chaotic behaviour of an ocean ecosystem model under seasonal external forcing. *J. Plankton Res.* **19**, 1495–1515.

Ryabchenko, V. A., Fasham, M.J.R., Kagan, B.A. & Popova, E.E. 1997. What causes short-term oscillations in ecosystem models of the ocean mixed layer? *J. Mar. Syst.* **13**, 33–50.

Ryabchenko, V. A., Gorchakov, V.A. & Fasham, M.J.R. 1998. Seasonal dynamics and biological productivity in the Arabian Sea euphotic zone as simulated by a three-dimensional ecosystem model. *Global Biogeochem. Cycles* **12**, 501–530.

Herring, P. J., Fasham, M.J.R., Weeks, A.R., Hemmings, J.C., Roe, H.S.J., Pugh, P.R., Holley, S., Crisp, N. & Angel, M.V. 1998. Across-slope relations between the biological populations, the euphotic zone and the oxygen minimum layer off the coast of Oman during the southwest monsoon (August, 1994). *Prog. Oceanogr.* **41**, 69–109.

Merrett, N. R. & M. J. R. Fasham, 1998. Demersal ichthyofaunal distribution in the abyssal North Atlantic revisited: the effect of sample size on ordination. *Mar. Ecol. Prog. Ser.* **173**, 267–274.

Fasham, M.J.R. 1998. JGOFS: the synthesis stage. US JGOFS News 9(2), 13.14.

Fasham, M. J. R., Boyd, P.W. & Savidge, G. 1999. Modeling the relative contributions of autotrophs and heterotrophs to carbon flow at a Lagrangian JGOFS station in the northeast Atlantic: The importance of DOC. *Limnol. Oceanogr.* **44**, 80–94.

Fasham, M.J.R. & Evans, G.T. 2000. Advances in ecosystem modelling within JGOFS. In *The changing ocean carbon cycle: a mid-term synthesis of the Joint Global Ocean Flux Study* (eds. H.W. Ducklow, J.G. Field & R. Hanson), pp. 417–446. Cambridge Univ. Press.

Popova, E. E., Ryabchenko, V.A. & Fasham, M.J.R. 2000. Biological pump and vertical mixing in the Southern Ocean: Their impact on atmospheric CO<sub>2</sub>. *Global Biogeochem. Cycles* **14**, 477–498.

Fasham, M.J.R., Baliño, B.M. & Bowles, M.C. 2001. A new vision of ocean biogeochemistry after a decade of the Joint Global Ocean Flux Study (JGOFS). *Ambio Special Rep.* **10**, 31 pp.

 Anderson, T.R., Spall, S.A., Yool, A., Cipollini, P., Challenor, P.G. & Fasham, M.J.R. 2001. Global fields of sea surface dimethylsulfide predicted from chlorophyll, nutrients and light. *J. Mar. Syst.* **30**, 1–20.

Martin, A. P., Richards, K.J. & Fasham, M.J.R. 2001. Phytoplankton production and community structure in an unstable frontal region. *J. Mar. Syst.* **28**, 65–89.

Yool, A. & Fasham, M.J.R. 2001. An examination of the "continental shelf pump" in an open ocean general circulation model. *Global Biogeochem. Cycles* **15**, 831–844.

Baliño, B. M., Fasham, M.J.R. & Bowles, M.C. 2001. Ocean biogeochemistry and global change: JGOFS research highlights 1988–2000. *IGBP Science* **2**, 1–32.

Flynn, K. J. & Fasham, M.J.R. 2002. A modelling exploration of vertical migration by phytoplankton. *J. theor. Biol.* **218**, 471–484.

Popova, E. E., Lozano, C.J., Srokosz, M.A., Fasham, M.J.R., Haley, P.J. & Robinson, A.R. 2002. Coupled 3D physical and biological modelling of the mesoscale variability observed in north-east Atlantic in spring 1997: biological processes. *Deep-Sea Res. I* **49**, 1741–1768.

Fasham, M. J. R. (ed.) 2003. *Ocean biogeochemistry*. *The role of the ocean carbon cycle in global change*. Berlin: Springer-Verlag, 297 pp.

Fasham, M. J. R. 2003. JGOFS: a retrospective view. In *Ocean biogeochemistry*. *The role of the ocean carbon cycle in global change*. (ed. M. J. R. Fasham), pp. 269-277. Berlin: Springer-Verlag.

Flynn, K. J. & Fasham, M.J.R. 2003. Operation of light-dark cycles within simple ecosystem models of primary production and the consequences of using phytoplankton models with different abilities to assimilate N in darkness. *J. Plankton Res.* **25**, 83–92.

Hemmings, J. C. P., Srokosz, M.A., Challenor, P. & Fasham, M.J.R. 2003. Assimilating satellite ocean-colour observations into oceanic ecosystem models. *Phil. Trans. Roy. Soc. Lond. A* **361**, 33–39.

Srokosz, M. A., Martin, A.P. & Fasham, M.J.R. 2003. On the role of biological dynamics in plankton patchiness at the mesoscale: an example from the eastern North Atlantic Ocean. *J. Mar. Res.* **61**, 517–537.

Hemmings, J. C. P., Srokosz, M.A., Challenor, P. & Fasham, M.J.R. 2004. Split-domain calibration of an ecosystem model using satellite ocean colour data. *J. Mar. Syst.* **50**, 141–179.

Fasham, M.J.R., Flynn, K.J., Pondaven, P., Anderson, T.R. & Boyd, P.W. 2006. Development of a robust ecosystem model to predict the role of iron on biogeochemical cycles: a comparison of results for iron-replete and iron-limited areas, and the SOIREE ironenrichment experiment. *Deep-Sea Res. I* **53**, 333–366. Popova, E. E., Coward, A.C., Nurser, A.G., de Cuevas, B., Fasham, M.J.R. & Anderson, T.R. 2006. Mechanisms controlling primary and new production in a global ecosystem model – Part I: Validation of the biological simulation. *Ocean Sci.* **2**, 249–266.

Wallhead, P. J., Martin, A.P., Srokosz, M.A. & Fasham, M.J.R. 2006. Accounting for unresolved spatial variability in marine ecosystems using time lags. *J. Mar. Res.* **64**, 881–914.

Anderson, T.R., Ryabchenko, V.A., Fasham, M.J.R. & Gorchakov, V.A. 2007. Denitrification in the Arabian Sea: A 3D ecosystem modeling study. *Deep-Sea Res. I* 54, 2082–2119.

Guirey, E. J., Bees, M.A., Martin, A.P., Srokosz, M.A. & Fasham, M.J.R. 2007. Emergent features due to grid-cell biology: Synchronisation in biophysical models. *Bull. Mathematical Biol.* **69**, 1401–1422.

Mitra, A., Flynn, K.J. & Fasham, M.J.R. 2007. Accounting for grazing dynamics in nitrogenphytoplankton-zooplankton models. *Limnol. Oceanogr.* **52**, 649–661.

Martin, A. P., Zubkov, M.V., Fasham, M.J., Burkill, P.H. & Holland, R.J. 2008. Microbial spatial variability: An example from the Celtic Sea. *Prog. Oceanogr.* **76**, 443–465.

