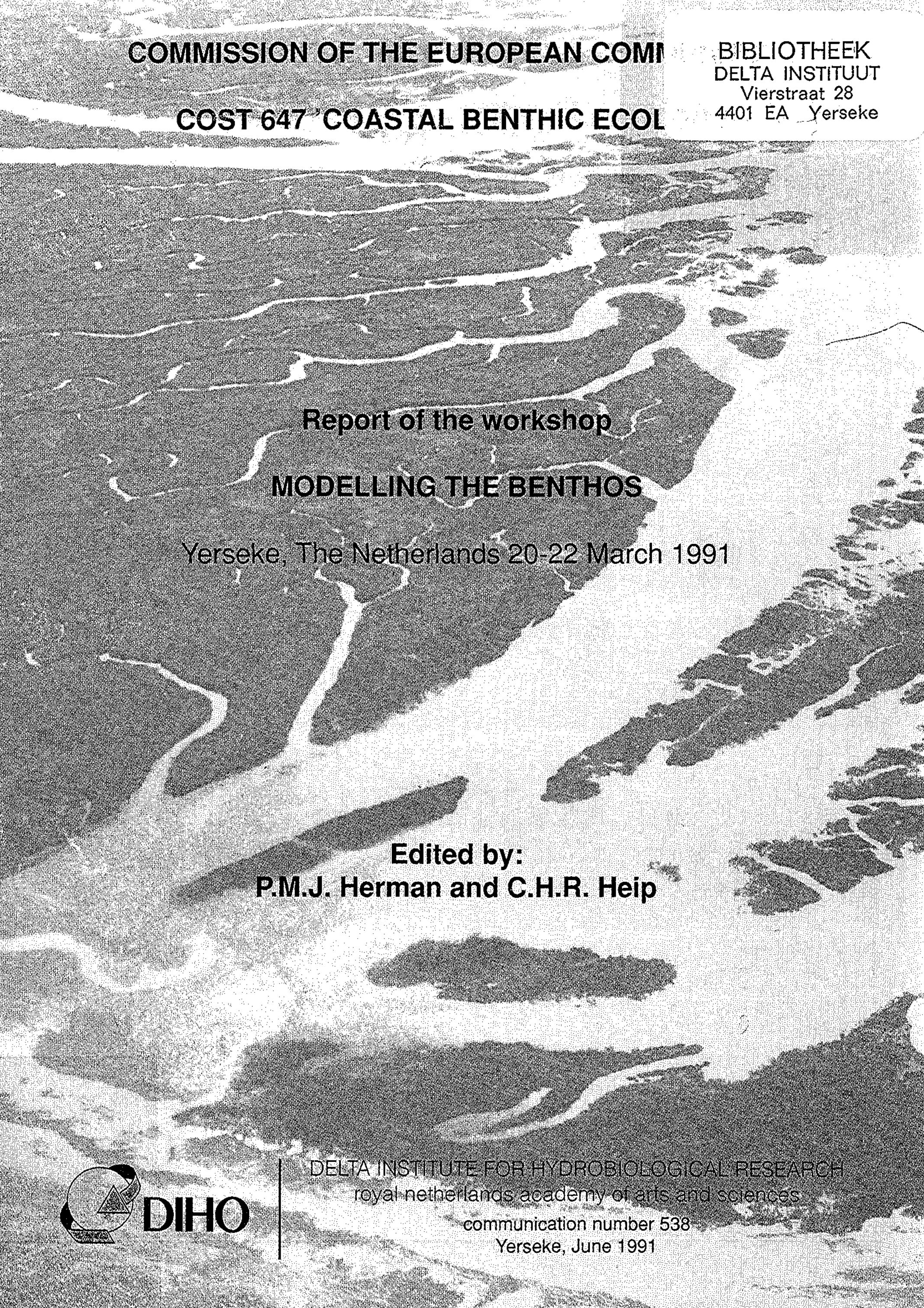


COMMISSION OF THE EUROPEAN COMM

COST 647 'COASTAL BENTHIC ECOL

Report of the workshop

MODELLING THE BENTHOS

Yerseke, The Netherlands 20-22 March 1991

Edited by:
P.M.J. Herman and C.H.R. Heip

DIHO
DELTA INSTITUTE FOR HYDROBIOLOGICAL RESEARCH
royal netherlands academy of arts and sciences
communication number 538
Yerseke, June 1991

COMMISSION OF THE EUROPEAN COMMUNITIES

COST 647 'COASTAL BENTHIC ECOLOGY'

Report of the workshop

MODELLING THE BENTHOS

Yerseke, The Netherlands 20-22 March 1991

Edited by:
P.M.J. Herman and C.H.R. Heip

DELTA INSTITUTE FOR HYDROBIOLOGICAL RESEARCH
royal netherlands academy of arts and sciences
communication number 538
Yerseke, June 1991

LIST OF PARTICIPANTS

W. Armonies
Biologische Anstalt Helgoland
Wattenmeerstation Sylt
D-2282 List
Germany

J. Baretta
NIOZ
P.O. Box 59
1790 AB Den Burg, Texel
The Netherlands

K.-G. Barthel
Commission Eur. Communities
Dir. Gen XII / E
Wetstraat 200
B-1049 Brussels
Belgium

B. Brinkman
RIN
P.O. Box 59
1790 AB Den Burg, Texel
The Netherlands

P. Chardy
IFREMER - Brest
BP 70
29263 Plouzane
France

J. Davey
Plymouth Marine Laboratory
Prospect Place
West Hoe, Plymouth
Devon PL1 3DH
United Kingdom

K. Essink
Ministry of Transport and Public Works, Tidal Waters Division
P.O. Box 207
9750 AE Haren
The Netherlands

C. Heip
Delta Institute for Hydrobiological Research
Vierstraat 28
4401 EA Yerseke
The Netherlands

P.M.J. Herman
Delta Institute for Hydrobiological Research
Vierstraat 28
4401 EA Yerseke
The Netherlands

J.N. Jensen
Nat. Env. Research Inst.
Jaegersborg Alle 1B
DK-2920 Charlottenlund
Denmark

S.A. de Jong
Ministry of Transport and Public Works, North Sea Directorate
P.O. Box 5807
2280 HV Rijswijk
The Netherlands

A. Josefson
Nat. Environmental Res. Institute
Jaegersborg Alle 1B
DK-2920 Charlottenlund
Denmark

P. Legendre
Dept. Biological Sciences
University of Montreal
C.P. 6128 Succ. A
Montreal, Quebec H3C 3J7
Canada

Jian Li
Zoology Institute
State University of Gent
K.L. Ledeganckstraat 35
B-9000 Gent
Belgium

J. van der Meer
NIOZ
P.O. Box 59
1790 AB Den Burg, Texel
The Netherlands

Y. Monbet
IFREMER - Brest
BP 70
29263 Plouzane
France

A. Nicolaidou
University 1
Zoological Laboratory
Panepistimiopolis
GR-17551 Athens
Greece

B. O'Connor
Aquafact International Services Ltd.
7, Innovation Centre
Galway
Ireland

T. Prins
Ministry of Transport and Public Works, Tidal Waters Division
P.O. 8039
4330 EA Middelburg.
The Netherlands

P. Radford
Plymouth Marine Laboratory
Prospect Place
West Hoe, Plymouth
Devon Pl1 3DH
United Kingdom

H. Scholten
Delta Institute for Hydrobiological Research
Vierstraat 28
4401 EA Yerseke
The Netherlands

W. Silvert
Bedford Inst. of Oceanography
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2
Canada

A. Smaal
Ministry of Transport and Public Works, Tidal Waters Division
P.O. 8039
4330 EA Middelburg
The Netherlands

K. Soetaert
Brussels Free University
Pleinlaan 2
1050 Brussel
Belgium

M. Thessalou-Legaki
University 1
Zoological Laboratory
Panepistimiopolis
GR-17551 Athens
Greece

E. Thiébault
Station biologique de Roscoff
BP 74
29680 Roscoff Cedex
France

M. van der Tol
Ministry of Transport and Public Works, Tidal Waters Division
P.O. Box 439
4330 AK Middelburg
The Netherlands

CONTENTS

OBJECTIVES OF THE WORKSHOP

Peter M.J. Herman and Carlo Heip

Delta Institute for Hydrobiological Research
Vierstraat 28, 4401 EA Yerseke, The Netherlands

AIMS

Within the COST 647 project it has become increasingly clear that it is not possible to understand benthic dynamics from a purely population dynamical point of view. The concept of the benthos as an isolated subsystem governed by internal interactions (and 'key species') is not sufficient to understand the often widely divergent evolutions in the benthos of closeby stations.

In models of the major carbon and nutrient flows in ecosystems the benthos is a difficult part to handle. There is a lack of operational concepts for modelling work : what are relevant functional groups, important processes and major environmental determinants? How can these be translated into models and measured in experimental conditions or field populations? Apart from conceptual difficulties, technical problems arise because the (macro)benthos has much larger characteristic time scales than the pelagos and the benthic microbiota from which it depends.

The Yerseke workshop was set up to bring together modellers and field workers to discuss new ways towards understanding benthic dynamics. Discussion between scientists following the analytical and the observational path aimed at the formulation of new ideas for closer cooperation.

The workshop focused on meio- and macrobenthic dynamics. We are, of course, aware of the importance of other processes, e.g. in the benthic microbiological world. For this workshop, however, we want to consider them part of the 'outside world'. This implies that relations with microbiological processes (e.g. feeding, bioturbation) would be viewed from one side only : that of the macro- and meiobenthos.

QUESTIONS

Participants were requested to contribute to the discussion by adressing questions relevant to the general objectives. A (non-exhaustive) list of such questions was posed :

- What are relevant functional groups to summarize multi-species data on benthos, with respect to their role in the ecosystem. How consistent are these groups in their reaction to the environment, in their major process rates etc...

- How can the occurrence of relevant functional groups be predicted ? What benthic community can be expected where, and why. How do settling processes influence the spatial distributions? Can this be derived from other components in an ecosystem model ?

- What are the major processes in the benthos, that should be incorporated in benthic models. ('If it is there, what does it do') What are the important rates in these processes. How can these rates be measured ? How are the processes regulated by other components in the environment (e.g. what regulates grazing or bioturbation rate ?)

- What are the spatial scales of importance to benthic dynamics, and can these be incorporated into models?

- What models are available now as tools for study of the dynamics of benthos? What is their theoretical basis, how do they work out in practice, where can they be improved ? How can technical difficulties, e.g. the differences in characteristic time scales, be solved?

- What do general ecosystem models expect as output from their 'benthic submodel', and what can they deliver as input (e.g. food concentration and quality etc....)

PARTICIPANTS

Participants came from 9 countries. The workshop brought together scientists with quite different backgrounds and specializations. Field biologists, experimental biologists, ecosystem modellers, statisticians confronted their views, concepts, methods. Of course, this did not lead immediately to a solution of all the problems addressed by this workshop. However, several of these questions were addressed directly by the presentations in the workshop. Contributions varied in approach from a review of the current state-of-the art to provocative statements of insufficiencies in current methods, from cautious incorporation of all relevant processes to experimental exploratory analysis of simplified models. The most interesting confrontation was between the statistical approach and the dynamical system simulation. Both approaches 'model' certain data sets, but come from different worlds. This *choc des cultures* yielded interesting ideas for further development.

The benthos is a particularly promising ecosystem component for methodological developments. Much effort has been devoted in the past decades to collect extensive data sets on benthic populations. On the other hand, the study of benthic processes needs conceptualization. The statistical study of patterns in the data hopefully could lead to simulation models which are better able to grasp the essence of the benthic dynamics. We hope that the discussions in the Yerseke workshop have helped towards achieving this goal.

TRANSPORT OF BENTHOS WITH TIDAL WATERS: ANOTHER SOURCE OF INDETERMINATION

Werner Armonies

Biologische Anstalt Helgoland, Wattenmeerstation Sylt, D-2282 List

ABSTRACT

In the Wadden Sea, many benthic species may actively enter the water column and drift around with the tidal currents. Consequently abundance in the sediment decreases where they start drifting and increases where they return to the sediment. During very calm weather, abundance changes in some species may be predictable or even partly reversible. In the latter case, high and low abundance of a species may regularly alternate in the same site at about weekly intervals. But already moderate wind may cause unpredictable changes of abundance, depending on both the topography of the habitat and the wind direction. Numerical abundance of drifters in the water column indicates that drifting is an essential part of lifestyle in at least some species such as the copepod Harpacticus flexus (copepodites and adults) or the bivalves Macoma balthica and Cerastoderma edule (juveniles of 1 to 6 mm length). Some of the consequences of the drifting of benthos for both ecological field studies and benthic modelling are, (1) A hydrographic submodel needs to be included in any benthos model. (2) Abundance of benthos capable of drifting may dramatically change over short periods. (3) These changes of abundance may be reversible; finding two times the same abundance at one site does not imply that abundance was constant over the intermittent period. (4) Species that are able to drift may exploit additional habitats for short periods and suffer from hazards absent in the sediment.

INTRODUCTION

Species abundance data are basic for any benthic model, either directly or indirect e.g. as biomass value. Apart from planktonic larvae, most of the benthic infauna is often regarded as quasi-sessile. Therefore, quantitative sampling is often restricted to a few periods of the year and abundance is estimated from these few counts. However, recent studies demonstrated that many benthic species may drift around with the tidal waters. These species include meio-fauna as well as macrofauna, and active swimmers as well as species which are unable to swim actively.

MEIOBENTHIC DRIFTERS

Some harpacticoid species such as *Harpacticus flexus* and *Tachidius discipes* were traditionally classified as being surface dwellers in the sediment. However, quantitative sampling of the water column above intertidal sandflats revealed that they are highly active swimmers, above all at night. In the special case of these species it is unknown why they enter the water column. Generally, feeding, mating, moulting, and escape from unfavourable conditions prevailing in the sediment are discussed. But whatever may be the reason, their swimming has a number of unexpected consequences.

(1) During rather calm weather, abundance of benthic swimmers in shallow waters above intertidal sandflats may exceed abundance of zooplankton in the same size class. On an average, abundance in the water column of small animals and their biomass may be at night about twice as high as during daytime (Fig. 1).

(2) While swimming, the specimens are transported with the tidal currents. This may lead to strange situations, e.g. when the tidal water above an upper intertidal sandflat area contained 3-times more "benthic" harpacticoids than the sediment (Fig. 2).

(3) Most meiobenthic swimmers strictly prefer the nighttime for their excursions into the water column and they return to the sediment at sunrise. Experimental shading of the sediment in the field indicates that this timing pattern is not caused by endogeneous factors but at least in part depends on light intensity (Fig. 3). Shading of the sediment by phytoplankton blooms had the same effect (Fig. 4) but specific differences appeard in the case of shading by seafoam (Fig. 5). Possibly some species are attracted by the foam which might serve as an additional food resource. As a result, the density of phyto-plankton may change the abundance of meiobenthos in the water column and hence transportation rates and local abundance in the sediment.

(4) Preferential swimming in the dark results in changes of abundance in the sediment, depending on the direction of the tidal waters during night. Nocturnal flood tides cause an onshore transport of meiobenthic swimmers and ebb tides an offshore transport (Fig. 6). As a result, abundance in the sediment may switch between low and high in about weekly intervals (Fig. 7). Such regularly alternating patterns are only found during periods with calm weather. Wind driven currents may change the transport direction of drifters in a rather unpredictable way (Fig. 8).

CONCLUSIONS FROM MEIOBENTHIC DRIFT

In taxa containing swimming species, single counts of abundance can only yield a snap-shot of continuous change. This is inappropriate for most field studies and gives unreliable input values for numerical models. A benthic model resticted to the sediment cannot predict the outcome and consequences of drifting. Therefore I suggest at least a hydrographic submodel should be included. Because of a significant response of meiobenthic swimmers to shading of the sediment by both phytoplankton and seafoam, a submodel on phytoplankton dynamics might be helpful for at least some species. Reliable abundance data for model input may be obtained by either very large scale spatial sampling or by periodical sampling of the studied habitats.

MACROBENTHIC DRIFTERS

Drifting in the water column above intertidal flats is not restricted to meiobenthos but also occurs in postlarval macrobenthic species. In a pilot study of a multidisciplinary ecosystem research project just starting now (SWAP = Sylter Wattenmeer Austausch Prozesse, meaning Exchange processes in the Wadden Sea around the Island of Sylt) the mud snail *Hydrobia ulvae*, the clam *Macoma balthica* and the cockle *Cerastoderma edule* proved to be abundant drifters. The bivalves were juveniles of 1 to 4 mm (cockles) or 1 to 6 mm (clams) length drifting with the help of mucus threads. Floating snails included all sizes. These species show dial, lunar and seasonal patterns of abundance in the water column.

Cockles were more abundant in nocturnal catches than during daytime while the reverse was true for mud snails (Fig. 9, 10). A lunar cycle was most pronounced in clams (Fig. 11) and still evident in cockles (Fig. 12) but the cycles are not the same. No lunar pattern is evident in drifting mud snails. Instead their abundance in the water column correlated significantly negative with wind velocity (Fig. 13, 14). This is due to wind driven currents which modify the direction of the tidal currents.

In July, an average of 3,000 and up to 10,000 individuals of the three species passed each meter of low tide line during a single tidal cycle. These numbers indicate that drift of postlarval age stages is essential for both distributional patterns and dispersal. At least in the bivalve species drifting seems to be part of the ordinary life-cycle.

CONCLUSIONS FROM MACROBENTHIC DRIFT

(1) Because of the seasonally high abundance of macrobenthic drifters in the water column above intertidal flats, I suggest drifting should be included in benthic models. And because of the temporal rhythms of water column entrance and their dependence on topography, hydrography, and meterology, respective submodels are also needed. Together with the consequences on modelling derived from meiobenthic drift, the result is an ecosystem model rather than an independent benthos model.

(2) At least in the case of macrobenthos, migrations cover the entire Wadden area from the high tidal flats to the shallow subtidal. With respect to migrations, this seems to be the least possible size of a modelled area.

(3) All the examples on drifting benthos derived from shallow waters of the Wadden Sea. Because of a lack of studies which performed periodic sampling

on very short time scales, close to nothing of these migrations was known a few years ago. Today the same still applies to deeper subtidal sites. Since many of the species living in the Wadden Sea also occur in the subtidal, migrations of benthic animals may also occur at these sites. Instead of the tidal currents, residual currents might be more effective in these deeper waters.

Fig. 1. Composition of Mesozooplankton above a tidal flat of the northern Wadden Sea during a dial and a nocturnal high tide

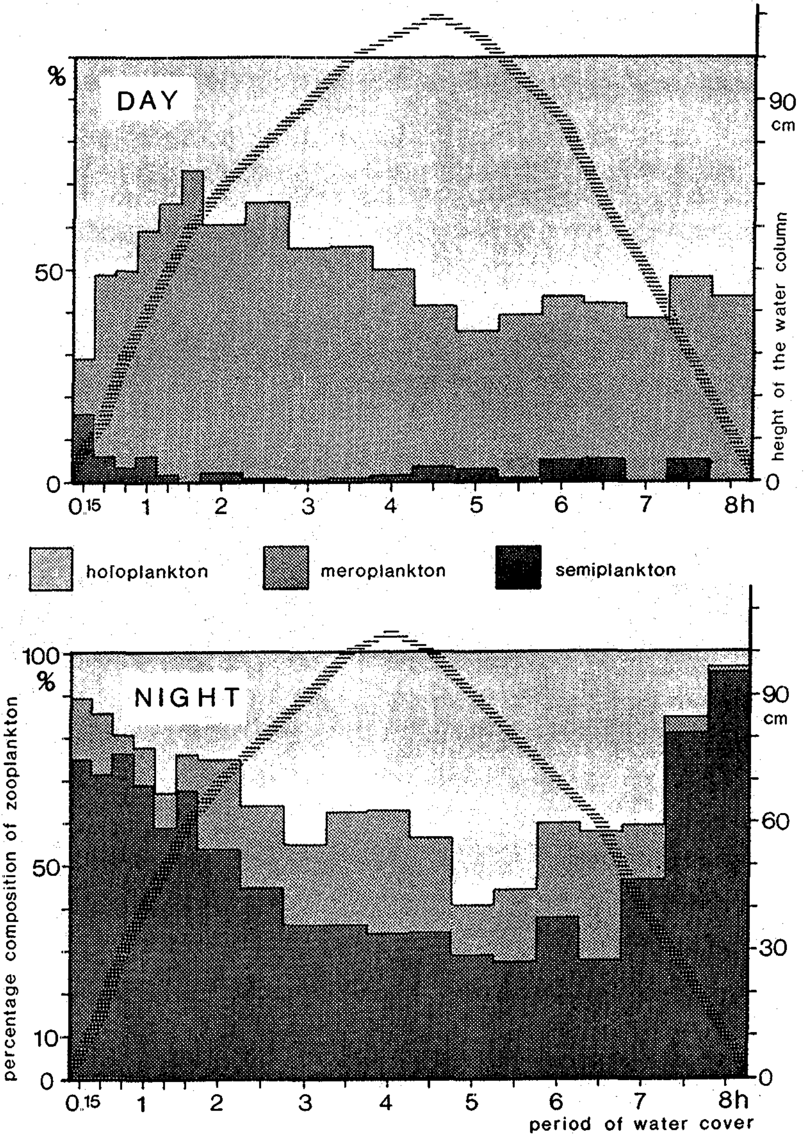
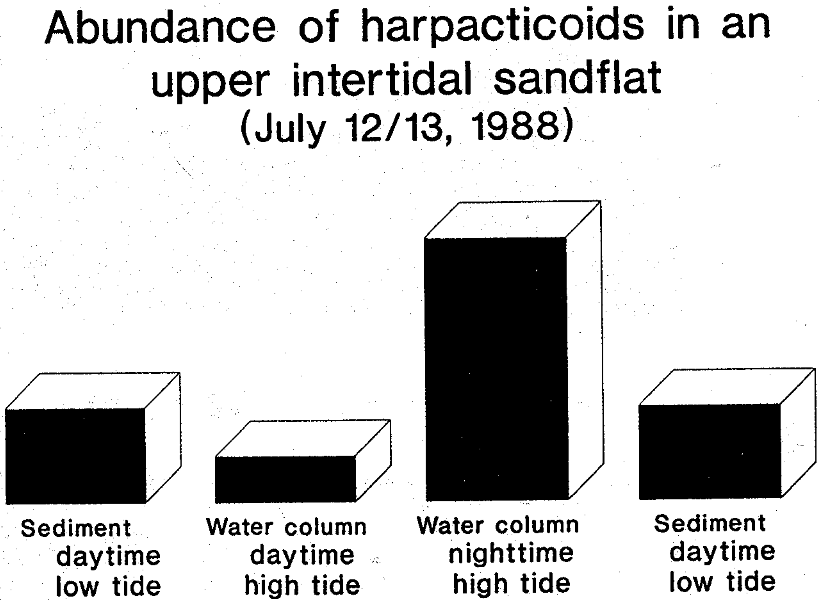


Fig. 2. Abundance of meiobenthic harpacticoids in the water column above a high intertidal sand flat during a nocturnal high tide and in the sediment during the preceding and following low tides. The 3-fold higher abundance refers to actively swimming specimens which were imported from seaward sites



During the nocturnal high tide, the water column contained 3-fold more harpacticoids than the sediment during both the preceding and succeeding low tides

Fig. 3. Shading of sandy intertidal sediment by a black box during daytime increases abundance of meiobenthic swimmers in the water column. Transparent boxes served as a control

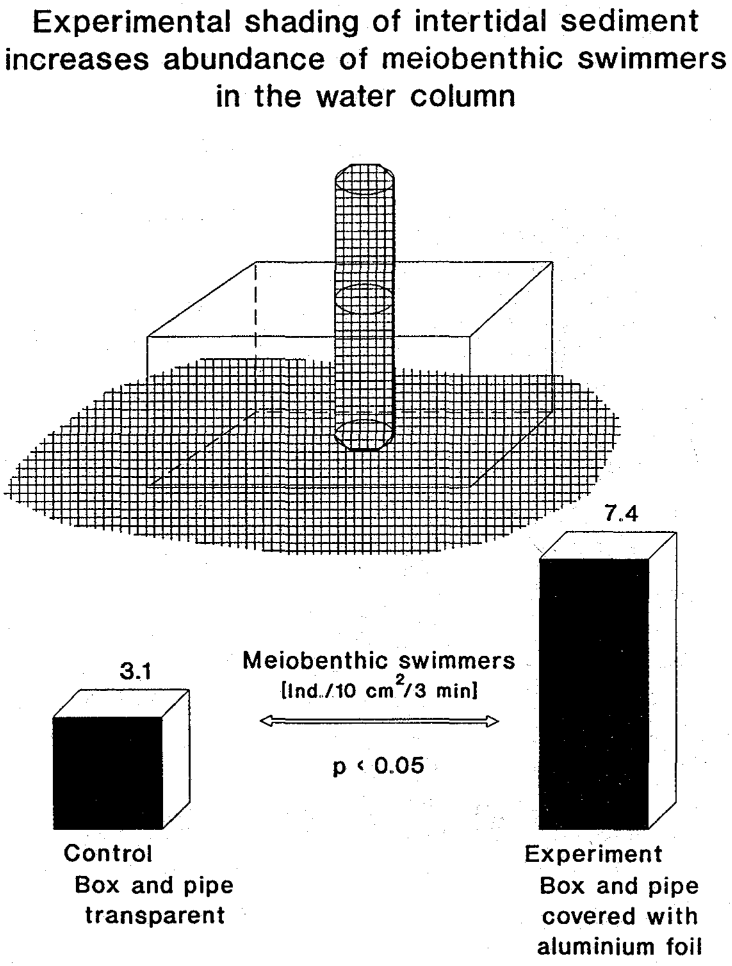


Fig. 4. Shading of the sediment by *Phaeocystis* colonies increases abundance of meiobenthic swimmers in the water column

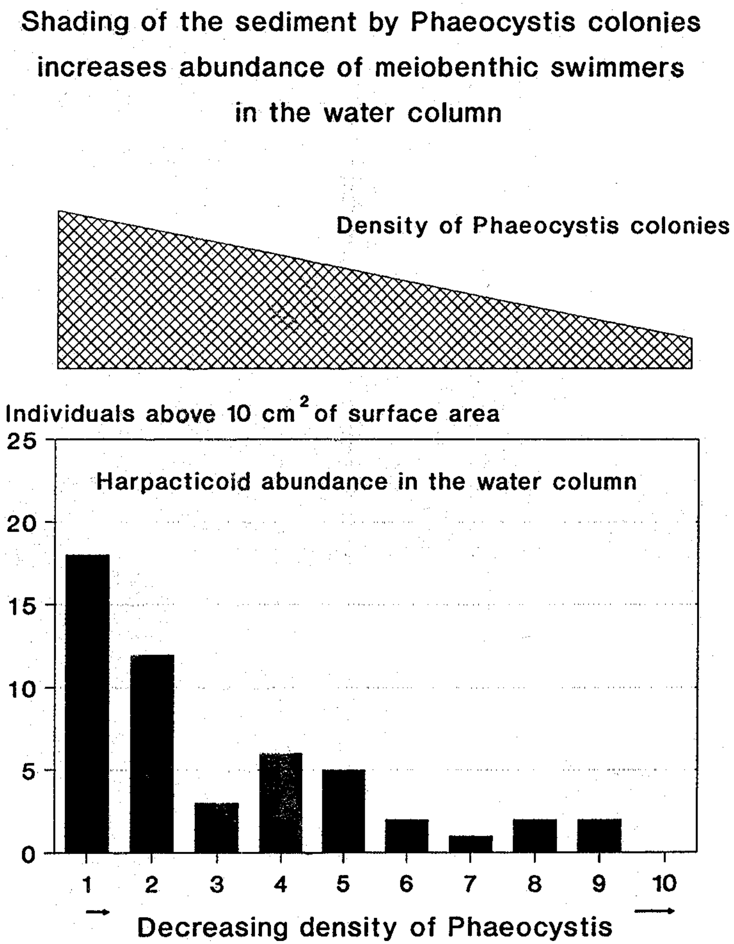


Fig. 5. Differential response of two meiobenthic harpacticoid species towards shading by seafoam

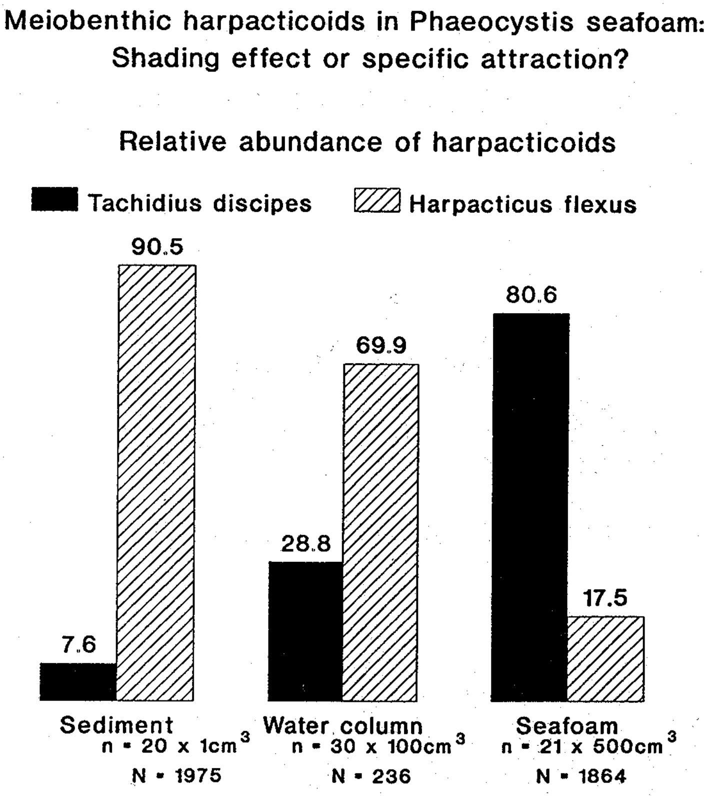
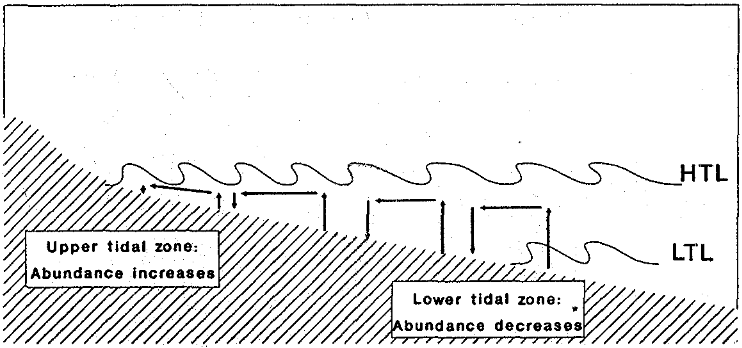


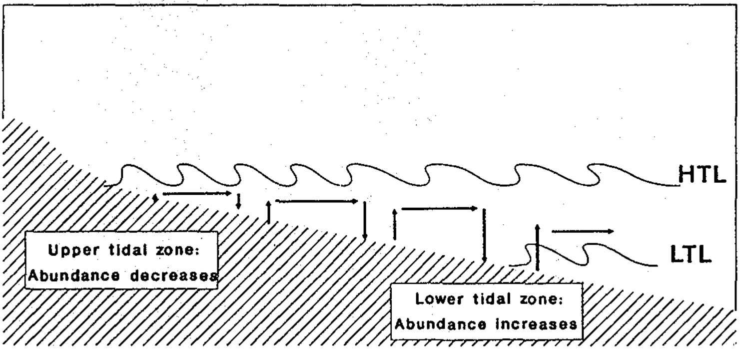
Fig. 6. The direction of transport of meiobenthic drifters depends on the state of the tide

Meiobenthic drift during nocturnal swimming

(1) Onshore transport during nocturnal flood tides

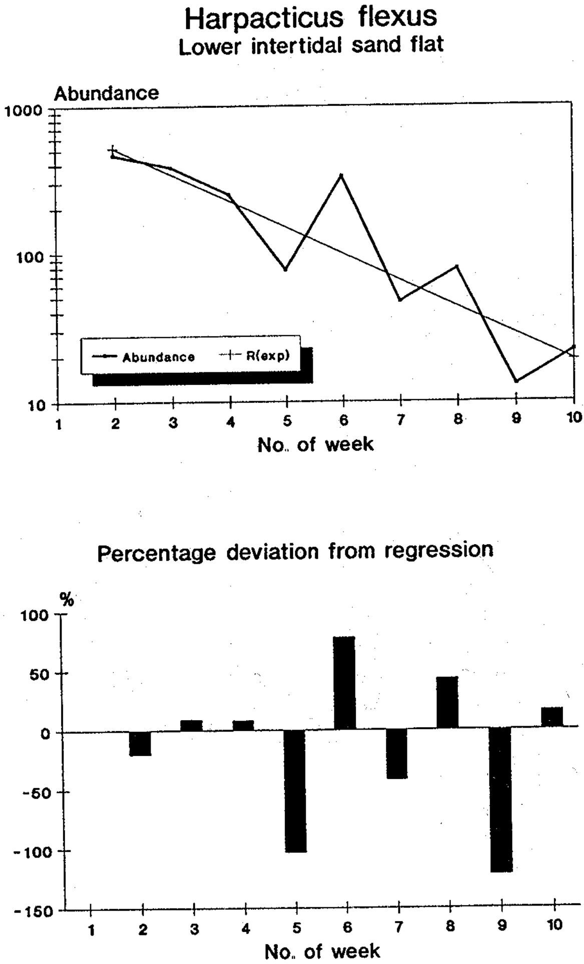


(2) Offshore transport during nocturnal ebb tides



* unless compensated for by subtidal imigration

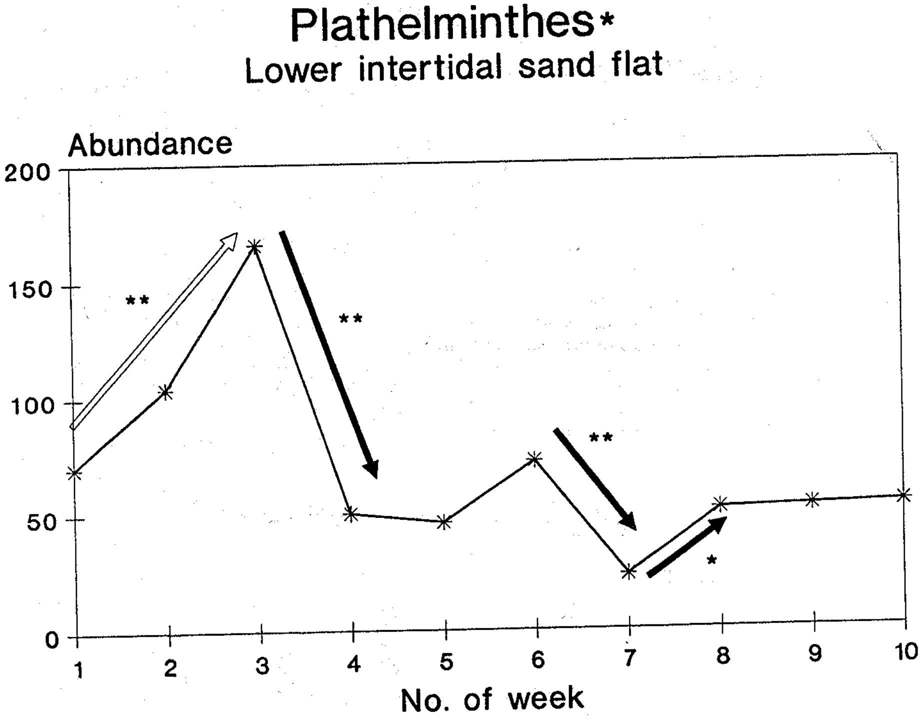
Fig. 7. Abundance of *Harpacticus flexus* in the sediment of a sandy lower intertidal site. Periodical abundance changes result from the differential direction of transport with the tidal waters during nocturnal swimming



Harpacticus flexus
Lower intertidal sand flat

Percentage deviation from regression

Fig. 8. Abundance of plathelminths in the sediment of a lower intertidal sand flat sampled at weekly intervals. Changes of abundance are statistically significant (arrows) but because of wind driven currents the direction of change is unpredictable



* without Pogaina suecica

Fig. 9. Abundance of mud snails in drift nets which were placed 20 cm above the sediment on a sandy tidal flat at low tide level. Abundance are numbers caught per 2 nets with an opening 20 cm in-diameter per high tide. Unpublished data, June/July 1990

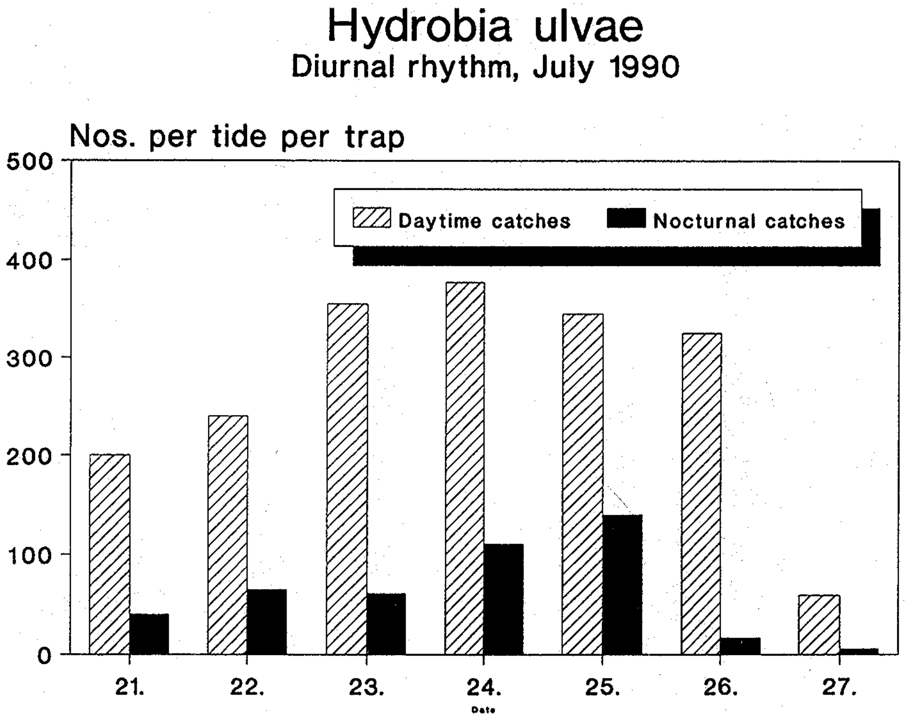


Fig 10. Abundance of cockles in drift nets. For further explanations see Fig. 9

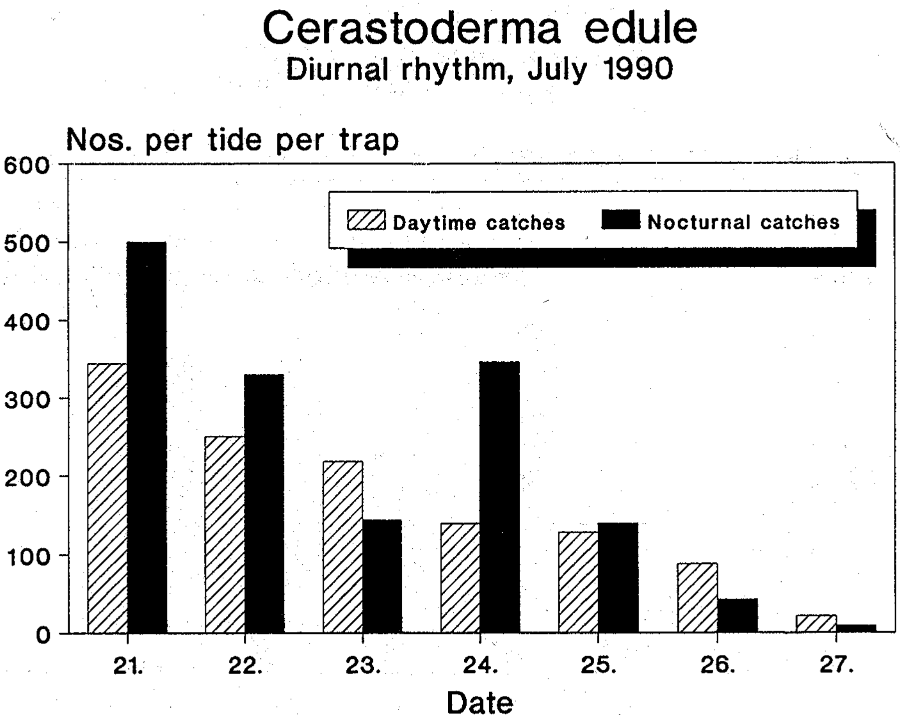
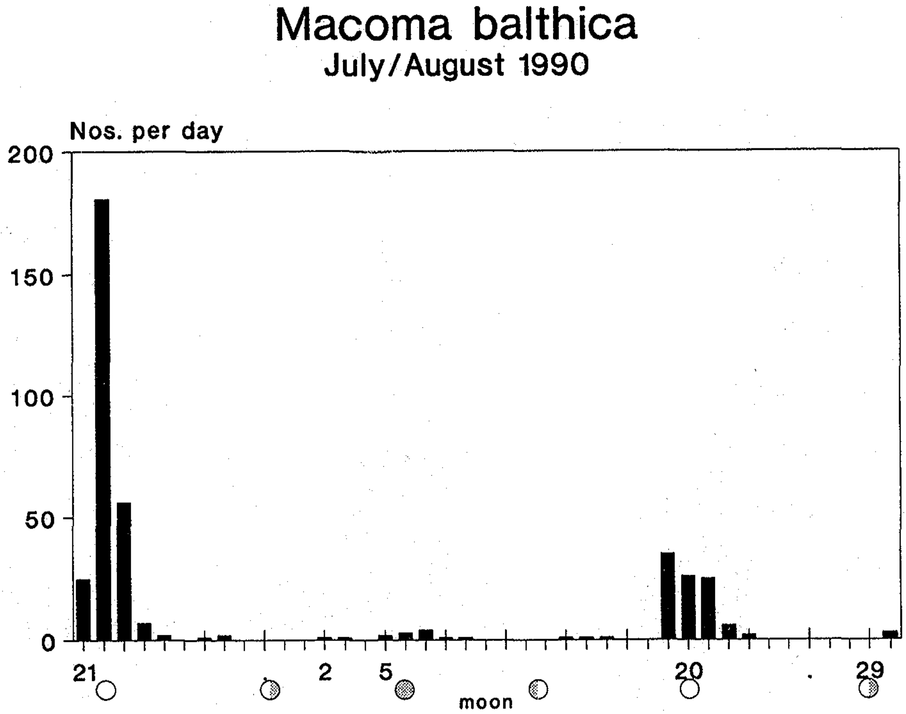


Fig.11. Lunar rhythms in drifting *Macoma balthica.* Clams preferentially entered the water column during new moon and were less affected by by an intermittend storm than other taxa (unpublished data, July/August 1990)



For their migrations clams prefer the new moon phase

Fig.12. Lunar rhythm in drifting *Cerastoderma edule*. Cockles prefer to enter the water column during the full and new moon spring tides (unpublished data, July/August 1990)

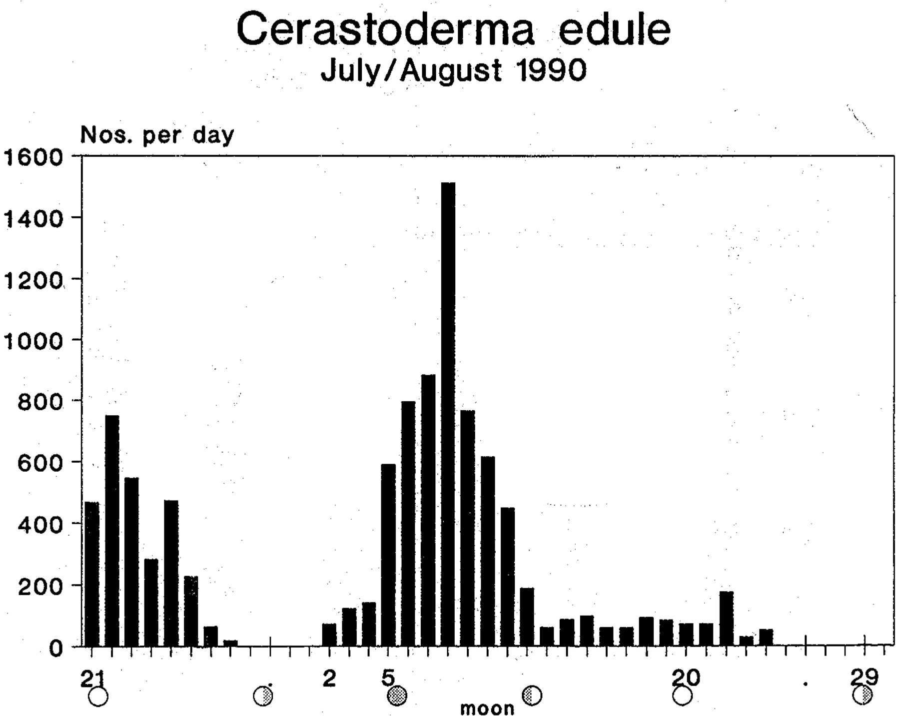


Fig.13. Abundance of mud snails in the water column decreases with increasing wind velocity

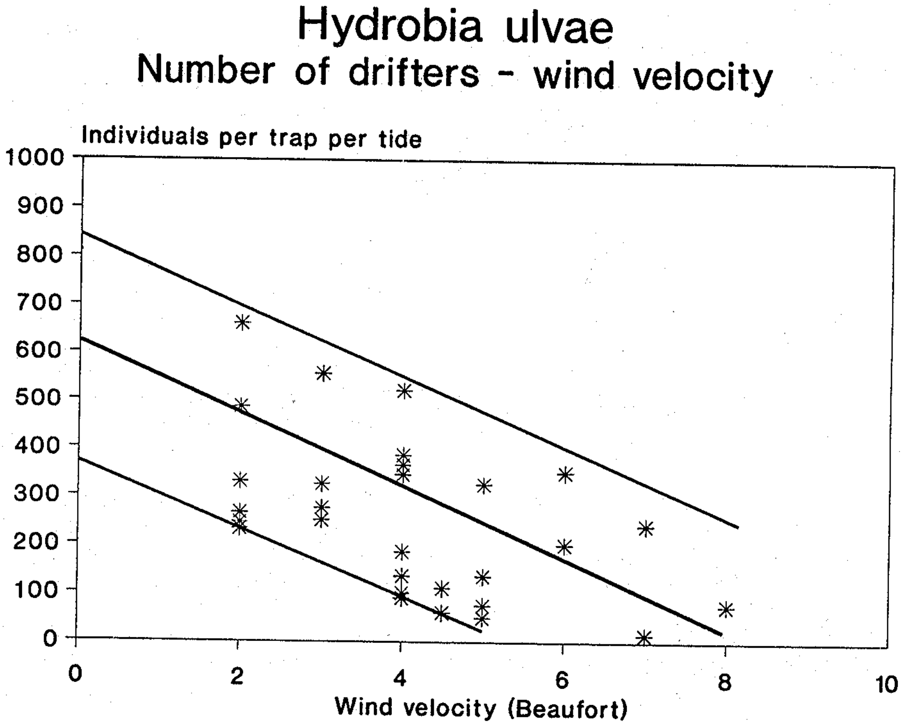
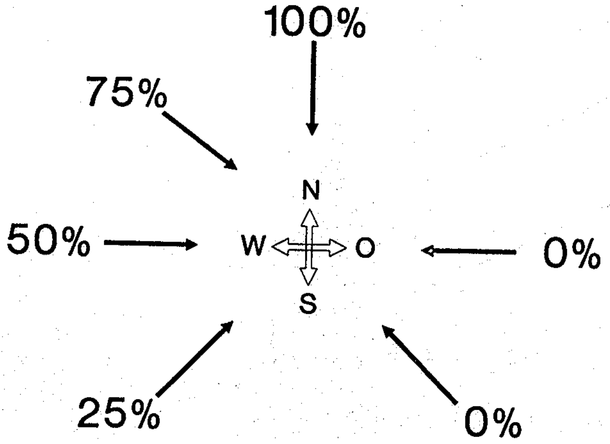


Fig.14. Relative abundance of mud snails in the water column correlates with the wind direction. Northern wind always yielded catches higher than overall mean, catches during periods with eastern wind were all beyond average. This is a consequence of the topography of the studied area



Hydrobia ulvae

Percentage of tides with the number of drifters higher than average sorted according to wind direction

NORTH SEA MODELLING

J.W. Baretta, P. Ruardij

Nederlands Instituut voor Onderzoek der Zee (NIOZ),
P.O. Box 59, 1790 AB Den Burg, Texel, NL

INTRODUCTION

A group of marine research institutes from countries around the North Sea has initiated a project ERSEM (European Regional Seas Ecosystem Model) to construct, calibrate and validate an ecosystem model of the North Sea under the umbrella of the Marine Science and Technology programme (MAST) of the EC.

The major participants in this project are:

- Nederlands Instituut voor Onderzoek der Zee, Texel (NIOZ)
- Plymouth Marine Laboratory, Plymouth (PML)
- Institut für Meereskunde, Hamburg (IfM)
- Marine Laboratory Aberdeen, Aberdeen (MLA)
- Water Quality Institute, Horsholm, DK (WQI)
- University of Oldenburg, Oldenburg (UO)
- Centre d'Estudis Avancats, Blanes, Spain (CEAB)
- University of Gothenburg, Gothenburg (UG)
- Askö Laboratory, Stockholm (AL)

The objective of this project is to provide a basis to support decision making in environmental quality and biological resource management by developing suites of modules for combination into ecosystem models aimed at answering particular biological and environmental management questions, pertaining to the North Sea. In particular we aim to address questions that are probably caused by eutrophication effects, such as the seasonal occurrence of anoxic conditions in stratified waters, changes in autotrophic and heterotrophic production and trends in relative nutrient availability.

The model suite will integrate the current views on the functioning of marine ecosystems into generic formulations of the processes by which carbon and nutrients (N, P, Si) are cycled in shelf seas, including the associated oxygen dynamics.

Existing models

Many generic formulations of marine ecological processes already exist. The participants in this project have themselves developed and published descriptions of various ecological processes (see references). Many more alternative process models have been published in the scientific literature elsewhere. The existing time-dependent horizontal box models for regions of the North Sea (Fransz & Verhagen, 1985; Mommaerts et al., 1984; Markus et al., 1988) have emphasized biological detail in the pelagic system at the expense of detail in physical structure and transport processes. These, and other models, describe the seasonal cycle of plankton dynamics using vertically integrated equations (cf. Pace et al., 1984); very few models include the vertical structure of the water column (Kiefer & Kremer, 1981; Stigebrandt & Wulff, 1987, Radach & Moll, 1989). To date, only a few attempts have been made to integrate into a single model all the processes which define a total coastal ecosystem (see Kremer & Nixon, 1978; Radford, 1979; Baretta & Ruardij, 1988; de Vries et al., 1988). The difficulty in achieving such a synthesis is to model each process with a similar degree of detail, since some system processes have been exhaustively researched and thus can be modelled with a lot of detail, whereas many other essential system processes have hardly been studied at all and thus only may be modelled very coarsely. As a consequence there are numerous vertically integrated plankton/nutrients models, but, for example, almost no models of benthic processes, nor of the "microbial loop" in coastal- and shelf ecosystems. Thus there is an urgent need for process studies, especially of the pelagic and benthic small food web, which may be expected to contribute significantly to nutrient regeneration.

The ability to simulate nutrient cycles is closely related to the ability to simulate plankton blooms. The present models are able to simulate the gross characteristics of the spring plankton bloom, the order of magnitude of the biomass produced and the timing of the bloom within a range of one to two months (Radach, 1983). Simulation of summer and fall blooms is less successful and in the simulated annual cycle they are usually underestimated. This is partly due to a lack of knowledge about nutrient regeneration, both in the water column and at the sediment-water interface, but also to the lack of coupling in the models between biology, chemistry and physics (Jones & Henderson, 1987).

To a large extent, the approach has been to treat nutrient dynamics within the framework of plankton dynamics, without taking into consideration chemical processes affecting the speciation and bio- availability of nutrients, and only partly taking into account the influence of sediment-water exchange processes. On the other hand, benthic nutrient dynamics are usually viewed from a pore-water perspective, focussing primarily on understanding and describing nutrient profiles and less on the actual fluxes across the sediment- water interface (e.g. Berner, 1980; Blackburn & Sörensen, 1988). As a consequence there are deficiencies in existing descriptions of the relationship between pelagic and benthic nutrient cycles, although some attempts have been made (Billen & Lancelot, 1988).

Simulation packages/languages

To reach the objective stated above, we need suitable tools, of which modelling software may be the most important one. Therefore, the first priority is to make available to all participating institutes a software environment suitable for model development and testing, including a model framework which can be used as a test-bed and at the same time defines the overall logical structure. This is essential because the structure of complex ecosystems is rather ill-defined. It ensures that, even though development is proceeding at different sites, we are working within the same system definition.

Such software, designed to facilitate ecological modelling, has proved invaluable to the successful completion of complex multidisciplinary studies (Radford 1971). Radford (1979) used the commercial simulation package "Continuous System Modelling Program" (IBM 1967) as a computing environment to model the Bristol Channel and Severn Estuary. More recently Baretta & Ruardij (1988) reported on the development of a package known as BAHBOE which they used to construct their Ems and western Wadden Sea models (EON, 1988). The WQI is developing a software package for modelling fjord ecosystems in collaboration with the Danish Hydraulic Institute (DHI). Delft Hydraulics has developed DELWAQ (Postma, 1988) as a general framework for water quality and ecological modelling.

These packages all have different strengths and weaknesses and to create an optimized software package is one of the tasks of this project. However, here the requirement is more for technology than science. The simulation software packages available to the project partners now or still under development will be compared early in the project and the combination of choice will be made available to project partners. PML will document, maintain and distribute this package.

However, to get the modelling itself started quickly, NIOZ and the University of Oldenburg will port the BAHBOE package to run under the UNIX operating system and distribute it to the project partners.

Model development

Marine ecosystem models usually have been produced by individuals or very small groups, with limited interaction between the modelling scientists and the experimentalists studying the various aspects of the system to be modelled. Such an approach has the drawback that it is very difficult for the experimentalists to set up their experiments such that the results may be used to test the model validity.

Only rarely have multidisciplinary teams of physicists, chemists, biologists and ecologists worked together closely to formulate a mathematical model of a marine ecosystem. The team approach has been used successfully in modelling estuarine ecosystems, however. Baretta & Ruardij (1988) describe the work of such a team which modelled the Ems Estuary. Similarly, the Severn Estuary has been modelled by a team from the Institute for Marine Environmental Research (now PML) (Radford, 1979).

An effective way to integrate the efforts of such a team into mathematical models is a workshop approach (cf. Holling, 1978). The definition of how the various processes are to be modelled and the testing of the resulting modules, will be done at a series of modelling workshops where modelers and experimentalists together interact on-line with the model as they have implemented it. Obviously, model development and refinement will not be confined to the duration of these workshops, but acceptance testing and inclusion of modules into the final model suite will be done at the workshops, thereby closely involving non-modelling, experimental scientists into the whole process.

THE STRUCTURE OF THE MODEL

The model comprises three submodels, each describing the dynamics of a subsystem:

- The pelagic submodel, containing descriptions of the major biological and chemical processes in the water column.
- The benthic submodel, describing the biological and chemical processes in the sediment underlying the water column.
- The physical submodel, which describes the physical processes in the water column (stratified or homogeneous) and, by incorporating vertical transport processes, also couples the pelagic and benthic system. This submodel thus ensures the integration of the physical environment and biological and chemical dynamics of the pelagic and benthic systems.

The model structure described here defines a box of water and underlying sediment and what happens in there. Though this box may be of arbitrary surface area and volume, it is clear that a regional sea such as the North Sea cannot be modelled as one box since the North Sea is far from homogeneous. We can take the morphological differences into account by spatially differentiating the whole sea into a number of such boxes (we propose using the ICES-boxes) and driving the physical interactions (mainly transport processes) between the boxes through the physical submodel.

An important aspect of this structure is that the pelagic and the benthic submodel together, representing the dynamics in the water column of an arbitrary area and its underlying sediment, are formulated exactly the same in all boxes but their behaviour will depend on the physical conditions in the boxes. In other words, the spatially and temporally different effects of horizontal and vertical transport processes, generated by the physical submodel, produce differences in the biological and chemical dynamics.

The physical submodel is in its turn forced with the outputs from (physical) circulation and dispersion models of the North Sea.

BIOLOGICAL AND CHEMICAL COMPONENTS OF THE MODEL

The Pelagic submodel

1. Primary producers

Data will be obtained to test several published algorithms which predict primary production rates. Specifically, the relationship described by Jordan & Joint (1984) for phytoplankton from the English Channel will be tested for a wide variety of conditions in the North Sea. This relationship suggests that depth-integrated primary production can be estimated from values of surface irradiance and depth-integrated chlorophyll concentration. In this respect, data from remote sensing platforms such as CZCS may be used profitably in combination with sea-truth data to calibrate primary production models. Since remote sensing data on chlorophyll concentrations are acquired synoptically, and produce average values for large areas, they are very suitable for use in testing and calibration of primary production models.

The proposed algal growth model derives from published work on the photosynthesis and nutrient-limited growth of algae in pure culture, possibly that on "cell quota control" and "threshold limitation" of growth by Droop (1983) and others (Tett, 1987; Tett & Droop, 1988). Algal growth is made to depend on the cellular content of the limiting nutrient, or on net photosynthesis, whichever is most restricting. In addition to predicting seasonal cycles of "bulk" phytoplankton it will simulate the growth of mixed algal communities, including for example diatoms, microflagellates and dinoflagellates in order to model plankton blooms of various types of algae, viz. Phaeocystis sp. This approach will open the possibility to model some of the features of seasonal succession in the phytoplankton community.

An operational model of mixed plankton communities will be made available by NIOZ as a starting point. In view of the probable impact of zooplankton grazing on phytoplankton communities, close collaboration with researchers of MLA studying zooplankton is anticipated.

2. The pelagic small food web

Recently, an important change in our perception of marine ecology has come about with the recognition of the importance of marine bacteria and the "microbial loop" (Azam et al., 1983; Fenchel, 1988). A re-evaluation of the role of bacteria and other micro-organisms in the food web is therefore desirable. Recent reviews (e.g. Joint & Morris, 1982; Smetacek & Pollehne, 1986) emphasized the importance of these components of the planktonic system characterized by high microbial biomass (Le B. Williams, 1982) and rapid division rates, which in conjunction imply high algal and bacterial turnovers. It has been shown that bacteria may pass on twice as much organic carbon to the next trophic level as the herbivorous zooplankton. These indications of the importance of the microbial loop in marine carbon flow and nutrient regeneration underscore the importance of modelling the microplankton components.

3. Zooplankton

Several models have already been developed, involving both zooplankton and larval fish (Hay et al., 1988; Heath, 1988; Jones and Henderson, 1988), but in this project the aim is to describe prey ingestion in terms of predator behaviour and to evaluate the partitioning of ingested carbon and/or nitrogen into growth and reproduction, and losses through respiration, excretiŏn and defecation. Data on the distribution and abundance of predatory macrozooplankton (jellyfish and fish larvae) in the North Sea are available at MLA. These will be used to develop foraging models. Valuable data on macro- and mesozooplankton grazing, reproduction and excretion rates are available from the Autumn Circulation Experiment, and from other studies carried out at MLA (Checkley, 1984; Fuiman and Gamble, 1988; Gamble and Hay, 1988).

The benthic submodel

The benthic submodel will in the first instance have three components: the small foodweb, macrobenthos and nutrient cycling.

The rationale for this is that in the generally soft sediments of the North Sea benthic biological activity is dominated by micro- and meiofauna, both in terms of carbon flows and in the nutrient fluxes. However, serious problems may be expected in formulating, testing and validating mathematical modules of almost any aspect of the benthic system, due to a lack of quantitative data and working hypotheses on benthic processes in coastal and shelf-sea ecosystems.

1. The benthic small food web

The small food web is an important element in nutrient regeneration in the benthic system. It differs essentially from its pelagic counterpart since it represents the slower part of the nutrient cycle, due to the longer transport paths. With its strong chemical and biological gradients, the benthic system has a vertical structure that enables its different layers to interact. As a result there are many types of micro-environments which differ in their oxidation potential, resulting in different microbial activities. These micro-environments are connected by diffusion processes in such a way that the gradients are self-maintaining.

The driving force is the (seasonal) input of organic matter, produced in the pelagic system. This module will describe the mineralization dynamics as mediated by the biological components of the small food web and its time delays and efficiency.

2 Macrobenthos

The deposit-feeding macrobenthos is a major link between the benthic small food web and higher trophic levels in the system. Also the suspension-feeding macrobenthos directly affects the pelagic system in shallow areas. The dynamics and behaviour of elements in the macrobenthos are much less well understood than most other system components. Indeed, only recently adequate data on the distribution and abundance of macrobenthic species (de Wilde et al., 1988; Eleftheriou & Basford, 1989) have become available for the North Sea. At present, productivity estimates are primarily based on empirically derived production/-biomass data (de Wilde et al., 1984) with little effort to derive dynamic models of macrobenthic production processes. In the absence of a well established body of theory, data or modelling history, it is not possible to outline a process oriented submodel at this stage. As a first step, a forum is required in which participating scientists can discuss and explore alternative approaches to modelling the macrobenthos. From these discussions a preliminary model will be formulated, which will serve as the starting point for model development.

3. Nutrient Cycling

In this project we will focus on the identification and conceptual modelling of the chemical mechanisms and processes, in order to describe the relationship between the biology of the North Sea and the nutrient chemistry. This represents a first step towards forecasting the response of the system to long-term changes like eutrophication (Berg & Radach, 1985; Malmgren-Hansen, 1984; Stigebrandt & Wulff, 1973; Wulff & Rahm, 1988).

The main emphasis will be on chemical phenomena (complexation, precipitation, sorption) relevant to the functioning of the ecosystem (Owens et al., 1986). In the modelling of the nutrient sediment-water interaction special attention will be paid to sedimentation of particulate forms and to regeneration of inorganic components to the water-column. The nutrient submodel should be able to provide a correct estimation of nutrient removal from the North Sea ecosystem by chemical and biochemical processes, mainly within the sediments (denitrification, precipitation of stable compounds).

Almost all data concerning nutrients in the North Sea are derived from the water--column (Brockman et al., 1988), with only few experimental data on the sediment--water nutrient exchange processes (Rutgers van der Loeff, 1980). Information on removal of nutrients from the ecosystem is restricted to denitrification off the Belgian coast (Billen, 1978). However, chemical processes in the watercolumn, in the benthos and at the sediment-water interface may substantially influence the nutrient cycling and consequently the functioning of the ecosystem (Wollast & MacKenzie, 1983; Froelich et al., 1982; Koike & Sörensen, 1988; Raaphorst et al., 1988).

Higher trophic levels

The inclusion of the higher trophic levels into full scale ecosystem models is desirable from a systems-management point of view. Large predatory animals in the ecosystem have the capacity to modify the structure of the system, and are of exceptional social, economic and political importance. It is therefore considered important to make a concerted effort to improve our capability in higher trophic level modelling as part of this project. It is recognized, however, that although higher trophic levels may have a large impact on system structure, the energy and nutrient flows through these levels are relatively insignificant. Thus, realistic incorporation of higher trophic levels into ecosystem models is difficult, when these models focus on energy- and nutrient-fluxes.

1. Fish populations and fish/benthos interactions

Fish models will be developed at MLA in conjunction with the University of Aberdeen. The models will attempt to simulate the dynamics of the whole fish community, taking into account predation interaction with the benthos and plankton in addition to interactions within the fish assemblage. The first approach will be to aggregate fish species into functional groups, groups with similar ecological characteristics, by using multi-variate analysis of habitat characteristics, prey preferences and growth rates.

PHYSICS-ECOLOGY INTEGRATION

The physical oceanographic climate of the North Sea is such that it can only be represented by hydrodynamic models with a very fine resolution in space and time. However, once such a model has been constructed, the results may be parameterized for the larger scales appropriate to ecosystem modelling. Such a parameterization, especially with regard to the temporal and spatial distribution of nutrients, is the objective of the efforts of the Institut fur Meereskunde in Hamburg. In this way, combined with a submodel simulating the combined effects of wind and irradiance on the vertical structure of the water column, the main effects of physical processes on ecosystem functioning will be incorporated in the model.

Forcing functions and boundary conditions

External forcing of the system will be incorporated in the model in the form of time-dependent data sets e.g. of river run-off, terrestrial inputs of nutrients and organic matter. These data need to be collated along with other forcing functions, notably incident solar radiation and water temperature.

The boundary conditions for all dissolved and pelagic components of the ecosystem which are subject to transport processes across the system boundaries are less likely to be immediately available. For this reason PML and MLA will make an effort to provide data on nutrients, chlorophyll, and turbidity together with measurements of zooplankton abundance along the northern and western boundaries of the North Sea. This would supplement data sets already being collected along the southern boundary. Data for the eastern boundary will be collected by the Swedish and the Danish participants and will be collated by WQI. Other data already collected under the scientific programmes of the project partners will provide suitable validation data for the North Sea model in the main body of the North Sea. Both PML and NIOZ are participating in the NERC North Sea project which has run monthly surveys in the Southern and Central North Sea for a period of 15 months, from Aug 1988 up to October 1989. Another long-term set of boundary conditions on the Continental coast (river discharges and element concentrations therein) will be available through the cooperation of the DGW of Rijkswaterstaat and Delft Hydraulics (Postma et al., 1987). ^pg;

FINAL REMARKS

Natural systems are complex, subtle and difficult to comprehend. Numerical simulation of these systems is possible only if we make strong, simplifying assumptions and ignore much of the variability. The consequence of doing so is to produce models which give considerable insights but little predictive power. The variable behaviour of the natural ecosystem, much of it due to the stochastic, inherently unpredictable, forcing of the system provides an envelope of uncertainty about our understanding of natural systems and about our quantitative knowledge of their average behaviour. If we can reduce this envelope of uncertainty by including major sources of this variability into our models and thereby increase our understanding of the cause and effect relationships in the system, this project will have brought us a step closer to realizing the objective stated in the introduction.

REFERENCES

Azam, F., T. Fenchel, J.G. Field, J.S. Gray, I.A. Meyer-Reil & F. Thingstad (1983). The ecological role of water column microbes in the sea. Mar. Ecol. Progr. Ser. 10: 257-263.

Baretta J.W. & P. Ruardij, (eds.) 1988. Tidal Flat Estuaries, Simulation and analysis of the Ems estuary. Ecol. Studies 71, Springer Verlag: 353 pp.

Berg, L. & G. Radach (1985). Trends in nutrient and phytoplankton concentrations at Helgoland Reede (German Bight) since 1962. ICES C.M. 1985/L.2.

Berner, R.A. (1980). Early diagenesis, a theoretical approach, Princeton University Press, Princeton N.J.: 64-77.

Billen, G. (1978). A budget of nitrogen recycling in North Sea sediments off the Belgian coast. Est.Coast. mar. Sci. 7: 127- 146.

Billen, G. & C. Lancelot (1988). Modelling benthic nitrogen cycling in temperate coastal ecosystems. In: T.H. Blackburn & J. Sörensen (eds). Nitrogen cycling in coastal marine environments. Wiley, Chichester: 341-378.

Blackburn, T.H. & J. Sörensen (1988) (eds). Nitrogen cycling in coastal marine environments. Wiley, Chichester: 1451.

Brockman, U., G. Billen & W.W.C. Gieskes (1988). North Sea nutrients and eutrophication. In: W. Salomons, B.L. Bayne, E.K. Duursma & U. Fürstner (eds). Pollution of the North Sea. Springer, Berlin: 348- 383.

Checkley, D. (1984) Relation of growth to ingestion for larvae of Atlantic herring Clupea harengus and other fish. Mar. Ecol. Prog. Ser. 18: 215-224.

Droop (1983). Botanica Marina, 26: 99-112. Emerson, S., R. Jahnke & D. Heggie (1984). Sediment-water exchange in shallow water estuarine sediments. J. Mar. Res. 42: 709-730.

Eleftheriou, A. and D.J. Basford, (1989). The macrobenthic infauna of the offshore northern North Sea. J. mar.biol. Ass. U.K. 69: 123- 143.

EON(1988). The ecosystem of the western Wadden Sea: field research and mathematical modelling. NIOZ-rapport 1988-11: 139 pp.

Fenchel, T. (1988) Marine Plankton Food Chains, Ann. Rev. Ecol. 19: 19-38.

Fransz, H.G. & J.H.G. Verhagen (1985). Modelling research on the production cycle of phytoplankton in the Southern Bight of the North Sea in relation to riverborne nutrient load. Neth. J. Sea Res. 19: 241-250.

Froelich, P.N., N.A. Luedtke, G.R. Heath & T. de Vries (1982). The marine phosphorus cycle. Am.J. Scie 282: 475-511.

Fuiman, L. and J. Gamble (1988). Predation by Atlantic herring sprat and sandeels on herring larvae in large enclosures. Mar. Ecol. Prog. Ser. 44: 1-6.

Gamble, J. and S. Hay (1988). Predation by the scyphomedusan Aurelia aurita on herring larvae in large enclosures; effects of predator size and prey starvation. ICES Early Life History Symposium, Paper No. 52. (Rapp. P.-v. Réun. Cons. int. Explor. Mer., in press).

Hay, S., G. Evans and J. Gamble (1988). Birth, growth and death rates for enclosed populations of calanoid copepods. J. Plankton Res. 10: 431-454.

Heath, M. (1988). A modelling and field study of grazing by herring larvae. ICES Early Life History Symposium, Paper No. 4. (Rapp.P.-v. R#un. Cons. int. Explor. Mer., in press).

Holling, C.S., (ed.) (1978). Adaptive environmental assessment and management. John Wiley, New York.

I.B.M. Application program 1967, System 360 continuous system modelling program (360A-CX-16X). Users Manual. IBM.

Joint, I.R. & R.J. Morris (1982). The role of bacteria in the turnover of organic matter in the sea. Oceanogr. Mar. Biol. A. Rev. 20: 65-118.

Jones, R. and E. Henderson (1987). The dynamics of nutrient regeneration and simulation studies of the nutrient cycle. J. Cons. int. Expor. Mer 43: 216-236.

Jones, R. and E.Henderson (1988). Simulation studies of fish larval survival. In: Towards a theory on biological physical interactions in the world oceans. Ed: Rothschild B.J., Kluwer Academic Publ.: 343-372.

Jordan, M.B. & I.R. Joint (1984). Studies on phytoplankton distribution and primary production in the western English Channel in 1980 and 1981. Contin. Shelf. Res., 3: 25-34.

Kiefer, D.A. & J.N. Kremer (1981). Origins of vertical patterns of phytoplankton and nutrients in the temperate, open ocean: a stratigraphic hypothesis. DSR 28A: 1087-1105.

Koike, I. & J. Sörensen (1988). Nitrate reduction and denitrification in marine sediments. In: T.H. Blackburn & J. Sörensen (eds). Nitrogen cycling in coastal marine environments. SCOPE. Wiley, Chichester: 251-274.

Kremer, J.N. and Nixon, S.W. (1978). A coastal marine ecosystem simulation and analysis. Ecological studies no. 24. Berlin: Springer Verlag, xi: 217 pp.

Malmgren-Hansen, A. (1984). Model calculations for Kattegat. Report from the Danish Environmental Protection Agency No. 59. (In Danish).

Markus, A.A., P.C.G. Glas and A.v.d. Giessen (1988). A simulation model of phytoplankton and water quality in the Southern Bight of the North Sea. ICES--paper CM1988/C:44, Hydrography Committee.

Mommaerts, J.P., G. Pichot, J. Ozer & Y. Adam (1984). Nitrogen cycling and budget in Belgian coastal waters: North Sea areas with and without river inputs. Rapp. P.-v. Réun. Cons. int. Explor. Mer 183: 57-69.

Owens, N.J.P., R.F.C. Mantoura, P.H. Burkill, R.J.M. Howland, A.J. Pomeroy and E.M.S. Woodward (1986). Nutrient cycling studies in Carmarthen Bay: phytoplankton production nitrogen assimilation an d regeneration. Mar. Biol. 93: 329-342.

Pace, M.L., J.E. Glasser & L.R. Pomroy (1984). A simulation analysis of continental shelf food webs. Mar. Biol. 82: 47-63.

Postma, L. (1988). Delwaq. Users manual. Delft Hydraulics: 180 pp.

Postma, L, J.M. de Kock, A.A. Markus and J.A.v. Pagee (1987). Long term and seasonal water quality modeling of the North Sea and its coastal waters. ICES--paper CM1987/C:39, Hydrography Committee.

Raaphorst, W. van, P. Ruardij & A.G. Brinkman (1988). The assessment of benthic phosphorus regeneration in an estuarine ecosystem model. Neth. J. Sea Res. 22: 23-36.

Radach, G. (1983). Simulation of phytoplankton dynamics and their interactions with other system components during FLEX'76. In: J. Sündermann & W. Lenz (eds.). North Sea Dynamics. Springer Verlag Berlin-Heidelberg: 584-610.

Radach, G. & A. Moll (1989). State of the art in algal bloom modelling. EEC Workshop on "Eutrophication and algal blooms in North Sea coastal zones, the Baltic and adjacent areas", Brussels, 26-28 October 1988. Water Pollution Research Reports (in press).

Radford, P.J. (1971). The simulation language as an aid to ecological modelling. Mathematical Models in Ecology (ed. J.N.R. Jeffers) Proc. Symp. Bristol Ecological Society: 277-296.

Radford, P.J. (1979). Some aspects of an estuarine ecosystem model GEMBASE. State of the art in Ecological Modelling (ed. S.E. Jörgensen) Proceedings of the ISEM conference on ecological modelling, Copenhagen, 1978. International Society for Ecological Modelling pub.: 301-322.

Rutgers van der Loeff, M.M. (1980). Nutrients in the interstitial waters of the Southern Bight of the North. Neth. J. Sea Res. 14: 144-171.

Stigebrandt, A. and F. Wulff (1987) A model for the dynamics of nutrients and oxygen in the Baltic proper. Journal of Mar. Res. 45: 729-757.

Smetacek, V. and F. Pollehne (1986). Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia 26: 401-428.

Tett (1987). Symposia Soc. for General Microbial 41: 387-425.

Tett & Droop (1988). CRC Handbook of Laboratory Model Systems for Microbial Ecosystems. Ed. Wimpenny, CRC Press, Florida, 2: 177- 233.

Vries, I. de, F. Hopstaken, H. Goossens, M. de Vries, H. de Vries and J. Heringa (1988). GREWAQ: An ecological model for Lake Grevelingen. Documentation report T0215-03, Delft Hydraulics: 242 pp.

Wilde, P.A.W.J. de, E. Berghuis & A. Kok (1984). Structure and energy demand of the benthic community of the Oysterground, Central North Sea. Neth. J. Sea Res. 18: 143-159.

Wilde, P.A.W.J. de & G.C.A. Duineveld (1988). Macrobenthos van het Nederlands Continentale Plat verzameld tijdens de ICES "North Sea Benthos Survey" April 1986. NIOZ Rapport 1988.

Williams, P.J. Le B. (1982). Microbial contributions to overall plankton community respiration studies in CEE's. In: G.D. Give and H.R. Reeve (eds.). Marine Mesocosms: Biological and Chemical Research in Experimental ecosystems, Springer Verlag, Berlin.

Wollast, R. & F.T. MacKenzie (1983). The global cycle of silica. In: S.R. Aston (ed). Silicon geochemistry and biogeochemistry. Academic Press, London: 39-76.

Wulff, F. and L. Rahm (1988). Long-term, Seasonal and Spatial Variation of Nitrogen, Phosphorus and Silicate in the Baltic: An Overview. Mar. Environm. Res. 26: 19-37.

DYNAMIC SIMULATION *VERSUS* STEADY-STATE MODEL: AN ALTERNATIVE STRATEGY TO MODEL THE BENTHIC FOOD WEB

Pierre Chardy[1], Jean Claude Dauvin[2], Philippe Gros[1], Yves Monbet[1]

[1]IFREMER, B.P. 70, 29280 Plouzané, France
[2]MNHN, 75231 Paris Cedex 5, France

ABSTRACT

The benthic component of a marine ecosystem is usually regarded as a trophodynamic system. In the framework of ecological modelling, most benthic submodels have dealt with simulation analysis, the behaviour of the state variables being described by a set of differential equations integrated over time.

One of the difficulties of simulating the benthic food web is emphasized by the fact that simple linkage between two compartments (donor and recipient), appears to be more and more unrealistic as soon as the upper levels of the food web are concerned. The dynamic response of macrobenthic compartments, which consist in long living and slow reproducing species, cannot be described only by "growth-related" processes. Other processes as spawning and recruitment are important regulating factors. This leads to develop increasingly complex models which require detailed population studies.

On the other hand, steady-state models give an oversimplified picture of the food web. Such approach would seem legitimate as far as the objectives are to approximate average annual flows for large spatial scale studies. Despite the roughness of the approach, it provides a convenient tool for the summarization of extensive data in term of budget. The use of inverse method, recently investigated by Vézina and Platt (1988), allows to face the fundamental limitation of the low ratio of observations to unknowns, and to take the uncertainty of the parameter into account, as well as the variance of the observations.

Advantages and limitations of these two possible approaches, applied to benthic systems, are investigated in the case study of a subtidal fine sand community of the western English Channel.

INTRODUCTION

Ecosystem model practice was traditionally dominated by plankton dynamics. The benthic subsystem was commonly either ignored or considered as a marginal component, restricted to a detritic box with a remineralisation rate.

Nevertheless, some fundamental questions such as global flux studies, living resource management, nutrient regeneration and eutrophication processes, contaminant flows throughout the living matter, legitimate the development of benthic submodels.

Most of our experience in that field comes from generic ecosystem models such as GEMBASE, the General Ecosystem Model for the Bristol Channel and the Severn Estuary (Radford, 1981), and more recently, the Ems Estuary model (Baretta and Ruardij, 1988) which represents the first attempt to model the major benthic processes as fully as the pelagic ones. Modelling the benthos is a new task within the scope of ecosystem modelling. Among the numerous questions related to this topic (relevant functional groups, major processes, spatial scales....), we propose to discuss briefly the basic alternative approach "*dynamic simulation versus steady state model*" applied to subtidal benthic fine sand communities, commonly distributed in the Northwestern European seas.

DYNAMIC SIMULATION : the case study of *Abra alba* community, bay of Morlaix.

This case study is an attempt to simulate the seasonal variations of major benthos compartments over one year. Previous studies, developed in this area by Cabioch (1968), Boucher (1983), Dauvin (1984, 1988, 1989, 1990), Riaux-Gobin *et al.* (1989), produced a complete database of monthly values of the major benthic compartments, exhibited in the conceptual flow diagram, Fig. 1. The bulk of information gathered in the bay of Morlaix provides an opportunity to simulate the benthic biomass response to environmental fluctuations. The proposed model is basically a trophodynamic point model (Chardy and Dauvin, in preparation). Forcing functions are the sedimentation rate of organic carbon (Fig. 2) , benthic primary production and the temperature effect ($Q_{10} = 2$). Transfer of carbon between compartments is expressed by universal biological processes : input is ingestion; outputs are predation, respiration, egestion and non-predatory mortality. Parameters are derived from known P/B ratios or literature. Most of them would require extensive discussion, but this chapter is mainly concerned with the consistency of

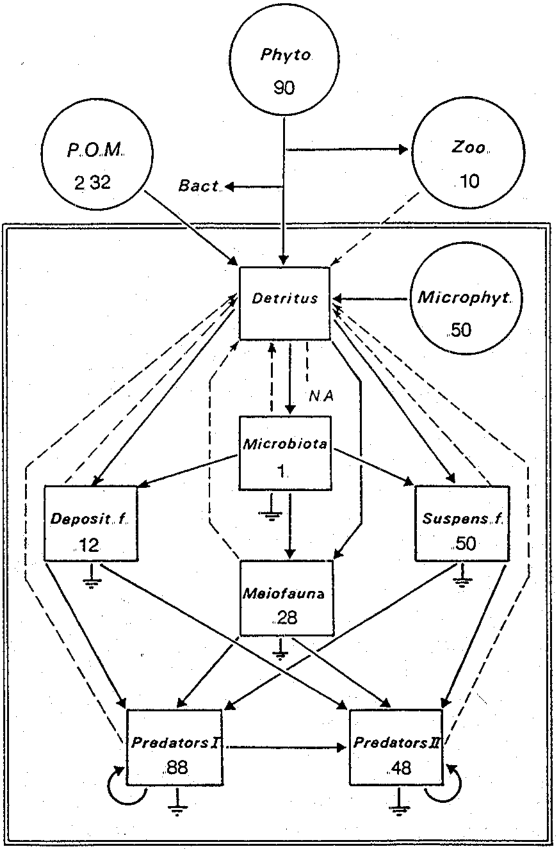
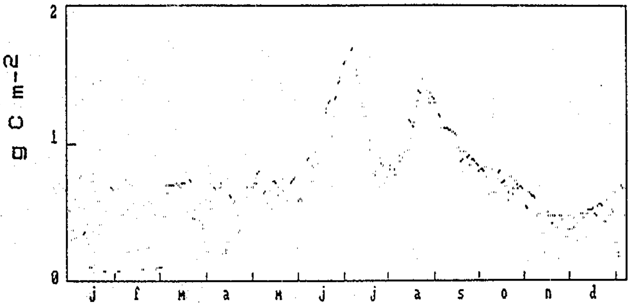
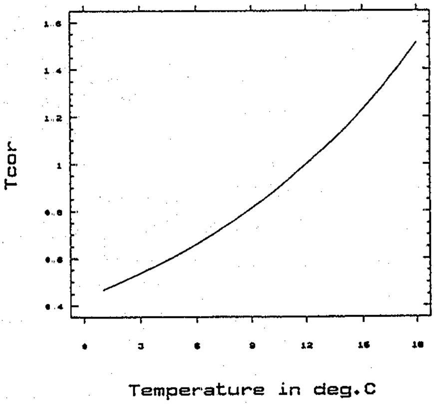


Figure 1. BAY OF MORLAIX. Conceptual flow diagram of the model.
Exogeneous variables ares in circles; endogeneous variables ares in boxes.

→: trophic fluxes. - - →: feaces + non predatory mortality.
⏚ : respiration. ═══ : boundary of the benthic system.
P.O.M.: particulate organic matter. Phyto. : phytoplancton.
Zoo. : herbivorous zooplancton. Microphyt. : microphytobenthos.
N.A. : non assimilated.
Annual average biomasses in g C.m^{-2}



NET SEDIMENTATION in g C m^{-2} d^{-1}



Tcor = EXP(.069*(Temperature-12))

Q10 = 2

Figure 2. BAY OF MORLAIX. Forcing functions.

the seasonal cycle simulation of the state variables.

Fig. 3 gives the simulation of the 7 benthic compartments. The seasonal cycle of bacteria is reasonably well simulated and strongly related to the input of labile organic carbon. The magnitude of the annual variations is quite realistic, but the maximum peak in June appears much too early and is over-estimated. The meiofauna compartment follows the general dynamics of the bacteria, with a much smoother profile from spring to the end of summer. The shape of the suspension feeder curve is in good agreement with the observations, the maximum of biomass being shifted to the autumn period. The last three compartments are not adequately simulated. The mean annual values fit the observations but the seasonal fluctuations are out of phase.

These results suggest that food availability and temperature factors are insufficient to simulate the dynamics of the "upper part' of the benthic food web which may be affected by other regulating factors such as spawning and recruitment.

Spawning and recruitment effects can be introduced in the simulation insofar as the knowledge of the life cycle of the major populations of the macrofauna compartments is available. Periods of spawning and recruitment for macrofauna have been derived from the work of Dauvin (1984, 1990). The spawning process may be simulated as the release of energy equivalent to the annual gonad production into daily portions over a period of spawning. The recruitment effect is more subtle to include in the simulation. Settlement of larvae makes a very small contribution in terms of biomass (Baretta & Ruardij, 1988). But, the mean individual weight of the compartment is significantly modified and the basic metabolic rates, as an exponential function of individual weight, are strongly affected. The conceptual importance of the size-structured approach in ecosystem modelling has a strong theoretical basis (Silvert, 1984, 1988). this viewpoint is illustrated by the variations of mean individual weight of *Abra alba* population (Fig. 5), established from size frequency distributions and the specific size-weight allometric relationship during the year 1980 (Dauvin, 1984). Variation of P/B ratio is calculated using the function defined by Schwinghamer *et al.*, 1986 (Fig. 5). Magnitude of variation of the P.B ratio during an annual cycle varies between 0.4 and 4.

From these observations, we can expect that recruitment effect may be an important regulatory mechanism.

Results of the simulation introducing spawning and recruitment effects are given in Fig. 4.. In this new version, the dynamics of the first three compartments (microbiota, meiofauna, suspension-feeders) are not modified. But the correspondence between data and model is more acceptable for higher trophic levels, particularly for carnivore I and carnivore II compartments. this example reflects the need for further investigations in the field of regulatory mechanisms for the benthic submodels : uptake regulation for fast turnover compartment and fecundity and

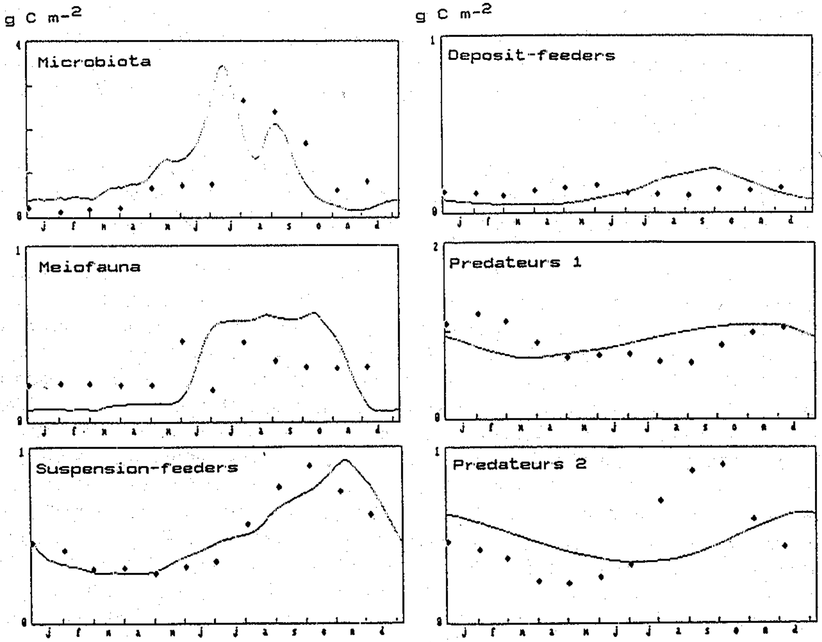


Figure 3. BAY OF MORLAIX. Simulated biomasses of the benthic compartments.
Observations : ◆
Simulation : ——

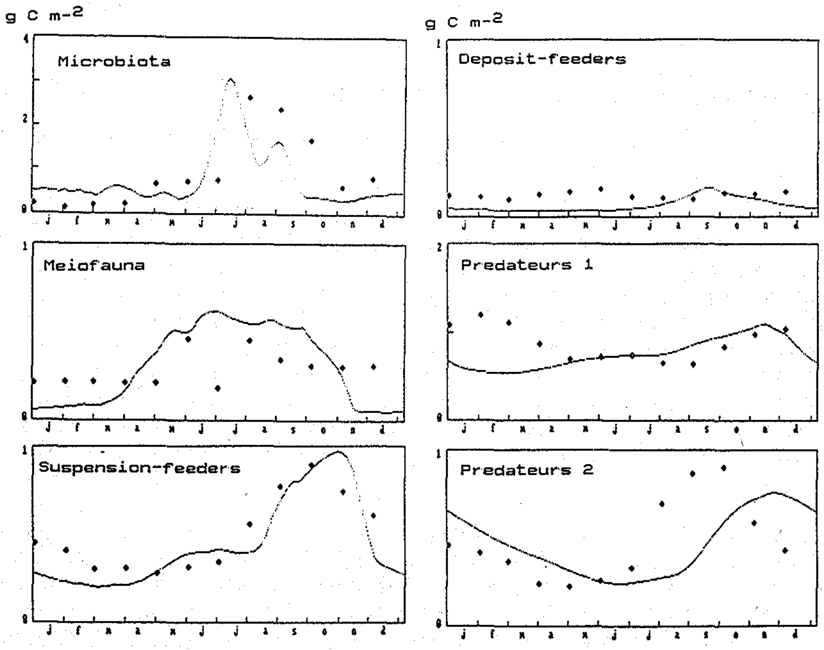


Figure 4. BAY OF MORLAIX. Introduction of spawn and recruitment effects.
Observations : •
Simulation : ——

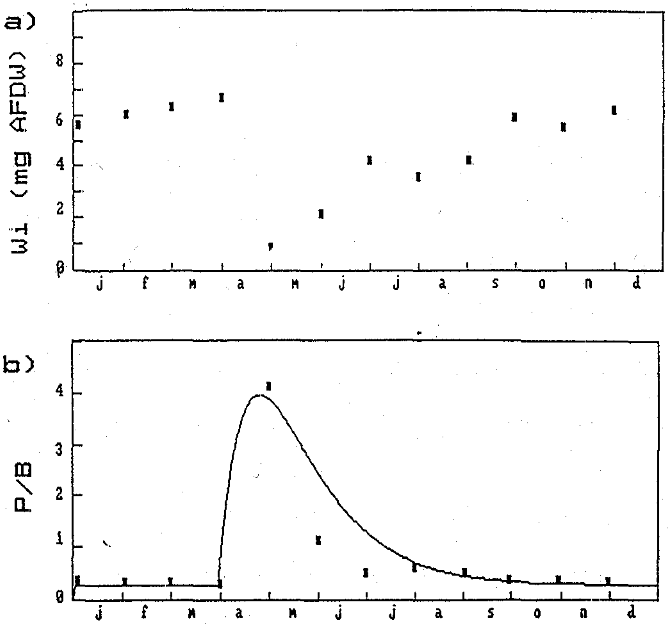


Figure 5. BAY OF MORLAIX.

a) Variations of the monthly individual weight of Abra alba population over an annual cycle (derived from Dauvin, 1984).

b) Calculed 'Production/Biomass' ratio using the function established by Schwinghamer et al. (1986): $P/B = W_i^{-0.304}$

recruitment processes for long living species compartments. The dynamics of macrobenthic component cannot be satisfactorily described only by growth-related processes.

But recruitment is still a central problem in population dynamics and cannot be simulated by a simple formulation. An explicit description of the recruitment processes is probably out of the scope of the ecosystem modelling field, at this state of our knowledge.

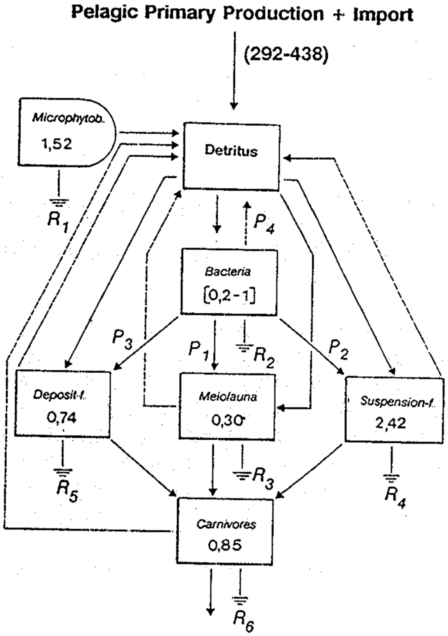
STEADY-STATE MODEL : the case study of *Tellina fabula* community, Bay of St. Brieuc.

The opposite of a simulation analysis, which provides time dependent variations of the standing stocks, is the steady-state model which appears as a brute-force approach, giving an over-simplified picture of the food web. Basically, this approach provides average annual flows between compartments. The methodology is related to the "input-output analysis" attributed to Leontief (1951) and was first applied to economic systems. Recent applications to coastal marine ecosystems have been proposed by Klepper and Van de Kamer (1988) for estimating the carbon budget of the Oosterschelde estuary. St. Brieuc *Tellina fabula* community study is an illustration of a steady-state model solved by the inverse procedure. Basic principles of the inverse problem in food web research have been discussed by Vézina and Platt (1988).

A numerical model gives the behaviour of the state variable from known parameter values, whereas the inverse method uses the observations of the state variables to estimate the parameter values. This approach corresponds well to the state-of-the-art benthic submodel, in which standing stocks are commonly measured on an annual basis, without any seasonal variation, and database parameters are approximated from production/biomass ratios, with a high level of uncertainty.

In order to illustrate the interest of such a method, a comparison between direct flux measurements and results generated from the model is presented.

Three global flow measurements are available (Gros *et al.*, 1990) : net sedimentation of organic carbon measured with sediment traps, bacterial production using the tritiated thymidine incorporation method, and community oxygen consumption measured with an *in situ* respiration chamber. Uncertainty of such measurement is defined by the confidence limits of the calculated mean values ($t = 0.05$).
The solutions of an optimal balanced budget for two input values corresponding to the upper and lower boundaries of the measured annual sedimentation rate is given in Fig. 6.



GLOBAL FLOWS	*Measurements*	*Model output*
Total Respiration:	(118 - 276)	(117 -155) $(R_1+R_2+R_3+R_4+R_5+R_6)$
Bacterial Production:	(44 - 204)	(103 - 118) $(P_1+P_2+P_3+P_4)$

Figure 6. BAY OF ST BRIEUC. Conceptual flow diagram.
Comparison between the uncertainty ranges of direct measurements and calculations from the steady-state model.
Flows ares expressed in g C.m^{-2} .y^{-1}

The results clearly indicate that the uncertainty range of the measured fluxes is much larger than the interval between the maximum and minimum values generated by the model. As previously indicated by Klepper and Van de kamer (1987) about the Oosterschelde case, the method leads to a considerable reduction in the uncertainties of the estimate of fluxes by direct measurements.

CONCLUDING REMARKS

The simulation modelling approach provides an elegant solution for understanding the benthic community response to environmental factors, particularly food supply input from surrounding waters. Detailed information can emerge about the partitioning of the available food among functional groups having the same feeding strategy, or about the time lag between donor and recipient compartments. But benthic submodels contain many regulation mechanisms with parameters that are poorly known. Long term dynamic compartments need further information on regulation factors such as the recruitment process, which cannot be explicitly modelled. Furthermore, simulation analysis is meaningful only if seasonal variations of the standing stocks are available, which is not commonly the case for benthic communities.

The steady-state approach is of particular interest in the perspective of global flux studies, dealing with annual budget estimates. Because the system is underdetermined, powerful mathematical methods as inverse techniques are very attractive. Direct estimates of most flows in the benthic system are not available. Even when global fluxes are accessible by measurement (such as total community respiration), the results are instantaneous and punctual. This leads to unacceptably large uncertainties when this information is integrated over an annual time scale. Inverse technique can be applied to reduce the uncertainty of major flows by seeking the extreme solutions for a particular benthic system.

REFERENCES

Baretta, J.W. and P. Ruardij. 1988. Carbon flows in the western Wadden Sea : Model calculations. Scient. ar. 53 : 523-529.

Boucher, G. 1983. Evolution du peuplement du meiobenthos des sables fins sublittoraux de la baie de Morlaix. Oceanologica Acta n. sp. Actes 17e Symposium Européen de Biologie Marine, Brest. pp. 33-37.

Cabioch, L. 1968. Contribution á la connaissance des peuplements benthiques de la Manche occidentale. Cah. biol. mar. 9 : 493-720.

Chardy, P., Dauvin, J.C. (in prep.). Carbon flows in a subtidal fine sand community from the western English Channel. A simulation analysis.

Dauvin, J.C. 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la Baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz. Thèse Doct. Eta, Sci. nat., Univ. Pierre & Marie Curie, Paris. 468 pp. + 193 pp. annexes.

Dauvin, J.C. 1988. Rôle du macrobenthos dans l'alimentation des poissons démersaux vivant sur les fonds de sédiments fins de la Manche occidentale. Cah. biol. mar. 29:445-467.

Dauvin, J.C. 1989. La méiofaune temporaire d'un peuplement subtidal de sédiment fin de la Manche occidentale. Echantillonnage, composition qualitative et quantitative. Ann. Inst. Océanogr. Paris, 65 : 37-55.

Dauvin, J.C. 1990. Recrutement méiobenthique des principales espèces de Polychètes et de Mollusques Bivalves d'un peuplement subtidal de sédiments fins de la Manche occidentale. Cah. biol. mar. 31:201-224.

Gros, Ph., Blanchard, M., Chardy, P., Gentien, P., Hamon, D., Monbet, Y. 1990. Atelier franco-suédois sur l'environnement. Chambéry 30.09-03.10.1990, 18 pp.

Klepper, O., Van de Kamer, J.P.G. 1987. The use of mass balances to test and improve the estimates of carbon fluxes in an ecosystem. Mathematical Biosciences 85 : 37-49.

Leontief, W. 1951. The structure of the American economy, 1919-1939. Oxford University Press. 264 pp.

Radford, P.J. 1979. Some aspects of an estuarine ecosystem model GEMBASE. State-fo-the-art in Ecological Modelling (Ed. S.E. Jorgensen) - Proceeding of the ISEM Conference on ecological modelling, Copenhagen, 1978. International Society for Ecological Modelling pub. 301-322.

PROBLEMS OF MODELLING BIOTURBATION

John Davey

Plymouth Marine Laboratory, Prospect Place, The Hoe
PLYMOUTH PL1 3DH, United Kingdom

ABSTRACT

Bioturbation by macrofaunal animals modifies sediments in the benthic boundary layer in most marine environments with profound implications for both physical and chemical processes. Techniques for measuring rates of bioturbation in the laboratory and in the field, whether manifest as particle mixing or as irrigation of burrow structures, will be briefly reviewed.

With bioturbation quantified, aspects relevant to modelling are a matter of the aims of the model. For certain purposes, such as modelling the fate of pollutants, it may only be necessary to consider the bioturbation due to key species, while for more general purposes some estimate may be required of the bioturbation manifested by whole communities. Such divergent demands will be considered in the context of existing knowledge and practicalities.

INTRODUCTION

I must make it clear that I am addressing problems associated with the concept of bioturbation and how we may quantify it and not with problems in the modelling process per se. This is because I am a biologist with experience in researching bioturbation as a process. I am not, however, a modeller.

Let me also get out of the way difficulties with the word "bioturbation". I have seen this referred to as "a dreadful word". It certainly seems to upset some people. I fear I offer cold comfort. The word bioturbation, whatever its etymology, is embedded in the literature with a permanence that we must accept. I propose no alternatives. Bioturbation it is going to have to be.

The construction of what I now have to say divides into three:
- what is bioturbation
- what is the state of the art in quantifying it
- for what purposes might we want to fit it into models

The best and shortest definition is attributable to American Alan Myers (1977) and runs:

'BIOLOGICALLY MEDIATED SEDIMENT-WATER INTERACTIONS'

Taking the first part: for all practical purposes bioturbation is mediated by the macrofauna. I exclude the meiofauna because, other than in extreme examples of low-energy environments such as the abyssal deep, any bioturbatory signal attributable to meiofaunal sized organisms will be completely swamped by macrofaunal bioturbation and hydrodynamic "noise". In fact bioturbation will, as a general rule, increase in significance as one moves from the deep sea, through the coastal zone and into estuaries. Since my experience has been almost exclusively with estuarine research what I have to say will reflect that bias, but I submit that the generality applies to any marine system with adjustments for scale and local community composition.

As to the "sediment-water interactions" I wish to address two aspects:

1. effects on physical characteristics - resuspension, porosity, etc
2. effects on chemical exchanges between sediments and water

There is a third aspect - the biological effects, which we may think of in terms of interactions between members of infaunal macrobenthic communities. One has only to recall the classic paper of Rhoads and Young (1970) and their "trophic group amensalism" hypothesis about deposit feeders rendering the sediment uninhabitable for suspension feeders. Since then there has been a productive field of research on many aspects of trophic and other interactions that frequently implicate bioturbation in structuring benthic communities. However in this presentation I shall concentrate first on the physical and chemical consequences and the tools at our disposal for quantifying them before going on to look at what questions we might be addressing when we incorporate bioturbation as a phenomenon into models. The physical and chemical consequences of bioturbation are intertwined, many of the chemical consequences flowing directly from the very nature of the physical ones.

MEASURING BIOTURBATION

I have spent much of the last six or seven years engaged in multidisciplinary studies of bioturbation and we have deployed and, in some instances devised, techniques for use both in laboratory microcosms and under field conditions. Since I do not have time to be comprehensive I make no apology for confining myself to a brief review of our work in Plymouth for the purposes of illustrating how some of the important facets of bioturbation may be quantified. The numbers of scientists contributing in this field are many. I am simply confining myself to that about which I know the most!

Depending on the particular behavioural characteristics of a given species, reworking may result in sediments being homogenised or differentiated. By using sediment markers - I have tried both microscopic glass beads that mimic sediment particles and fluorescent dyes that stain sediment particles - sediment budgets can be arrived at typically in units such as grams (of sediment) processed per animal (or unit of biomass) per unit of time.

Both the reworking of sediments and the construction of permanent or semi-permanent burrow structures may change physical characteristics of sediments, again in either direction. Thus sediments may be rendered more porous and liable to resuspension or more compacted and less liable to resuspension. Such characteristics may be measured in various ways, such as by the use of falling cones, penetrometers or devices that test the shear strength of the sediments.

But when burrow structures are extensive, one of the most important consequences is the effective increase in the total surface area of the sediments across which chemical exchange processes can take place. I am personally a little concerned at some of the looser estimates of this effect that have, regretably, been bandied about in the literature. Let us be clear: if every square centimetre of a mudflat is replicated by a second square centimetre of burrow walls underneath it, i.e. if the effective surface area is doubled, that alone represents a potentially massive increase. In practise few examples are likely to exist of more than ten-fold increases and 2 or 3 fold increases are the order of the day. One of the best demonstrations of this phenomenon is the modelling of burrows by resin casting. This is a technique that works particularly well in the field so that highly realistic figures can be put on the extent of burrow surfaces.

In the laboratory I have also used real-time X-radiography of thin section tanks or "cuvettes" to follow the sequence of burrow construction by Nereis diversicolor and established behavioural aspects of burrow construction and maintenance that relate to particular population densities.

In the complete absence of bioturbation a typical clay/silt sediment would have a very shallow RPD (redox potential discontinuity) and anaerobic pathways of diagenesis would predominate at all depths below a few millimetres. Once bioturbating organisms open up the sediments to oxygen, whether merely by increasing porosity or, more fundamentally, by irrigating burrows to depths well below the otherwise prevailing RPD, the potential for rate changes to diagenetic processes and to exchanges with the water column are large and may typically be two orders of magnitude greater than rates associated with purely diffusion-led chemistry.

Working in microcosms with undisturbed sediment cores from many different sites in the Tamar estuary system, we have developed a variety of techniques to quantify these chemical exchanges in relation to specific bioturbational activities. Our chemists have designed, tested and deployed with elegant success a ten level pore-water sampler (Watson & Frickers, 1991). The in situ deployment of this device in microcosms or in inter-tidal flux chambers means access to repeatable pore-water profiles of more or less anything carried in solution. Our electronics experts have designed a superbly user-friendly device for deploying self-heated thermistors to detect irrigation currents in and out of animal burrows in laboratory microcosms which can be used not only to record patterns of irrigation activity but to trigger feedback mechanisms to automatically sample irrigation fluids emanating from animal burrows for subsequent chemical analysis (Davey et al 1990). We have already deployed this technique not only to measure the impact of burrowing animals on nutrient and heavy metal exchanges across the sediment-water interface but to monitor the performance of such animals when the system is subjected to pollutant stress (Davey, 1991).

In summary, a wide range of research techniques is available for putting good numbers on almost every aspect of bioturbation.

MODELLING BIOTURBATION

What then are the questions raised by the need to incorporate bioturbation as a rate-defined process into mathematical models? The usefulness of models lies in their ability to predict future states of a system, including those that might arise from particular perturbations. Clearly we can expect to model bioturbation chiefly in terms of the redistribution of sediment particles and the enhancement of chemical fluxes between the sediment and the water column via pore fluids. The biological consequences are ultimately a matter of community structure and the direction in which that may be changing, probably over the longer term.

Models concerned with the movement of sediments on a seasonal basis, with rates of accretion or erosion; models that look at the input of particular chemical species to a sedimentary system and which seek to predict the eventual fate of that species in the system; these are the models we can cater for by identifying the major bioturbating species present and providing sediment reworking budgets, irrigation rates and scales of burrow construction characteristic of those species. In effect we can confine ourselves to "key species", the community dominants like Arenicola, Nereis, various bivalves etc. whose "bioturbational signatures" are rapidly becoming a part of the standard literature.

But the closer we look at the animal-sediment-water system the more complex we perceive it to be. At the beginning of my talk I deliberately played down the role of the meiofauna. I am not unaware of a school of thought that says the meiofauna have been overlooked in the investigation of bioturbation. I think it fair to argue that their direct influence on sediment particle reworking is minimal next to that of macrofaunal bioturbators, and that likewise their effect on any increase of sediment-water surface areas by burrow construction is also minute. However, a phenomenon such as the erodibility of a fine-grained sediment depends on a host of factors. At a microscopic level the condition of individual sediment particles in terms of bacterial colonisation and the presence of mucus coatings and other secretions from meiofaunal animals, especially nematodes, - and probably also from diatoms - could influence physical properties. Moreover it has been suggested to me, only very recently, that erodibility may be a property that shows variation on a microscale dimension, with the top tenth of a millimetre of a very fine sediment being physically different in important respects from the next layer of particles down. Our understanding of the relationship between biological activities and such minutae of physical properties is probably embryonic. While the meiofauna may thus be dismissed from the definition of "bioturbators" they may nevertheless be responsible for effects which are a part of the equation of bioturbation produced by macrofauna.

I have also not addressed, largely because of lack of time, the ramifications of biological feedback from bioturbation. Bioturbating organsims clearly influence their own community structure. In any model that wishes to address the consequences of such major perturbations as the construction of tidal barrage or major industrial redevelopment, we might consider that modelling bioturbation on the basis of a few key species in the existing system would be quite inadequate. Changes to macrobenthic community structure might have to be predicted and bioturbation modelled as a community attribute. It has always been easier to research bioturbation species by species, but community approaches have always been a part of this field and may yet come into their own in the future.

Twenty years ago Winston and Anderson (1971), working in the Great Bay system of New Hampshire (eastern seaboard, USA), did pioneering work with X-radiography to characterize bioturbation along an estuarine gradient across a spectrum of sediment types and macrobenthic communities. They found a gradual decrease in bioturbation with distance from the sea. There was no suggestion that this was a general rule, but the fact that I could document almost exactly the opposite for the Tamar estuary at least serves to illustrate that the interplay of sediment types and communities is complex. Thus we may need to perceive bioturbation as a community attribute, and obtain estimates that reflect not just the effects of the key species, but the consequences arising from the seasonal and spatial variability of all the organisms in that community. This is something we are currently doing for the Tamar estuary.

CONCLUSION

In conclusion I believe we have many useful and well-researched handles on bioturbation whereby we may quantify the rates of processes involved. But like most science, the more we learn the more we find there is to know. This should not make us despair. Whatever we can supply on bioturbation to go into models will hopefully come back to us in clearer ideas about where next we need to concentrate our research.

REFERENCES

Davey, J.T. 1991. Electronic monitoring of bioirrigation by estuarine infauna and its application to bioturbation and pollution studies. Symposium of the Zoological Society of London, No. 63 (in press).

Davey, J.T., Watson, P.G., Bruce, R.H. & Frickers, P.E., 1990. An instrument for the monnitoring and collection of the vented burrow fluids of benthic infauna in sediment microcosms and its application to the polychaetes Hediste diversicolor and Arenicola marina. Journal of Experimental Marine Biology and Ecology, 139:135-149.

Myers, A.C. 1977. Sediment processing in a marine sub-tidal sandy bottom community: I. Physical processes. Journal of Marine Research, 36:609-632.

Rhoads, D.C. & Young, D.K. 1970. The influence of deposit feeding organisms on sediment stability and trophic structure. Journal of Marine Research, 28:150-178.

Watson, P.G. & Frickers, P.E., 1991. A multilevel, in situ pore-water sampler for use in intertidal sediments and laboratory microcosms. Limnology and Oceanography, 35:1381-1389.

Winston, J.E. & Anderson, F.E. 1971 Bioturbation of sediments in a northern temperate estuary. Marine Geology, 10:39-49.

MODELLING THE BENTHOS - HOW TO DEAL WITH SOME PROBLEMS?

Karel Essink

Rijkswaterstaat, Tidal Waters Division, P.O. Box 207,
9750 AE Haren,The Netherlands

INTRODUCTION

When modelling the dynamics of benthic populations we need to have a good understanding of many biological processes, and even in a quantitative sense. Among such processes are the production and survival of eggs and larvae, success of settlement, growth, and intra- and interspecific interactions.

In modelling these processes many problems have to be solved. Not being a modeller myself, but having seen many long-term data sets of macrozoobenthos, I want to point at some of these problems. I am curious to learn how modellers are going to deal with these problems.

REPRODUCTION

Long-term data sets, such as available for Balgzand and Groninger Wad inter-tidal flats in the Dutch Wadden Sea (e.g. Beukema & Essink, 1986) have shown that in some species recruitment is high after severe winters; this occurred in 1979 and 1987 (Beukema, 1991). If we want to model such events in the dynamics of populations it is essential that we know what is exactly happening. Do the low temperatures during a severe winter stimulate the species concerned to produce more gametes, or is there a far greater survival of larvae and young recruits due to reduced abundance or late arrival of the predators of these young stages? Extensive experimental approach will be necessary before being able to model these processes.

Data from Balgzand intertidal flats also indicate that the abundance of small sized species, e.g. *Heteromastus filiformis, Nereis diversicolor, Scoloplos armiger*, has increased due to increasing eutrophication of the western Dutch Wadden Sea during the last two decades (Beukema, 1991). These species are relatively shortlived ones. Their increase in abundance may be explained by a decreased mortality of adults, causing an increased reproduction rate. An other possible explanation is that increased eutrophic conditions did favour reproduction success in one way or an other, increasing the number and also the fitness of recruits, and thereby the population abundance. It is likely that interspecific competition for food is involved, in which competitiion r-strategists will be at a favourable position. To be able to model this process we are dependent on information on interspecific competition and on fitness of offspring. Can we model this effect of eutrophication without such specific knowledge?

SETTLEMENT

For some species, e.g. *Cerastoderma edule* hydrodynamic conditions play an important role in settlement (cf. Baggerman, 1953; Kristensen, 1957). In general, sediment type and local hydrodynamics will be strongly correlated. However, some species are not always content with the locations of their primary settlement; if primary settlement occurs at a sediment type that is not completely satisfactory they may choose for a secondary settlement elsewhere. This is known for e.g. *Mya arenaria* (Kühl, 1951).

Apparently, hydrodynamic conditions at the very time of settlement are important in determining where post-larvae will settle. For some species that do not have the possibility of secondary settlement population dynamics will therefore to a certain extent be dependent on suitability of the site of primary settlement. This surely poses a problem in modelling. Can this problem be overcome, e.g. by the use of box-models?

MIGRATION

Distribution patterns of juveniles and adults of a species may be different, e.g. in *Arenicola marina Macoma balthica* (Dankers & Beukema, 1981) and *Mya arenaria* (Kühl, 1951). Settlement generally occurs in a more sheltered habitat (high, muddy flats). As specimens grow larger, they may migrate to less sheltered habitats, where they are able to maintain due to their larger size and living position deeper in the sediment. In *Macoma balthica* migration of juveniles takes place in the first winter; the intensity of this migration is strongly governed by low winter temperatures (Beukema & De Vlas, 1989).

Modelling the dynamics of populations of benthic species may therefore require inclusion of different habitats, and "transport" processes (possibly in the form of box-models?).

FEEDING

In modelling processes of growth it is important to identify the feeding type of the different benthic species. It would be very nice if we only had to distinguish between filter feeders (feeding on phytoplankton and detritus present in the water column), deposit feeders (feeding in microphytobenthos and detritus present in the sediment), and carnivores. Such a strict distinction, however, cannot be made. Several species show variability of mode of feeding. I give two examples. *Macoma balthica* is known to be a deposit feeder as well as a filter feeder (Hummel, 1985). Omnivorous *Nereis diversicolor* have two main feeding techniques: deposit feeding and mucous bag filter feeding. In addition, this species is a herbivore as well as a carnivore (Goerke, 1971). In muddy intertidal flats *N. diversicolor* appear to rely heavily on deposit feeding (Esselink & Zwarts, 1989).
Not only the type and quantity of food, but also the quality of food is important. For filter feeding *Macoma balthica* diatoms rather than *Phaeocystis pouchetii* or orther flagellates will be the most important food source (Beukema & Cadée, 1990). Moreover, the caloric content (as measure of nutritional value) of suspended matter, taking together live and dead organic matter, seems to be a determining factor in the biomass and production of bivalves in estuaries (Laane, Etcheber & Relexans, 1987).

So, modelling of growth processes in macrozoobenthos has to deal with a fair amount of variability. In the benthic submodel of the ecosystem model of the Ems Estuary only deposit feeders and filter feeders were distinguished as functional groups. With respect to non-living organic matter labile, detrital and refractory organic compounds were distinguished (Baretta & Ruardij, 1988).

OVER WINTER SURVIVAL

Some macrozoobenthic species are sensitive to low temperatures during winter, e.g. *Lanice conchilega Nephtys hombergii* more species will be affected in abundance by the mechanical damage due to ice-scouring in winters. The effect of low winter temperatures varies with the height of the intertidal flats where the species are living (Beukema, 1984). In subtidal macrozoobenthos survival during a severe winter proved correlated to the level and duration of low temperatures (Beukema et al., 1988).

So, for some species variation of severeness of winters is an important factor in dynamics of population size. This should not be disregarded in modelling.

INTRA- AND INTERSPECIFIC INTERACTIONS

In regulation of numbers in a population intra- as well as interspecific interaction processes may be important.

Regarding intraspecific interactions I want to refer to results obtained in the French Programme National de Déterminisme du Recrutement showing that in adult populations of *Cerastoderme edule* settlement of postlarvae and succesfull development of juveniles is counteracted (Bachelet et al., 1991). Adult cockles have been shown to be predators of settling cockle larvae (André, 1991).
Interspecific interactions are known or assumed to exist in a number of species. The predator *Nephtys hombergii* may significantly reduce the numbers of other polychaetes, e.g. *Scoloplos armiger* and *Heteromastus filiformis* (Beukema, 1987; Schubert & Reise, 1986). *Carcinus maenas* may prevent the development of dense beds of *Cerastoderma edule* (Jensen & Jensen, 1985), whereas high densities of *C. edule* were found to negatively affect numbers of *Corophiumm volutator* (Jensen, 1985). In the Dollard (Ems Estuary) Essink & Kleef (1988) assume a negative interaction between the polychaetes *Nereis diversicolor* and *Marenzelleria viridis*.
But even when we are able to model these known interspecific interactions, we are not sure that we did not miss an important one, which even may cause the model to explode. Is there any experience in this field?

Aknowledgement.

Thanks are due to Gerard M. Janssen (Tidal Waters Division, Haren, NL) for his comments on a draft of this contribution.

REFERENCES

André, C., 1991. Influence of adult density on recruitment in Cerastoderma edule (Bivalvia). Proceedings 25th European Marine Biology Symposium, Sept. 1990, Ferrara, Italy (in press)

Bachelet, G., J. Guillou & P.J. Labourg, 1991. Adult-larval and juvenile interactions in the suspension feeding bivalve, Cerastoderma edule: field observations and experiments. Proceedings 25th European Marine Biology Symposium, Sept. 1990, Ferrara, Italy (in press)

Baggerman, B., 1953. Spatfall and transport of Cardium edule L. Arch. Néerl. Zool. 10: 315-342.

Baretta, J. & P. Ruardij, 1988. Tidal flat estuaries. Simulation and analysis of the Ems Estuary. Ecological Studies Vol. 71, Springer Verlag, Berlin etc., pp. 353.

Beukema, J.J., 1984. Zoobenthos survival during severe winters at high and low tidal flats in the Dutch Wadden Sea. In: J.S. Gray & M.E. Christiansen (eds.), Marine biology of polar regions and effects of stress on marine organisms. J. Wiley, Chichester: 351-361.

Beukema, J.J., 1987. Influence of the predatory polychaete Nephtys hombergii on the abundance of other polychaetes. Mar. Ecol. Prog. Ser. 40: 95-101.

Beukema, J.J., 1991. Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea. Proceedings 7th International Wadden Sea Symposium, Oct. 1990, Ameland, The Netherlands (in press).

Beukema, J.J., & K. Essink, 1986. Common patterns in the fluctuations of macrozoobenthic species living at different places on tidal flats in the Wadden Sea. Hydrobiologia 142: 199-207.

Beukema, J.J., J. Dörjes & K. Essink, 1988. Latitudinal differences in sur-vival during a severe winter in macrozoobenthic species sensitive to low temperatures. Senckenbergiana marit. 20: 19-30.

Beukema, J.J. & G.C. Cadée, 1990. Growth rates of the bivalve Macoma balthica in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. Mar. Ecol. Prog. Ser (in press).

Beukema, J.J. & J. de Vlas, 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve Macoma balthica from the Wadden Sea to the North Sea. Mar. Ecol. Prog. Ser. 52: 193-200.

Dankers, N. & J.J. Beukema, 1981. Distributional patterns of macrozoobenthic species in relation to some environmental factors. In: N. Dankers, H. Kühl & W.J. Wolff (eds), Invertebrates of the Wadden Sea. Balkema, Rotterdam: 69-103.

Esselink, P. & L. Zwarts, 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of Nereis diversicolor. Mar. Ecol. Prog. Ser. 56: 243-254.

Essink, K. & H.L. Kleef, 1988. Marenzelleria viridis (Verril, 1873)(Polychaeta: Spionidae): a new record from the Ems Estuary (The Netherlands/Federal Republic of Germany). Zoölogische Bijdragen, Leiden 38: 1-13.

Goerke, H., 1971. Die Ernährungsweise der Nereis-Arten (Polychaeta, Nereidae) of the German coasts. Veröff. Inst. Meeresforsch. Bremerh. 13: 1-50.

Hummel, H., 1985. Food intake of Macoma balthica (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 19: 52-76.

Jensen, K.T., 1985. The presence of the bivalve Cerastoderma edule affects migration, survival and reproduction of the amphipod Corophium volutator. Mar. Ecol. Prog. Ser. 25: 269-277.

Jensen, K.T., & Jensen, J.N., 1985. The importance of some epibenthic predators on the density of benthic macrofauna in the Danish Wadden Sea. J. Exp. Mar.

Biol. Ecol. 89: 157-174.

Kristensen, I., 1957. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Néerl. Zool. 12: 351-453.

Kühl, H. 1951. Über die Siedlungsweise van Mya arenaria. Verh. d. dtsch. Zool. Ges. Wilhelmshaven: 385-391.

Laane, R.W.P.M., H. Etcheber & J.C. Relexans, 1987. Particulate organic matter in estuaries and its ecological implication for macrobenthos. Mitt. Geol.-Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderband 64: 71-91.

Schubert, A. & K. Reise, 1986. Predatory effects of Nephtys hombergii on other polychaetes in tidal flat sediments. Mar. Ecol. Prog. Ser. 34: 117-122.

COMMUNITY OXYGEN BUDGETS OF SEAGRASS BEDS AND MICROBAL MATS ON THE BANC D'ARGUIN, MAURITANIA

S.A. de Jong[1], P.A.G. Hofman[2], A.J.J. Sandee[3], P.H. Nienhuis[1]

[1]Ministry of Transport and Public Works, North Sea Directorate
P.O. Box 5807, 2280 HV Rijswijk, The Netherlands

[2]P.C.van Hall Instituut, Verlengde Hereweg, 9721 AJ Groningen, The Netherlands

[3]Delta Institute For Hydrobiological Research,
Vierstraat 28, 4401 EA Yerseke, The Netherlands

ABSTRACT

During May 1988 a study on the oxygen budgets of seagrass beds and microbial mats was carried out at the Banc d'Arguin, Mauritania. Bell jar and microelectrode measurements were carried out simultaneously in the intertidal and subtidal zones to determine the relative contribution of each algal class. From the microelectrode data in situ measurements are compared with P-I curves.

On the upper intertidal flats, which were extremely muddy, mats of Vaucheria sp. alternated with spots of benthic diatoms, whereas at the intertidal zone of the sandy beaches only diatoms were found. Gross production of the latter group of microalgae ranged between 225 and 490 mg C m^{-2} d^{-1}. Intertidal and subtidal zones with the seagrasses Zostera noltii Hornem. and Cymodocea nodosa were distinguished. Only Z. noltii was present in both the intertidal and subtidal zone up to a depth of 1-2 m; below that depth C. nodosa dominated at sufficient irradiance. Daily gross production rates ranged between 1960 and 4240 mg C m^{-2} d^{-1} for Z. noltii and 2960 mg C m^{-2} d^{-1} for Cymodocea. At ca. 4 to 6 m depth subtidal microalgae, dominated by green algae, were responsible for 880 to 2615 mg C m^{-2} d^{-1}. Over the entire light receiving zone total gross production rates ranged from 5900-6860 mg C m^{-2} d^{-1}. The consumption lay between 3720 and 5140 mg m^{-2} d^{-1}. From these data net production rates of 1240 to 2980 mg C^{-2} d^{-1} were calculated.

From the seagrass species C. nodosa had the highest productivity, 30 mg C g AFDW^{-1} d^{-1}, whereas that of Z. noltii was 19 ± 4 mg C g AFDW^{-1} d^{-1} (n=4). Up to a biomass of 200 g AFDW m^{-2} no decline of the production per unit biomass was seen due to self-shading. From in situ measurements the overall productivity of intertidal benthic diatom mats was 10 mg C mg chl-a^{-1} d^{-1} at the mud flat and 22 mg C mg chl-a^{-1} d^{-1} at the more sandy beaches. On the mud flats the contribution of Vaucheria mats and seagrass present in intertidal pools must be significant since respiration exceeded diatom production by a factor 2. Productivity for the subtidal green algae varied between 30 and 64 mg C mg chl-a^{-1} d^{-1}.

Due to the prevailing NE winds organic matter is transported from the desert. In SW direction a gradual increase is seen in gross production of each algal class as well as the amount of detritus. Furthermore the seagrass ecosystem has high turnover rates in each zone.

BENTHIC DYNAMICS IN THE SKAGERRAK-KATTEGAT AREA SUGGEST MAJOR IMPORTANCE OF LARGE-SCALE, PELAGIC PRODUCTION RELATED FACTORS.

Alf B. Josefson and Jorgen Nørrevang Jensen

National Environmental Research Institute
DK-2920 Charlottenlund, Denmark

ABSTRACT

Quantitative data on macrobenthos collected in the two decades 1970 and 1980 in the Skagerrak and northern half of the Kattegat show similar temporal changes in the scale of hundreds of kilometers for major population variables.

Biomass showed a general increase and a major part of the increase in the non-echinoid proportion was due to two species, the suspension-feeding ophiuroid Amphiura filiformis and the deposit-feeding polychaete Heteromastus filiformis. Both species showed a marked increase in abundance in the first half of the 1980s. Data on somatic growth for Amphiura suggest higher growth rates in the 80s than in the 70s despite higher total biomass and abundance in the latter decade. Also growth showed a major increase in the beginning of the 80s.

The most simple explanation of the observed changes is that they represent a biostimulation event mediated by major food pulses, i.e. sedimenting organic matter, to the bottoms in the actual period. This interpretation is supported by data on water drainage from surrounding land areas and nutrient input to the sea, which showed high values during a number of years during the observed increases in the benthos.

Our interpretation is in accordance with the view of benthos as a compartment being intimately coupled to pelagic production, rather than being a detatched system living its own life.

INTRODUCTION

While there is a general agreement that many coastal areas in northwestern europe in recent years are experiencing eutrophication (e.g. Rosenberg 1985), there is currently a discussion about wether this also is the case in more open sea areas, such as the North Sea and Skagerrak-Kattegat area (Gray 1990). Previous investigations in both of these areas have shown that benthic biomass has increased in recent years in most places also at open sea stations (Rosenberg et al. 1987, Josefson 1990, Kroncke 1990) . At the same time it is clear, at least in the Skagerrak-Kattegat area, that the input of nutrients to, as well as winter concentrations of nutrients in, the sea has increased (Andersson & Rydberg 1988, Ærtebjerg et al. 1990). Although the stages of energy flow between nutrient levels in the surface waters and possible effects on the bottom essentially is in a black box, there seem to be few alternate explanations to an increased pelagic production and increased sedimentation to account for the increased benthic biomass.

While previous work has shown that there has been a general increasing trend in the area for totals and amphiuroids in the last 15 years (Josefson 1990), there has been no attempt to closer examine agreement in variation patterns between stations at the species level. Long-term comparison of faunal similarity, based on all species, at station 1 in this study and a similar station off the Northumberland coast suggested a major shift between the 1970s and the 1980s (Austen et al. 1991).

In this contribution we provide further support for the 'enrichment hypothesis' as one explanation of recent changes in the benthos in the Skagerrak-Kattegat area. We present time series data on abundance and biomass of the two species *Amphiura filiformis* and *Heteromastus filiformis* which are two of the most important species accounting for the biomass increase in this area. In addition we present data on individual growth and production of the former species. The data were gathered at stations situated over a distance of more than 250 km.

MATERIAL AND METHODS

Seven stations at water depths between 50 and 300 m were selected in the Skagerrak - Kattegat area (Fig. 1). The rationale for selection was that the time series from these stations are the only ones from open sea stations that exist, to our knowledge, with appr. annual samples and spanning over the shift between the 1970s and 1980s. The method used was traditional quantitative sampling and sieving on a 1 mm screen. The descriptions of the sites and methods used has been given elsewhere (Josefson 1990). The position of station 7 was from 1982 changed appr. 6 nautical miles to the north to a place at appr. the same water depth.

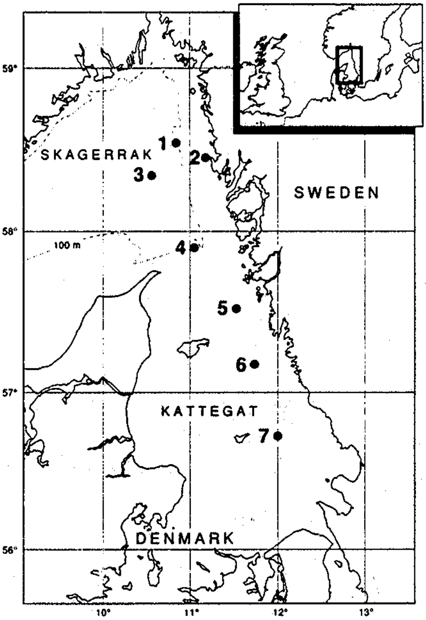


Fig. 1. *Map with sample stations*

RESULTS

Abundance and biomass

Changes in abundance of *Amphiura filiformis* at 6 of stations are shown in Fig.2. A common variation pattern with an increase from 1980 to the middle of the decade seems evident at most stations. To test if there was an overall correlation between the different time series, Friedmans' two-way anova by ranks (Sokal & Rohlf 1981) was used on data from the period 1979-1987. If more than one observation was available from the same year the mean was calculated, and if data was missing from one single year the mean was taken of the preceeding and the following year. When more than one years data in sequence was missing the mean from the closest following year was used. The results from the test (Table 1) showed significant covariation between the stations, irrespective if all stations were used or station 2 was excluded.

In Fig. 3 the time series on abundance of *Heteromastus filiformis* are shown. As was the case for the foregoing species there seemed to be a general increase in the first half of the 1980s. Testing for concordance (Table 1) showed significant covariation between stations irrespective if the 'aberrant' station 2 was excluded or not. When the biomass (wet weight) of this species was tested (Table 1) significant covariation was shown only when station 2 was excluded.

Biomass values of *Amphiura filiformis* were not available, so instead biomass of both *Amphiura filiformis* and *Amphiura chiajei* combined was tested for concor-

Fig. 2. Changes over time of *Amphiura filiformis* abundance at six stations in the Skagerrak - Kattegat area. Error bars are two standard errors. From station 3 the curve is shown for the amphiuroid *Amphilepis norvegica*.

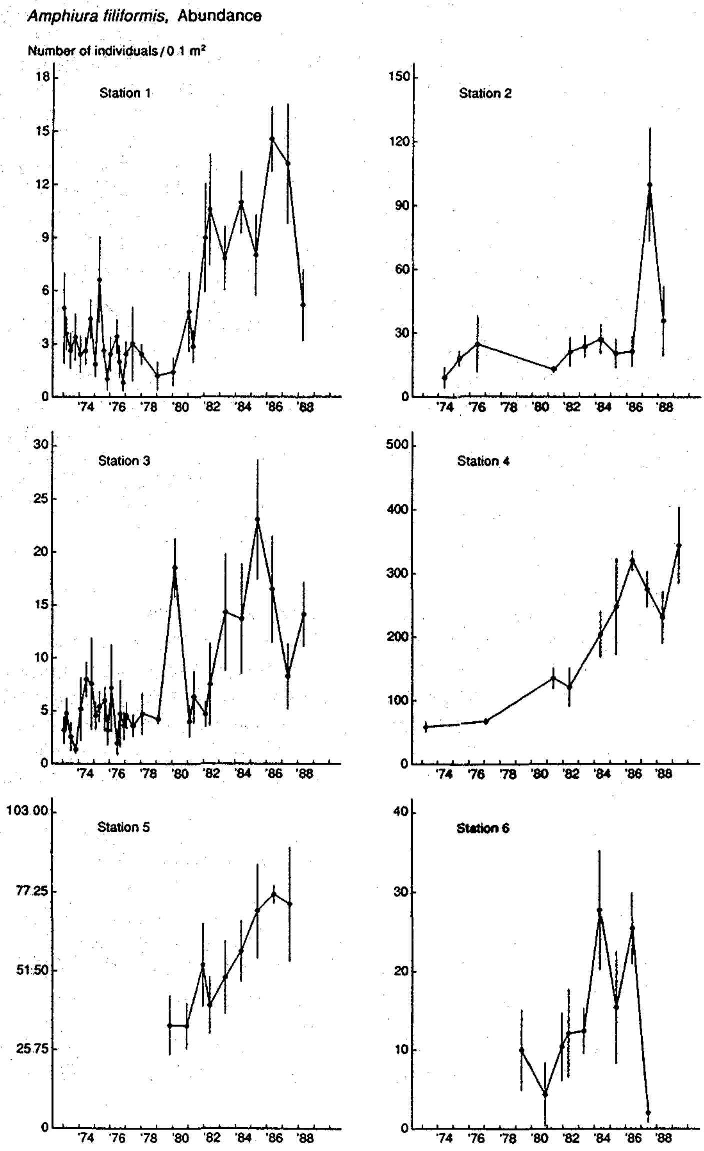


Fig. 3. Changes over time of *Heteromastus filiformis* abundance at six stations in the Skagerrak - Kattegat. Error bars are two standard errors.

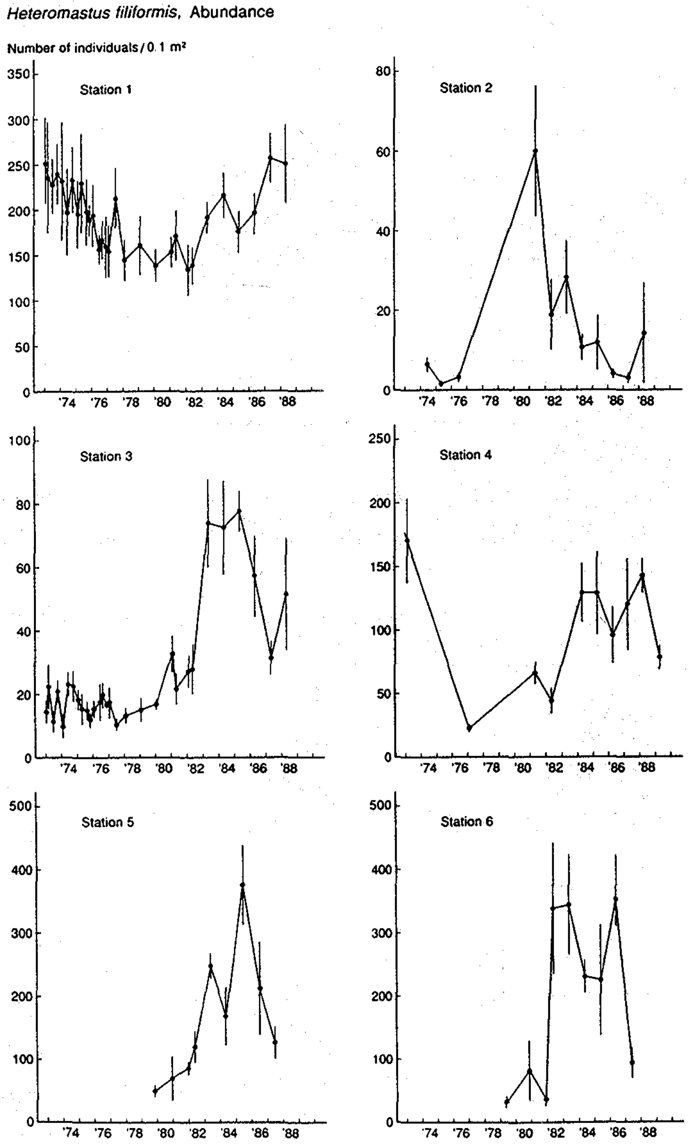


TABLE 1.

Results of testing for concordance of abundance and biomass of *Amphiura filiformis* and *Heteromastus filiformis* between stations in the Skagerrak-Kattegat over the period 1979 - 1987 (Friedmans' two-way anova by ranks). n = number of stations, and when n = 6 station no 2 has been excluded. P = likelyhood of no concordance, Sign. = level of significance, ** = P < 0.01, * = P < 0.05, ns = P > 0.05.

Variable	n	Test statistic	P	Sign.
Amphiura filiformis abundance	7	21.55	0.0058	**
	6	17.64	0.0241	*
Amphiura spp. biomass	7	24.54	0.0019	**
	6	20.44	0.0088	**
Heteromastus filiformis abundance	7	16.15	0.0402	*
	6	25.65	0.0012	**
Heteromastus filiformis biomass	7	10.47	0.2337	ns
	6	17.39	0.0263	*

dance (Table 1). Significant covariation between stations was shown with both combinations of stations.

The proportions accounted for by the two species are shown in Figs 4 and 5. It seems that from these figures that both species has increased also in a relative sense at many of the actual stations.

Fig. 4. Cumulative graphs showing proportions for *Amphiura filiformis* and *Heteromastus filiformis* of total number of individuals at seven stations in the Skagerrak - Kattegat. From station 3 data are shown for *Amphilepis norvegica*.

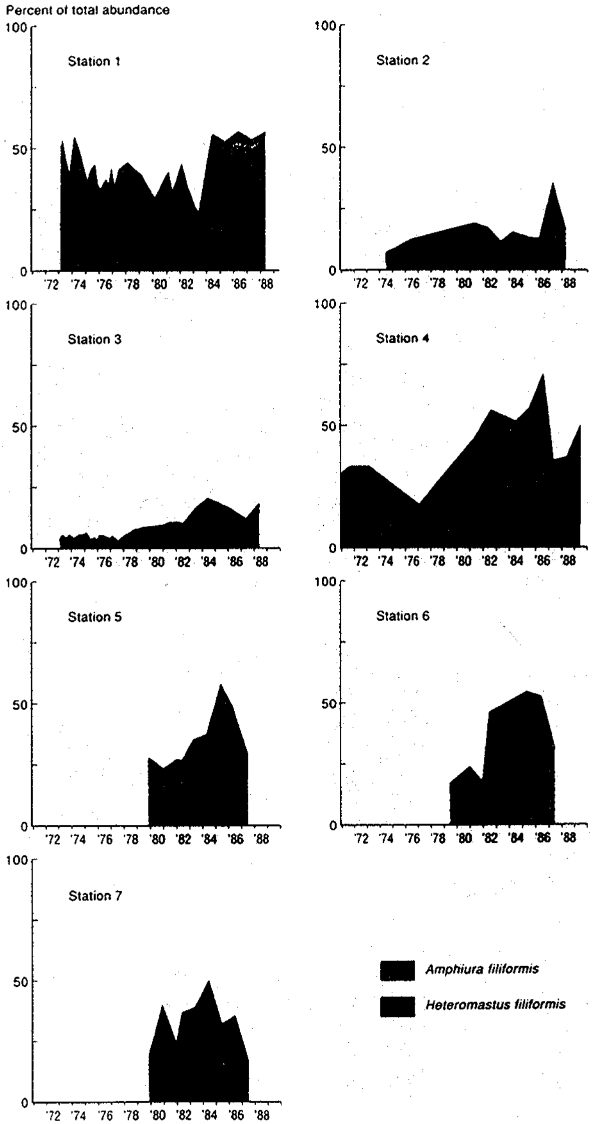
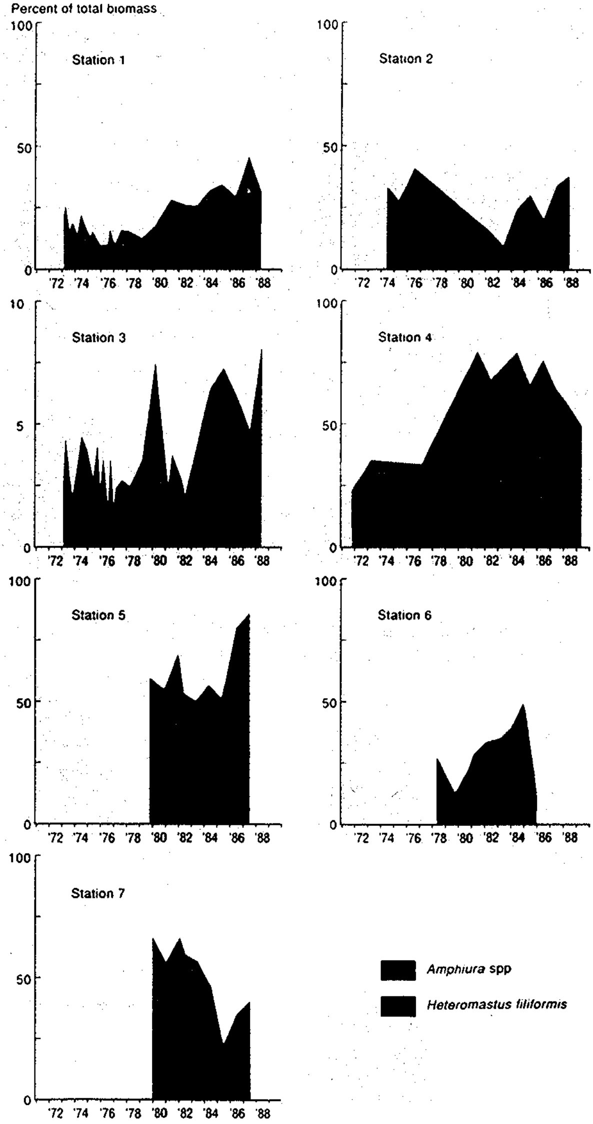


Fig. 5. Cumulative graphs showing proportions for *A. filiformis* and *H. filiformis* of total wet weight when echinoids were excluded at seven stations. See previous figure for further information.



Growth

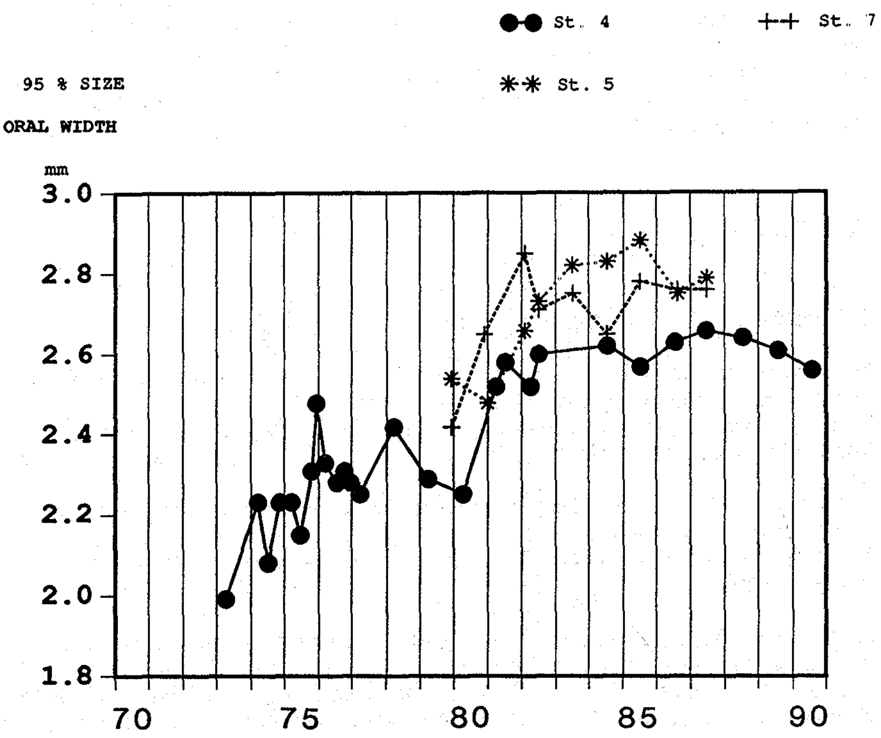


Fig. 6. Change over time of 95 % size (explained in the text) of *Amphiura filiformis* at stations 4 , 5 and 7.

From three of the stations individual growth of *Amphiura filiformis* was estimated from size frequency histograms. The details of this study is given in Josefson & Jensen (MS). As a measure of change in the maximum size we used the 95 % size, which is the upper size limit for 95 % of the individuals starting with the smallest individual. In practice this measure largely reflect changes in mean size of the composite cohort of the oldest individuals. The changes with time of this measure from the 3 stations are shown in Fig. 6. Also here a covariation between stations seems apparent and an increase in growth occurred in the beginning of the 1980s starting with 1980.

Estimating somatic growth of the cohort of 'recruits', the O-group, of *A. filiformis* was only possible at station 4. Fig. 7 shows increments of disc diameter and the size specific growth rates in periods of appr. a years length at this station from the two last decades. The data are at best minimum values (see Josefson & Jensen (MS) for explanation). The absolute growth seems clearly higher in the 1980s than in the 1970s, and this is particularily evident in terms of wet weight (Fig. 7 b,c). The size specific growth rates (sensu Ricker 1979) were not lower in the latter decade.

SYNTHESIS

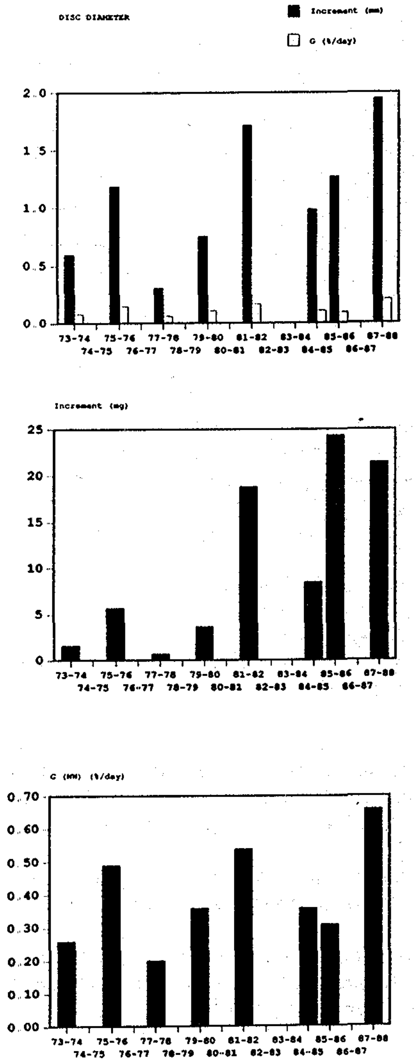
The results from the investigations presented here suggest that:

There is a remarkably high degree of covariation between stations of abundance and biomass in both species over the period 1979 - 1987.
There has been a general increase in abundance during the first half of the 1980s.
There are no apparent differences in the timing of the increase between the two species.
Growth of adult *Amphiura filiformis* at 3 of the stations showed a marked increase in the period 1979 - 1983.
Absolute growth of the O-group of *A. filiformis* at station 4 was higher in the 1980s than in the 1970s.

All these changes have occurred when at the same time total biomass have increased. If we assume that benthos, at these relatively great depths often is food limited, the changes in the beginning of the 1980s could be interpreted as a response to increased sedimentation of degradable organic material as a consequence of increased primary production. It may be more than a coincidence that the benthic increases occurred in a period when nutrient input to the sea was particularily high and oxygen deficiency was recognised for the first time in the Kattegat. During the period 1975 - 1988 the concentrations of nutrients before the spring bloom in southern Kattegat were higher in all years in the 1980s than in the 1970s (Ærtebjerg et al 1990). The highest concentrations were measured in 1981.

While we recognize that there are other possible explanations for the observed benthic changes, such as changed predation by demersal fish, they can probably only account for a part of the phenomenon. As such, the large-scale nature of the variations make biological interactions less likely to be the underlying cause than extrinsic factors. There are unfortunately no reliable data, to our knowledge, on changes in demersal fish stocks during the actual time period. Whereas *Amphiura*

Fig. 7. Somatic growth estimates for a mean sized individual in the 0-group of the *Amphiura filiformis* population at station 4. Estimates are for periods of appr. one years length. a. Increments and size specific growth rates in disc diameter. b. Increments of wet weight and c. weight specific growth rates.



may be predated on by haddock, cod and dab (Duineveld & van Noort 1986), *Heteromastus* is known to be less exposed to predation, at least as adult (e.g. Schaffer 1983). Yet the two species show similar abundance patterns. Climate has, through increased precipitation in the 1980s influenced the nutrient input from land through increased run-off, but there does not seem to be any apparent changes in other variables that can directly influence recruitment and growth in the benthos, such as temperature or salinity.

Some previous work suggest a tight coupling between pelagic production and the benthos in shallow water (e.g. Officer et al. 1982, Christensen & Kanneworff 1985). If our hypothesis of a coupling between winter nutrient levels and the benthic changes is valid, this implies that at least a part of the benthos is able to respond rapidly to production/sedimentation changes in the pelagial, also at relatively great depths. If so, our results reinforces the notion that accurate modelling of sedimentation of the pelagic primary production is essential in ecosystem models including benthos.

REFERENCES

Ærtebjerg, G., L.A. Jorgensen, P. Sandbech, J.N. Jensen and H. Kaas 1990. Marine områder - Vandmiljoplanens Overvågningsprogram 1989. Faglig rapport fra Danmarks Miljoundersogelser, nr. 8, 102 pp.(in Danish).

Andersson, L., L. Rydberg 1988. Trends in nutrient and oxygen conditions within the Kattegat: effects of local nutrient supply. - Estuar. coast. Shelf Sci. 26: 559-579.

Austen, M.C., J.B. Buchanan, H.G. Hunt, A.B. Josefson and M.A. Kendall 1991. Comparison of long-term trends in benthic and pelagic communities of the North Sea. - J. mar. biol. Ass. U.K. 71: 179-190.

Christensen, H., E. Kanneworff 1985. Sedimenting phytoplankton as major food source for suspension and deposit feeders in the Oresund. - Ophelia 24: 223-244.

Duineveld, G.C.A., G.J. van Noort 1986. Observation on the population dynamics of *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the southern North Sea and its exploitation by the dab, Limanda limanda. - Neth. J. Sea Res. 20: 85-94.

Gray, J.S. 1990. Statistics and the Precautionary Principle. Mar. Poll. Bull. 21: 174-176.

Josefson, A.B. 1990. Increase of benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s -effects of organic enrichment? - Mar. Ecol. Prog. Ser. 66: 117-130.

Josefson, A.B., J.N. Jensen (Manuscript). Increased growth of *Amphiura filiformis* in the 1980s supports the hypothesis of organic enrichment in the Kattegat-Skagerrak area! - To be subm. to Mar. Biol.

Kröncke, I. 1990. Macrofauna standing stock of the Dogger Bank. A comparison: II. 1951-1952 versus 1985-1987 Are changes in the community of the northeastern part of the Dogger Bank due to environmental changes? - Neth. J. Sea Res. 25: 189-198.

Officer, C.B., T.J. Smayda and R. Mann 1982. Benthic filter feeding: a natural eutrophication control. - Mar. Ecol. Prog. Ser. 9: 203-210.

Ricker, W.E. 1979. Growth rates and models. In: W.S. Hoar, D.J. Randall, D.J. Brett (eds): Fish Physiology 3: 678-743. Academic Press Inc.

Rosenberg, R. 1985. Eutrophication - the future marine coastal nuisance? - Mar. Poll. Bull. 16: 227-231.

Rosenberg, R., J.S. Gray, A.B. Josefson and T.H. Pearson 1987. Petersen's benthic stations revisited. II Is the Oslofjord and eastern Skagerrak enriched ? - J. exp. mar. Biol. Ecol. 105: 219 -251.

Shaffer, P.L. 1983. Population ecology of *Heteromastus filiformis* (Polychaeta: Capitellidae). - Neth. J. Sea Res. 17: 106-125.

Sokal, R.R., F.J. Rohlf 1981. Biometry, 2nd edn. W.H. Freeman & Co., San Francisco.

SPATIAL AUTOCORRELATION: TROUBLE OR NEW PARADIGM?

Pierre Legendre

Département de sciences biologiques, Université de Montréal,
C.P. 6128, succursale A, Montréal, Québec, Canada H3C 3J7

Preprint of a Paper submitted to Ecology as part of a Special Feature

INTRODUCTION

Spatial autocorrelation may be loosely defined as the property of random variables that are observed to take values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations. Autocorrelation is a very general property of ecological variables and, indeed, of all variables observed along time series (temporal autocorrelation) or across geographic space (spatial autocorrelation).

Most natural ecological phenomena display geographical patchiness, and it is found at all spatial scales - from microns to continental and ocean-wide scales. Picturing the spatial variation of the variable(s) under study in the form of a map shows the structure to be smoothly continuous, or else marked by sharp discontinuities. Most real-case studies concern only a part of a spatial structure, however; the special case where the part under study essentially looks like a gradient is discussed at more length in the Appendix.

The statistical problem that accompanies the spatial structuring of ecological data can be illustrated using the following common case of spatially autocorrelated data. The observed values of the variable of interest - for instance, species composition - are most often influenced, at any given locality, by the species assemblage structure at surrounding localities, because of contagious biotic processes such as growth, reproduction, mortality, migration, and so on. In such a case, since the value at any one locality can be at least partly predicted by the values at neighboring points, these values are not stochastically independent from one another. This may come as a surprise to ecologists who have been trained in the belief that nature follows the assumptions of classical statistics, one of them being the independence of the observations. However, field ecologists know from experience that living beings in nature are distributed neither uniformly nor at random; the same applies to the physical variables that we use to describe environments. Following hierarchy theory (Allen and Starr, 1982), we may look at the environment as primarily structured by large-scale physical processes - geomorphologic processes on land, currents and winds in fluid environments - that, through energy inputs, cause the appearance of gradients on the one hand, and of patchy structures separated by discontinuities (interfaces) on the other. These large-scale structures induce the formation of similar responses in biological systems, spatially and temporally. Within these relatively homogeneous zones, smaller-scale contagious biotic processes take place that cause the appearance of more spatial structuring through reproduction and death, predator-prey interactions, food availability, parasitism, and so on. Spatial heterogeneity is then functional in ecosystems, and not the result of some random, noise-generating process, so that it becomes important to study it for its own sake. One of the consequences is that ecosystems without spatial structuring would be unlikely to function. Imagine the consequences: large-scale homogeneity would cut down on diversity of habitats, feeders would not be found close to their food, mates would be located at random throughout the landscape, newborns would be spread around instead of remaining in favorable environments, and so on . Irrealistic as this may seem, this view is still common in many of our theories and models describing population and community functioning. This shift in views translates into a new paradigm for ecologists: spatial structuring is an important component for ecosystems. The first message of this paper is then that we have to revise our theories and models, to make them include realistic assumptions about spatial and temporal structuring of communities. The second message is that statistical concepts and techniques are now becoming available to handle such data.

Autocorrelation in a variable brings with it a statistical problem: it impairs our ability to perform standard statistical tests of hypotheses. The reason can best be illustrated using the case of the correlation coefficient. The problem lies in the fact that when both variables are positively autocorrelated, the confidence interval estimated by the classical procedure around a Pearson correlation coefficient is narrower than it is when calculated correctly, so that one declares too often that the coefficient is significantly different from zero (Fig. 1; see Bivand, 1980). With all other standard statistical tests, positive autocorrelation induces the same bias: computed test statistics are too often declared significant. Negative autocorrelation may produce the opposite effect, for instance in ANOVA. This problem is discussed in more detail by Cliff and Ord (1981).

This question can be contemplated from the point of view of the degrees of freedom: in classical statistical testing, one counts one degree of freedom for each independent observation, and this allows one to choose the statistical distribution appropriate for the given test. As we have seen above, the problem with autocorrelated data is their lack of independence, or in other words the fact that new observations do not each bring with them one full degree of freedom. Indeed,

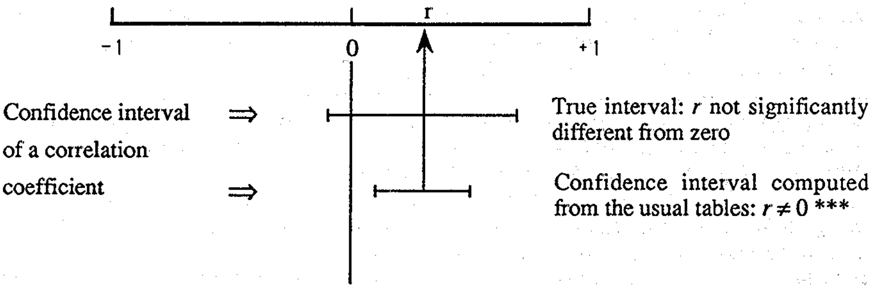


Fig. 1. Effect of spatial autocorrelation on tests of correlation coefficients for randomly generated, positively autocorrelated data.

knowledge of the variable's value at some locations gives the observer some prior knowledge of the value the variable will take at new locations. The consequence is that these new observations cannot be counted for one full degree of freedom. Corrections are available for the number of degrees of freedom and will be mentioned below.

The scope of this paper is threefold. First, I will show how spatial autocorrelation can be described and measured. Next, I will describe how valid tests can be performed. Finally, I will give substance to the new paradigm by presenting ways of introducing spatial structures into ecological modeling. The next paper of this Special Feature (Dutilleul and Fowler, 1991) addresses the companion problem of designing controlled experiments, especially in nature, in a spatially structured environment. The presence of spatial autocorrelation (two sites located at nearby locations are unlikely to be independent from one another) overlays the better--known problem that no two sites are exactly alike (pseudo-replication).

ASSESSING SPATIAL STRUCTURES

The analysis of spatial ecological patterns comprises two families of methods. Point pattern analysis is concerned with the distribution of individual objects through space - for instance individual plants or animals. The chief purpose of this type of analysis is to determine whether the geographic distribution of data points is random or not, and to describe the type of pattern, in order to infer what kind of process may have created the observed structure. From this family of methods, the quadrat-density and the nearest-neighbor methods have been widely used in vegetation science (Galiano, 1982; Carpenter and Chaney, 1983). Point pattern analysis will not be discussed further here, as it has been authoritatively reviewed by a number of authors listed in the last section of this paper.

Surface pattern analysis, on the other hand, is concerned with the study of spatially continuous phenomena. The spatial distribution of the variables is known, as usual, through sampling at discrete sampling stations. One or several variables are observed, each observation point representing its surrounding portion of space; the analysis of continuous transect data, such as echolocation data, is not specifically discussed here. Surface pattern analysis includes a family of methods designed to answer a variety of questions, which can be summarized under the following headings.

(1) Description of spatial autocorrelation - Ecologists are first interested to determine whether autocorrelation is present in their data, or not. The objective may be to demonstrate that no spatial autocorrelation is present (or remains, after extracting it: see below), in order to make valid use of the standard univariate or multivariate statistical tests of hypotheses. Or, they may be interested to demonstrate that spatial autocorrelation is present, in order to use it in their conceptual or statistical models. Spatial structures are first described through so-called structure functions which allow the description of the relationships for various distance classes. The most commonly used structure functions are correlograms, variograms and periodograms, which have been reviewed in more detail by Legendre and Fortin (1989). A correlogram is a graph where autocorrelation values are plotted in ordinate, against distance classes among sampling stations (localities) in abscissa. Correlograms (Cliff and Ord, 1981) can be obtained for single variables (Moran's I or Geary's c autocorrelation coefficients), or for multivariate data (Mantel correlogram: Sokal, 1986). In all cases, a test of significance is available for each individual autocorrelation coefficient plotted in the correlogram; this allows to determine whether a spatial structure is present in the data. The shape of the correlogram also indicates the type of spatial structure. In a semi-variogram (often called variogram for simplicity), the function of autocorrelation plotted in ordinate is called semi-variance, a measure closely related to Geary's c autocorrelation coefficient; in the geostatistical tradition, semi-variances are not tested for significance, although they could be through the test developed for Geary's c. Statistical models can be fitted to variograms (linear, exponential, spherical, Gaussian .) that allow to relate the observed structure to hypothesized generating processes. Since they measure the relationship existing between pairs of observation points located a certain distance apart, correlograms and variograms can be computed for preferential geographic directions, or in an all-directional way when the phenomenon is assumed to be isotropic in space. When the structure under study may be

assumed to consist of a combination of sine waves propagated through space, a Schuster periodogram can be computed. In periodograms, the abscissa is either a period, or its inverse, a frequency; the ordinate is the amount of variance explained by the Fourier series (sum of sines and cosines) with the given frequency or period. Two-dimensional periodograms can be plotted for all combinations of directions and spatial frequencies (Priestley, 1964; Ripley, 1981; Renshaw and Ford, 1984).

(2) Estimation and mapping - Structure functions require an interpretation. Since their shape may not correspond to a single type of spatial structure, they have to be complemented by maps of various kinds representing the spatial variation of the variable(s) of interest, or sometimes the variations of the variables' variance. Recent reviews for ecologists are Burrough (1987) and Legendre and Fortin (1989). Several programs are available for mapping (Table 1). The easiest way to obtain a contour map of a single variable is to use inverse-square-distance, which is but one case of moving average interpolation (Ripley, 1981), or other such interpolation methods. The older method of trend-surface analysis (Student, 1914), in which the variation of the variable of interest is expressed as a function of the geographic coordinates of the sampling locations, does not produce very accurate maps except in the most simple cases; it remains useful when ecologists want to remove a simple spatial structure, for instance a spatial trend, or large-scale patches, from their data, either because they want to study finer-scale spatial structures, or because they hope that after extracting the spatial component, no significant spatial structure will be left in the data (see also Appendix). The use of trend-surface functions in spatial modeling is also discussed below (equation 5). More sophisticated maps may be obtained by the geostatistical method of kriging, that makes use of variograms (above) to take the spatial autocorrelation into account during the interpolation process. [Among other applications, kriging is interesting for ecologists in that it allows an unbiased estimation of the amount of a resource available in a given area (stock assessment) even after non-random sampling; but this is by no means an easy task (Simard et al., submitted). Notice however that if one of the classical types of random sampling (Cochran, 1977) has been used in the survey sampling program, spatial means can be estimated in the usual way, using the design-based approach (de Gruijter and ter Braak, 1990).] Rough maps may be obtained by attributing to each locality the closest observed value (Thiessen or Dirichlet polygons method); or, sloping Delaunay triangles connecting triplets of observed points may be drawn in 3-dimensional plots; see Isaaks and Srivastava (1989). Finally, ecologists who are studying community structure, or other multivariate data sets, may not be interested in mapping individual species or variables. Representing the geographic variability of the whole data set can be done in either of three ways. The first one consists of computing a reduced-space ordination (correspondence analysis for species presence or abundance data; principal components or other

scalings for other data for which linear relationships may be assumed), and mapping the first few components separately; this method may fail to produce interesting maps, however, if the main components of the variability are not spatial. The second method, suggested by Legendre (1990), solves this problem; a canonical ordination (CCA or RDA: see below) of the multivariate data set is computed, constrained by a high-order trend surface equation; the resulting canonical variables are then mapped as above. The third method consists of using clustering techniques, with or without constraint of spatial contiguity, to divide the map into more homogeneous subsets; see the review by Legendre (1987).

Spatial and temporal autocorrelation are present jointly in historical biogeographic studies. Recent reviews include Wiley (1988a, b), Humphries et al. (1988), Brooks (1990) and Legendre (1990). The concept of correlograms has recently been extended by Gittleman and Kot (1990) to phylogenetic cladograms, in which the abscissa corresponds to systematic categories; besides phylogeneticists, cladograms are also used by cladistic biogeographers.

The additional objectives of performing valid statistical tests of hypotheses in the presence of autocorrelation, and testing statistical models that include spatial structure, are discussed in the following sections.

TESTS OF STATISTICAL SIGNIFICANCE VALID IN THE PRESENCE OF AUTOCORRELATION

When spatial autocorrelation has been demonstrated to be present in data, several solutions are open to the ecologist. First, one can attempt to remove the spatial dependency among observations so that the usual statistical tests can be used. This may be done either by removing samples until spatial independence has been attained (a solution which is not recommended because it implies a net loss of expensive information), or by filtering out the spatial structure using trend surface analysis (see sections above and below), or else by the method of spatial variate differencing (see Cliff and Ord, 1981, section 7.4).

The alternative is to modify the statistical method in order to take spatial autocorrelation into account; this is to be preferred when such a method is available, especially in cases where spatial structuring is seen not as a nuisance, but as a part of the ecological process under study (see Appendix). Cliff and Ord (1973) have proposed a method for correcting the standard error of the parameter estimates of the simple linear regression in the presence of autocorrelation. This method is extended to linear correlations, multiple regressions, and t-tests by Cliff and Ord (1981), and to the one-way analysis of variance by Griffith (1978, 1987). Cook and Pocock (1983) have suggested another method of correcting multiple regression parameter estimations by maximum likelihood, in the presence of spatial autocorrelation. Using a different line of approach, Legendre et al. (1990) have proposed a permutational method of analysis of variance for spatially autocorrelated data, in the common case where the classification criterion is a division of a territory into nonoverlapping regions, and one wants to test for differences among these regions. Bartlett (1978) has perfected a previously proposed mothod to correct for the effect of spatial autocorrelation due to an autoregressive process in randomized field experiments, by adjusting plot values by covariance on neighboring plots before the analysis of variance; see also the discussion by Wilkinson et al. (1983). [For experimental designs under heterogeneous field conditions, standard ANOVA may be appropriate even in spatially autocorrelated situations: see Dutilleul and Fowler (1991).]

A step forward is proposed by Clifford et al. (1989), who test the significance of the correlation coefficient between two spatial processes by modifying the estimation of both the standard error of the correlation coefficient and of the number of degrees of freedom. Empirical results show that their method works fine for positive autocorrelation; it could be generalized further, though, by applying to it the mathematics developed by Box (1954a, b) for the analysis of variance of repeated measurement data (time series). This is an area for promising future work.

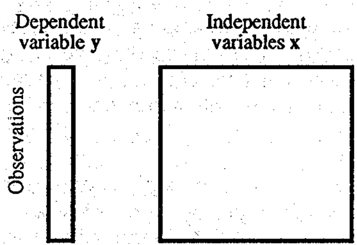
When methods specifically designed to handle spatial autocorrelation are not available, it is often possible to rely on permutational tests, where the significance is determined by some random reassignment of the observations; see Potvin and Roff (1991) for a review. This testing procedure does not rely on the standard assumptions of statistical tests (normality, homogeneity of variances, etc.), including the independence of the observations (Edgington, 1987). The Mantel test, used in a later section of this paper to model the effect of the data's spatial structure, is a permutation testing procedure. In complex problems, the difficulty of the permutation method lies in the designing of an appropriate randomization procedure.

INCLUDING SPATIAL STRUCTURE INTO MODELING: THE RAW DATA APPROACH

If spatial heterogeneity is so important for the functioning of ecosystems (Introduction), then models of ecosystem processes may fall short of being optimal unless they include the spatial organization of the players, populations and communities, among their predictor variables. Although this type of modeling is still in its infancy, two approaches have been proposed. The first one, described in this section, consists of expressing the spatial structure of the variables of interest as a linear combination of the geographic coordinates of the sampling stations. In the second approach (next section), the spatial structure is conveniently represented by a matrix of geographic distances among samples.

To understand how a spatial structure can be introduced into statistical models and combined with the environmental variables, we will look at various extensions of two classical approaches to data analysis: multiple regression and the analysis of variance. But let us first set the stage. In regression analysis (Fig. 2a), a set of independent, potentially predictive variables *x* are used to "explain" the variability of a dependent (or target) variable *y*. It is often postulated that the relationships can be described by a linear model of the form

(a) Multiple regression



(b) Analysis of variance

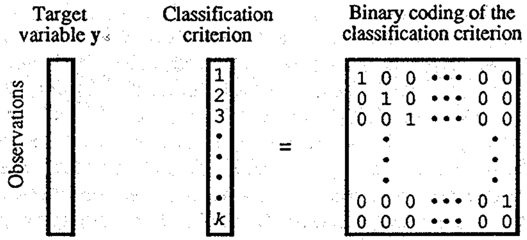


Fig. 2. Classical approaches to data analysis. (a) Multiple regression. (b) Single-classification analysis of variance (one-way ANOVA); there must be replicate observations within each group (not pictured).

$$y = \beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n + \varepsilon \qquad (1)$$

where ε represents the error term, which leads to estimates $\hat{y}$ of the values of *y* through the model :

$$\hat{y} = b_0 + b_1x_1 + \ldots + b_nx_n \tag{2}$$

In single-classification analysis of variance (one-way ANOVA), on the other hand, we are wondering how much of the target variable's variation can be explained by a classification criterion, through the decomposition model

$$SS_{total\ of\ y} = SS_{among\ groups} + SS_{within\ groups} \tag{3}$$

where the ***SS*** are the sums of squares designated by the subscripts; let us assume that there are replicate measurements within each class (group) of the classification criterion.

It is interesting to notice that the ANOVA variation partitioning can be computed using the multiple regression technology, provided that the classification criterion (***k*** classes) has first been coded into ***(k - 1)*** binary variables, as in Fig. 2b; ter Braak (1987) discusses this equivalence in more detail in an ecological framework. Ecologists can easily convince themselves of this equivalence by working out small examples on their favorite statistical package, using both methods; they will realize that the two ANOVA tables are identical.

The first extension of equation 2 is called partial regression analysis. It still applies to a single target variable **y**. In such an analysis (Fig. 3, arrows a), the explanatory potential which is specific to the matrix of environmental variables (r_1^2) can be studied after "partialling out" the site component. This preliminary operation can easily be done by regressing the binary site variables onto each environmental variable in turn and retaining only the regression residuals; the residuals are then used to model the target variable ***y***. In the same way, the specific effect of the site factor on ***y*** can be studied after partialling out the environmental variables' effect (r_2^2). Since the combined determination of both the environmental and the site variables on ***y*** (r_3^2) can also be computed, by multiple regression of ***y*** on both sets of predictive variables combined, the variation of ***y*** can be decomposed according to the following model:

$$SS_{total\ of\ y} = SS_{model} + SS_{residual} \tag{4}$$

where SS_{model} now contains three identifiable parts:

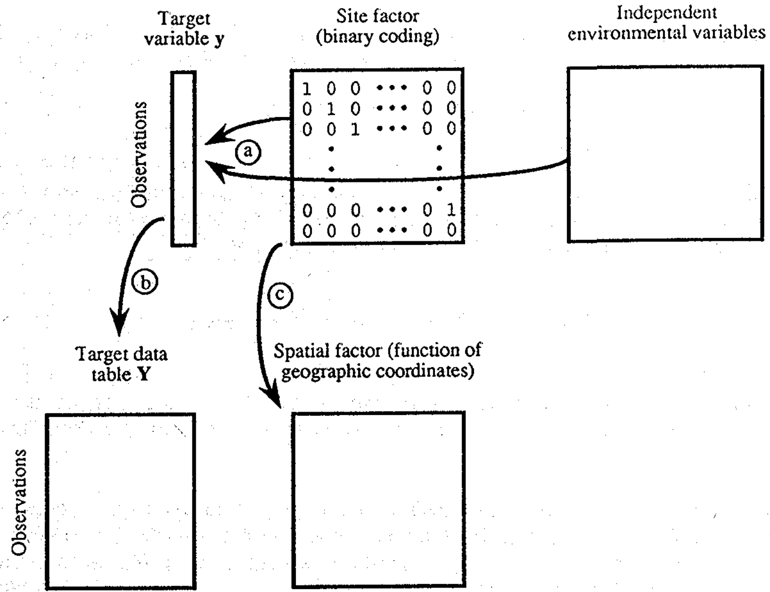


Fig. 3. Extensions of the linear modeling approach.
(a) Partition of the variance of y between the site factor and the environmental variables
(b) Explanation of a target data table instead of a single target variable, using canonical analysis.
(c) The "site factor" viewed as a "geographical location" factor; geographic coordinates are used instead of binary "site" variables.

1- The environmental variables fraction of the total variation of *y* is measured by the r_1^2 of the regression on the environmental variables after partialling out the binary site variables.
2- The among sites fraction is measured by the r_2^2 of the regression on the binary site variables after partialling out the environmental variables.
3- The interaction fraction is measured by $r_3^2-(r_1^2+r_2^2)$.

The second extension consists of using a whole table of target variables instead of a single one (Fig. 3, arrow b). There are then two alternatives. First, the regression coefficients of the dependent variables can be computed for all the dependent variables in *Y* at the same time, using the multivariate least-squares estimation equation $B = [X'X]^{-1} X'Y$ (Finn, 1974); the covariance structure of the dependent variables (*Y*) is not taken into account in this estimation. Alternatively, if *Y* is to be considered as a whole (when *Y* describes species assemblages, for instance), the statistical methods to use in place of multiple regression are called constrained ordination analyses by ter Braak (1987); two forms are of interest, depending on the nature of the data in the target data table: redundancy analysis and canonical correspondence analysis, both of which pertain to the canonical correlation family of methods. Redundancy analysis (RDA: van den Wollenberg, 1977) is to be used in the linear context, when the Euclidean distance is appropriate to represent the among-point relationships. Canonical correspondence analysis (CCA: ter Braak, 1986) is used in the unimodal context, when the chi-square distance is appropriate to describe the relationships among samples, as it is the case for species presence/absence or abundance data.

The third extension consists of replacing the table of binary site variables by a table of variables describing their spatial relationships (Fig. 3, arrow c), when the problems calls for that. Following Legendre (1990), Borcard et al. (in press) have suggested to use some high-order polynomial function of the geographic coordinates of the sampling locations, built from their *x* and *y* coordinates on a map, as is customary in trend-surface analysis. A third-order trend surface regression equation would have the form

$$f(x,y) = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \quad (5)$$

If we suppose that all the variables have been standardized, then there is no intercept term b_0 to worry about. Adding more and more terms into this polynomial equation should bring decreasing returns. Several stopping rules can be imagined. One of them would be to test for the added amount of explained variation when increasing the order of the equation, as in polynomial regression; spatial autocorrelation should bias the test of statistical significance, however. A variant is to include only the terms of each order (power 1, power 2, etc.) whose slope parameters (*b*) are significant; Borcard et al. (in press) have used this method to partition

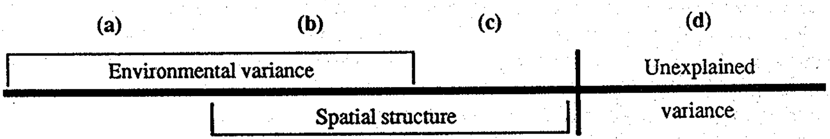


Fig. 4. Variance partitioning of the target data table; fraction (b) is the intersection of the environmental and spatial components.

the variation of multivariate target tables (using partial CCA) and of single ecological target variables (using partial multiple regression) into spatial and environmental components. Another stopping criterion is to increase the order of the polynomial trend-surface equation until the univariate correlogram of the residual surface, or the Mantel correlogram of the multivariate data set, becomes statistically non--significant. Four fractions of the variation can be identified, as above (Fig. 4); they can also be mapped and modeled separately if needed:

(a) Non-spatial environmental variation.
(b) Spatially structured environmental variation.
(c) Spatial variation of the target variable(s) that is not shared by the environmental variables.
(d) Unexplained, non-spatial variation.

The third fraction, 'c', is of special interest, since it points to a fraction of the variability that can be associated with a precise spatial structure - it is described by a function of the spatial coordinates ***x*** and ***y*** and may be mapped if necessary (Borcard and Legendre, in prep.) - but is not explained by the environmental variables at hand. In some cases, other environmental variables might be discovered that explain this fraction of variation. In other cases, this spatial fraction of variation may refer to biotic processes within the population or community that forms the target variable or data table, or to interactions of this population or community with other parts of the biotic community (disturbance dynamics, competition, predation, etc.).

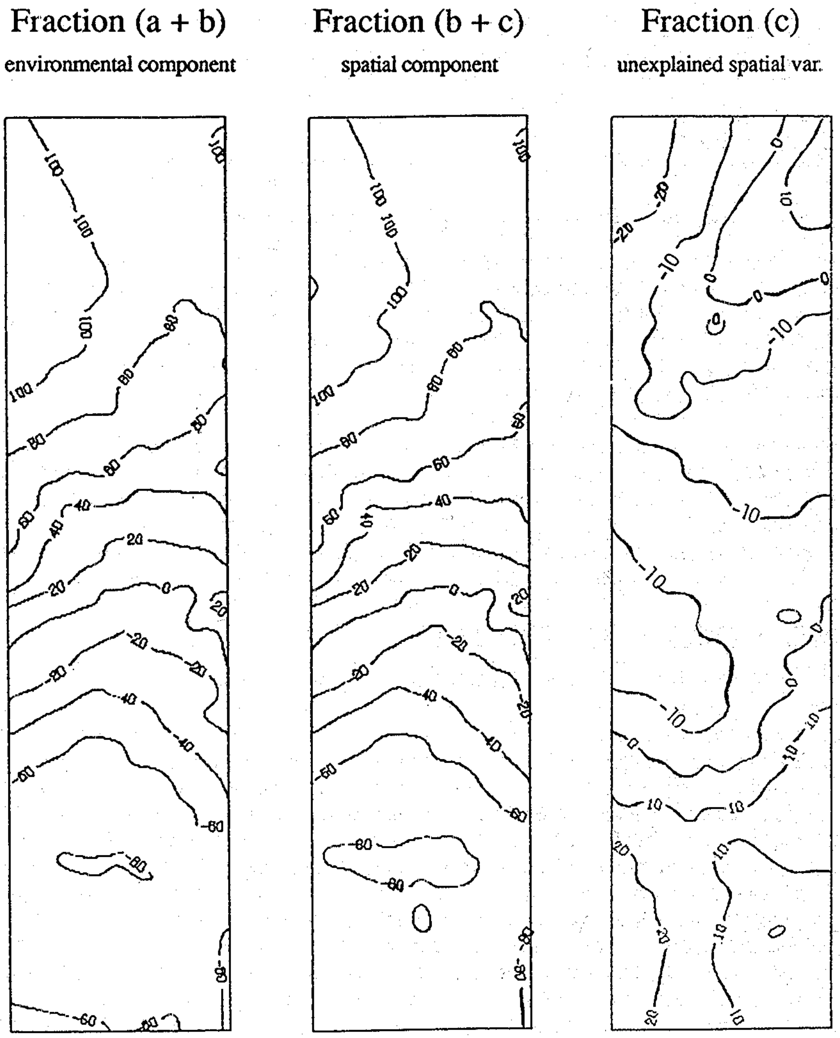
When fraction 'a' is very small, a false significant coefficient of determination could result if the common part 'b' was not partialled out, as it is the case in the many analyses where a target variable or data table is modeled by a set of environmental variables. Causality could falsely be attributed to the environmental variables, when in fact the correlation results from a common spatial structure present in both the dependent and independant data sets. This problem is discussed at some length by Legendre and Troussellier (1988).

Several examples of this partitioning procedure have been provided by Borcard et al. (in press). One of them concerns a community of Oribatid mites in a peat blanket in Québec, in a rectangular area located between a bog lake and the surrounding forest. The variance of the 35 taxa submitted to analysis was partitioned using five environmental variables on the one hand, and the following trend surface equation obtained by a forward selection procedure, on the other:

$$f(x,y) = b_1x + b_2y + b_4xy + b_5y^2 + b_9y^3 \tag{6}$$

Results of the partition obtained by partial canonical correspondence analysis are summarized in Table 1; notice that the interaction, 'b', between the two sets of

Fig. 5. Maps of the first canonical axes of fractions (a + b) [environmental component], (b + c) [spatial component], and (c) alone [unexplained spatial variation] of the Oribatid mite species data table. The lake shore is at the top of the map, the forest border at the bottom. The sampling area is 2.5 x 10 m. Contour values are not comparable among maps.


Fraction (a + b)
environmental component

Fraction (b + c)
spatial component

Fraction (c)
unexplained spatial var.

Table 1. Partition of the variation of the Oribatid mite assemblage.

Source of variation of the species data table	Fraction of variation
(a) Non-spatial environmental	13.7 %
(b) Spatially-structured environmental	31.0 %
(c) Non-environmental spatial	12.2 %
(d) Unexplained	43.0 %

independent variables is properly quantified. Fig. 5 presents three maps of the first canonical axes of various fractions of variation of the species data table. Notice the similarity between the maps for (a + b) and (b + c), which confirms the large amount of information (b) shared by these two maps. Notice also how different the map for (c) is from the other two; its significance is discussed in more detail in Borcard and Legendre (in prep.).

Legendre (1990) presents another example that simply involves canonical correspondence analysis instead of the partial form. The method is used to obtain an ordination of a species abundance data table which is constrained to be consistent with the geographic relations expressed by the trend-surface equation (5). The purpose is to obtain maps of the spatial structure component (called b + c above) of the data set, drawn from the canonical axes, as in the second map of Figure 5.

INCLUDING SPATIAL STRUCTURE INTO MODELING: THE MATRIX APPROACH

Another approach will now be presented to include "space" as a predictor in statistical models, on an equal footing with the usual set of environmental variables. The spatial structure can naturally be represented by a geographic distance matrix among sampling stations - or some modification of such a matrix, for instance some sort of a connection matrix (see below). In the typical case, the geographic (Euclidean) distance is computed for all pairs of sampling stations, based on their geographic coordinates, and assembled into a "spatial" distance matrix. If the biological and the environmental variables could also be represented in the form of distance matrices, then all three matrices could be compared by some form of correlation. Fortunately, a whole array of resemblance functions are available to compute these matrices (Sneath and Sokal, 1973; Orlóci, 1978; Legendre and

Legendre, 1983, 1984; Gower, 1985; Gower and Legendre, 1986); they are adapted to the different mathematical types of data (binary, qualitative, quantitative, mixed types), to the inclusion or exclusion of double-zeros, to the Q (comparison of objects) or R (comparison of variables) modes of analysis, and so on, so that one can model the correct concept of "resemblance" for the problem at hand.

Before going into the details of this modeling method, I need to introduce the Mantel test (1967), also called the Quadratic Assignment Procedure in psychometrics (Hubert and Schultz, 1976); this is the basic statistical instrument presently used for comparing distance matrices. In its basic form, the Mantel statistic is the sum of the cross products of the corresponding distances in two matrices. The Mantel statistic can easily be normalized to take values between -1 and +1, by first standardizing each of the distance matrices separately before computing the sum of cross-products; the Mantel statistic then becomes equivalent to a Pearson product-moment correlation coefficient. Because of the dependencies among values in a distance matrix, this correlation coefficient cannot be tested in the usual way. It is tested instead against a distribution of values obtained by randomly permuting the rows and columns of one of the distance matrices and recomputing the coefficient, each case corresponding to one of the possible realizations of the null hypothesis (Mantel, 1967). It should be noticed that a correlation between two distance matrices is not equivalent to the correlation between the two variables behind these matrices, or to the canonical correlation between two data tables; while canonical correlation analysis measures the correlation between two data tables, a matrix correlation r_{AB} measures to what extent the variations in the distances of matrix ***A*** correspond to the variations in ***B***. Other statistics have been suggested instead of Mantel's, to measure the correspondence between distance matrices: Dietz (1983) and Hubert (1985) have suggested nonparametric correlation coefficients, while Jackson (submitted) has worked from Procrustes statistics. As a suggestion for future work, a power analysis of these statistics should be performed to help decide among them, under various conditions.

The next step needed for causal modeling was the development of the partial Mantel test procedure by Smouse et al. (1986). The partial Mantel statistic, noted $r_{AB\cdot C}$, allows testing for the correlation between matrices ***A*** and ***B***, controlling for the effect of a matrix ***C***. With the same caveat as above, a partial Mantel statistic is to be interpreted much in the same way as a partial correlation, since the algebra is the same. The first role of a partial test is to check for possible false correlations, before interpreting data in a causal framework. Legendre and Troussellier (1988) have proposed to transfer to distance matrix modeling the bulk of knowledge acquired in causal analysis, and in particular the predictions made about the values of the simple correlations (De Neufville and Stafford, 1971) and the partial correlations (Legendre and Legendre, 1983, 1984) for different causal models. Fig. 6 provides the expectations for all possible causal models involving three matrices, in terms of the three simple and the three partial Mantel test values that can be computed.

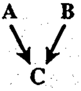
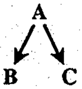
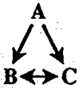
Model	**Expectations of the model**	**Model**	**Expectations of the model**
	$AC \neq 0$ $BC \neq 0$ $AB = 0$ $AB{\bullet}C \neq 0$ $BC{\bullet}A \neq 0$ $AC{\bullet}B \neq 0$ $AC{\bullet}B \geq AC$ $BC{\bullet}A \geq BC$		$AB \neq 0$ $BC \neq 0$ $AB \geq AC$ $AC{\bullet}B = 0$ $AB{\bullet}C \neq 0$ $BC{\bullet}A \neq 0$ $AB{\bullet}C \leq AB$ $BC{\bullet}A \leq BC$ $AB \times BC \approx AC$
	$AB \neq 0$ $AC \neq 0$ $AB{\bullet}C \neq 0$ $AC{\bullet}B \neq 0$ $BC{\bullet}A = 0$ $AC{\bullet}B \leq AC$ $AB{\bullet}C \leq AB$ $AB \times AC \approx BC$		$AB \neq 0$ $AC \neq 0$ $BC \neq 0$ $AB{\bullet}C \neq 0$ $AC{\bullet}B \neq 0$ $BC{\bullet}A \neq 0$

Fig. 6. Predictions of the four possible models of causal relationships involving three matrices, in terms of the expected results of the simple and partial Mantel tests. For simplicity, r_{AB} is noted AB, and so on. Stating that a relation is equal to zero means that the computed value should not be significantly different from zero, and conversely.

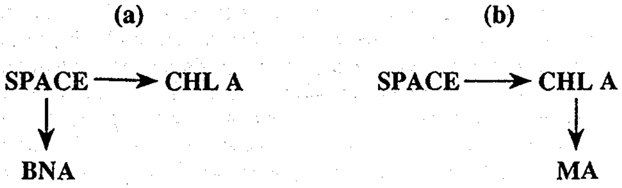


Fig. 7. Representation of the models supported by the data, (a) for the BNA, and (b) for the MA heterotrophic bacteria.

Ecological applications of this technique to models that include geographic distances are found in Burgman (1987), Legendre and Troussellier (1988), and Legendre and Fortin (1989); other interesting applications of the partial Mantel test to anthropology and population genetics are found in Sokal et al. (1986, 1987). In the paper by Legendre and Troussellier (1988), the question is whether the well--established relationship between environmental heterotrophic bacteria and phytoplankton biomass (measured by chlorophylle a, CHL A) holds for two identifiable components of the bacterial heterotrophic community of a marine lagoon: the BNA bacteria, which are presumably of continental origin, and the MA, expected to be mostly of marine origin (abbreviations as in the original publication). Both bacterial variables are well correlated to CHL A, but this could be the result of a common spatial structure created by currents. The spatial structure is represented by a matrix, called SPACE, of Euclidean (or geographic) distances among the 63 sampling stations. The Mantel and partial Mantel statistics computed to choose

Table 2. Above the diagonal: simple Mantel statistics and associated probabilities. Below the diagonal: partial Mantel statistics, controlling for the effect of the third matrix, and associated probabilities. Tests of significance are one-tailed. Upper part: analysis of the BNA - CHL A - SPACE relations. Lower part: analysis of the MA - CHL A - SPACE relations.

	BNA	CHL A	SPACE
BNA	----	0.258 *	0.521 *
CHL A	-0.006 ns	----	0.505 *
SPACE	0.468 *	0.449 *	----
	MA	CHL A	SPACE
MA	----	0.325 *	0.223 *
CHL A	0.252 *	----	0.505 *
SPACE	0.073 ns	0.469 *	----

* : Mantel test significant ($p < 0.001$); ns : test not significant

between the two models are reported in Table 2. The non-significant partial Mantel relationship between BNA and CHL A, when the effect of SPACE is held constant, points to the model in Figure 7a, which contradicts the hypothesis of control of the continental heterotrophs by phytoplankton; on the contrary, the non-significant partial Mantel relation between MA and SPACE, when CHL A is held constant, points to the model in Figure 7b, which supports the hypothesis of phytoplankton control for the marine heterotrophs.

Progress is still to be made in this elementary form of modeling. Spatial relationships can be construed in other ways than as an Euclidean distance matrix. Authors have used transformations such as the inverse, or the inverse of the square of the Euclidean distance, that give more importance to the small distance values (Jumars et al., 1977); other authors prefer to use connection schemes such as rook's of king's connections (Cliff and Ord, 1981) for regular grids of samples, and Gabriel graphs or Delaunay triangulations (Upton and Fingleton, 1985) for irregularly spaced points. An important step will be to learn how to analyze the n-independent-matrix case, and to extend this type of analysis into path analysis; a proposal in this respect has already been made by Krackhardt (1988) for the special case of autocorrelated network data.

CONCLUSION

Studying spatial structures is both a requirement for ecologists who deal with spatially distributed data, and a challenge. It is the new paradigm for field ecologists interested in exploratory data analysis or in modeling ecological phenomena. Fortunately, statistical methodology is rapidly developing to assist us in doing so. As we have seen, most of the theories and models that we rely on to understand ecosystems assume, explicitly or not, some spatial structuring of the environment and of the biological communities. Until recently, we have been bound to ignore this by lack of appropriate methods for analyzing and modeling our data. This led us to stretch our statistics beyond their basic assumptions; and worse, we were overlooking one of the most important determinants of the functioning of ecosystems. This is easily realized when including the spatial structure into models of ecological systems: by doing so, the amount of explained variation often jumps to unexpected heights. This means, on the one hand, that it may be of no use to try to increase the fraction of explained variation by looking at more environmental variables, when the explanation of this fraction of the variability, that emerges of the analysis as unexplained spatial variation (fraction c in Fig. 4), is to be found in population or community-based spatial processes. It also means that much better predictions can obtain by including the spatial structure as such among the predictive variables. This will be done even more efficiently when nonlinear methods of modeling are introduced into spatial analysis.

FURTHER READING AND APPLICATIONS

Important references to the topics discussed above are the following. For point pattern analysis: Pielou (1977), Cicéri et al. (1977), Getis and Boots (1978), Ripley (1981, 1987), and Upton and Fingleton (1985). For surface pattern analysis: Cliff and Ord (1981), Ripley (1981), Upton and Fingleton (1985, 1989), Griffith (1987), as well as the review paper by Legendre and Fortin (1989). For kriging and other mapping methods: the books of David (1977), Journel and Huijbregts (1978), and Isaaks and Srivastava (1989), as well as the review paper by Lam (1983). On canonical ordination, required reading is the chapter by ter Braak (1987). Table 3 lists computer programs available from researchers to carry out the computations of the methods described in this paper; most of these methods are not available in major statistical packages. This list of programs is not exhaustive.

ACKNOWLEDGMENTS

This is a contribution of the Groupe d'Écologie des Eaux douces, Université de Montréal. Development of the raw data approach to spatial modeling, as well as the preparation of this Review, have been done during tenure of a Killam Research Fellowship of the Canada Council. This work was also supported by NSERC grant No. A7738.

LITERATURE CITED

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy - Perspectives for ecological complexity. Univ. of Chicago Press, Chicago.

Bartlett, M.S. 1978. Nearest neighbour models in the analysis of field experiments. Journal of the Royal Statistical Society series B 40: 147-174.

Bivand, R. 1980. A Monte Carlo study of correlation coefficient estimation with spatially autocorrelated observations. Quaestiones Geographicae 6: 5-10.

Borcard, D., P. Legendre, and P. Drapeau. 1991. Partialling out the spatial component of ecological variation. Ecology (in press)

Borcard, D., and P. Legendre. Environmental control and spatial structure in an Oribatid mite community (Acari, Oribatei). (In preparation)

Box, G.E.P. 1954a. Some theorems on quadratic forms applied in the study of analysis of variance problems, I. Effect of inequality of variance in the one-way classification. Annals of Mathematical Statistics 25: 290-302.

Box, G.E.P. 1954b. Some theorems on quadratic forms applied in the study of analysis of variance problems, II. Effects of inequality of variance and correlation between errors in the two-way classification. Annals of Mathematical Statistics

25: 484-498.

Brooks, D.R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. Systematic Zoology 39: 14-30.

Burgman, M.A. 1987. An analysis of the distribution of plants on granite outcrops in southern Western Australia using Mantel tests. Vegetatio 71: 79-86.

Burrough, P.A. 1987. Spatial aspects of ecological data. Pages 213-251 in Jongman, R.H.G., C.J.F. ter Braak, and O.F.R van Tongeren [eds.] Data analysis in community and landscape ecology. PUDOC, Wageningen.

Carpenter, S.R., and J.E. Chaney. 1983. Scale of spatial pattern: four methods compared. Vegetatio 53: 153-160.

Cicéri, M.-F., B. Marchand, et S. Rimbert. 1977. Introduction à l'analyse de l'espace. Collection de Géographie applicable. Masson, Paris.

Cliff, A.D., and Ord, J.K. 1973. Spatial autocorrelation. Pion, London.

Cliff, A.D., and Ord, J.K. 1981. Spatial processes: Models and applications. Pion, London.

Clifford, P., S. Richardson, and D. Hémon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45: 123-134.

Cochran, W.G. 1977. Sampling techniques, 3rd. ed. Wiley, New York.

Cook, D.G., and S.J. Pocock. 1983. Multiple regression in geographical mortality studies, with allowance for spatially correlated errors. Biometrics 39: 361-371.

David, M. 1977. Geostatistical ore reserve estimation. Developments in Geomathematics, 2. Elsevier Scient. Publ. Co., Amsterdam.

de Gruijter, J.J., and C.J.F. ter Braak. 1990. Model-free estimation from spatial samples: a reappraisal of classical sampling theory. Mathematical Geology 22: 407-415.

Dietz, E.J. 1983. Permutation tests for association between two distance matrices. Systematic Zoology 32: 21-26.

Dutilleul, P., and N. Fowler. 1991. Spatial heterogeneity and the design of ecological field experiments. Ecology (this volume).

Edgington, E.S. 1987. Randomization tests, 2nd ed. Marcel Dekker Inc., New York.

Finn, J.D. 1974. A general model for multivariate analysis. Holt, Rinehart and Winston, New York.

Galiano, E.F. 1982. Pattern detection in plant populations through the analysis of plant-to-all-plants distances. Vegetatio 49: 39-43.

Getis, A., and B. Boots. 1978. Models of spatial processes: an approach to the study of point, line and area patterns. Cambridge Univ. Press, Cambridge.

Gittleman, J.L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Systematic Zoology 39: 227-241.

Gower, J.C. 1985. Measures of similarity, dissimilarity, and distance. Pages 397-405 in Kotz, S., and N.L. Johnson [eds.] Encyclopedia of Statistical Sciences, Vol. 5. Wiley, New York.

Gower, J.C., and P. Legendre. 1986. Metric and Euclidean properties of dissimilarity coefficients. Journal of Classification 3: 5-48.

Griffith, D.A. 1978. A spatially adjusted ANOVA model. Geographical Analysis 10: 296-301.

Griffith, D.A. 1987. Spatial autocorrelation: a primer. Association of American Geographers, Washington, D.C.

Hubert, L.J. 1985. Combinatorial data analysis: Association and partial association. Psychometrika 50: 449-467.

Hubert, L.J., and J. Schultz. 1976. Quadratic assignment as a general data analysis strategy. British Journal of mathematical and statistical Psychology 29: 190-241.

Humphries, C.J., P.Y. Ladiges, M. Roos, and M. Zandee. 1988. Cladistic biogeography. Pages 371404 in Myers, A.A., and P.S. Giller [eds.] Analytical biogeography - An integrated approach to the study of animal and plant distributions. Chapman and Hall, London.

Isaaks, E.H., and R.M. Srivastava. 1989. Applied geostatistics. Oxford Univ. Press, New York.

Jackson, D.A. PROTEST: A PROcrustean randomization TEST of community--environment concordance. Ecology (submitted).

Journel, A.G., and Ch.J. Huijbregts. 1978. Mining geostatistics. Academic Press, New York.

Jumars, P.A., D. Thistle, and M.L. Jones. 1977. Detecting two-dimensional spatial structure in biological data. Oecologia (Berlin) 28: 109-123.

Krackhardt, D. 1988. Predicting with networks: Nonparametric multiple regression analysis of dyadic data. Social Networks 10: 359-381.

Lam, N.S.-N. 1983. Spatial interpolation methods: A review. American Cartographer 10: 129-149.

Legendre, L., and P. Legendre. 1983. Numerical ecology. Developments in environmental modelling, 3. Elsevier Scient. Publ. Co., Amsterdam.

Legendre, L., and P. Legendre. 1984. Écologie numérique, 2ième éd. Tome 2: La structure des données écologiques. Masson, Paris et les Presses de l'Université du Québec.

Legendre, P. 1987. Constrained clustering. Pages 289-307 in Legendre, P., and L. Legendre [eds.] Developments in numerical ecology. NATO ASI Series, Vol. G 14. Springer-Verlag, Berlin.

Legendre, P. 1990. Quantitative methods and biogeographic analysis. Pages 9-34 in Garbary, D.J., and G.R. South [eds.] Evolutionary biogeography of the marine algae of the North Atlantic. NATO ASI Series, Vol. G 22. Springer-Verlag, Berlin.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Legendre, P., N.L. Oden, R.R. Sokal, A. Vaudor, and J. Kim. 1990. Approximate analysis of variance of spatially autocorrelated regional data. Journal of Classification 7: 53-75.

Legendre, P. and M. Troussellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnology and Oceanography 33: 1055-1067.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27: 209-220.

Orlóci, L. 1978. Multivariate analysis in vegetation research, 2nd. ed. Junk, The

Hague.

Pielou, E.C. 1977. Mathematical ecology, 2nd ed. Wiley, New York.

Potvin, C., and D.A. Roff. 1991. Distribution-free and robust statistical methods: Viable alternatives to parametric statistics? Ecology (this volume).

Priestley, M.B. 1964. The analysis of two dimensional stationary processes with discontinuous spectra. Biometrika 51: 195-217.

Renshaw, E., and E.D. Ford. 1984. The description of spatial pattern using two--dimensional spectral analysis. Vegetatio 56: 75-85.

Ripley, B.D. 1981. Spatial statistics. Wiley, New York.

Ripley, B.D. 1987. Spatial point pattern analysis in ecology. Pages 407-429 in Legendre, P., and L. Legendre [eds.] Developments in numerical ecology. NATO ASI Series, Vol. G 14. Springer-Verlag, Berlin.

Simard, Y., P. Legendre, G. Lavoie and D. Marcotte. Mapping, estimating biomass and optimizing sampling programs for spatially autocorrelated data: Case study of the Northern Shrimp. Canadian Journal of Fisheries and Aquatic Sciences (in press)

Smouse, P.E., J.C. Long, and R.R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic Zoology 35: 627-632.

Sneath, P.H.A., and R.R. Sokal. 1973. Numerical taxonomy - The principles and practice of numerical classification. Freeman, San Francisco.

Sokal, R.R. 1986. Spatial data analysis and historical processes. Pages 29-43 in Diday, E. et al. [eds.] Data analysis and informatics, IV. Proc. Fourth Int. Symp. Data Anal. Informatics, Versailles, France, 1985. North-Holland, Amsterdam.

Sokal, R.R., P.E. Smouse, and J.V. Neel. 1986. The genetic structure of a tribal population, the Yanomama indians. XV. Patterns inferred by autocorrelation analysis. Genetics 114: 259-287.

Sokal, R.R., H. Uytterschaut, F.W. Rösing, and I. Schwidetzky. 1987. A classification of European skulls from three time periods. American Journal of Physical Anthropology 74: 1-20.

Student [W.S. Gosset] 1914. The elimination of spurious correlation due to position in time or space. Biometrika 10: 179-180.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C.J.F. 1987. Ordination. Pages 91-173 in Jongman, R.H.G., C.J.F. ter Braak, and O.F.R van Tongeren [eds.] Data analysis in community and landscape ecology. PUDOC, Wageningen.

Upton, G. J. G., and Fingleton, B. 1985. Spatial data analysis by example. Vol. 1: Point pattern and quantitative data. Wiley, Chichester.

Upton, G. J. G., and Fingleton, B. 1989. Spatial data analysis by example. Vol. 2: categorical and directional data. Wiley, Chichester.

van den Wollenberg, A.L. 1977. Redundancy analysis. An alternative for canonical correlation analysis. Psychometrika 42: 207-219.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biological Review 42: 207-264.

Wiley, E.O. 1988a. Vicariance biogeography. Annual Review of Ecology and Systematics 19:513-542.

Wiley, E.O. 1988b. Parsimony analysis and vicariance biogeography. Systematic Zoology 37:271-290.

Wilkinson, G.N., S.R. Eckert, T.W. Hancock, and O. Mayo. 1983. Nearest neighbour (NN) analysis of field experiments. Journal of the Royal Statistical Society series B 45: 151-211.

APPENDIX : THE SPECIAL CASE OF GRADIENTS

Ecologists are often studying small sections of larger-scale autocorrelated spatial structures. These sections may look like gradients when, for instance, a mountain slope or a river bank is the focus of the study. This type of study is so widespread that it has led to a considerable amount of ecological literature on gradient analysis (Whittaker, 1967; ter Braak, 1987). Gradients, on the other hand, can be seen as a spatial structure that can easily be expressed as a simple function of the x and y geographic coordinates of the sampling stations, and extracted from the data before further analysis, thus satisfying the so-called stationarity condition. In order to disentangle "true" from "false" gradients, as they are termed in Legendre et al. (1990), we need to introduce a little notation.

In a "true" gradient, the value z_{ij} observed at any location (i,j) can be expressed as a function of its geographic coordinates x_{ij} and y_{ij}, plus an error term ε_{ij} which is independent from location to location. Thus, a linear gradient could be modeled by

$$z_{ij} = b_0 + b_1 x_{ij} + b_2 y_{ij} + \varepsilon_{ij} \qquad (7)$$

In a true gradient, the error terms at neighboring points are not correlated with one another. A true gradient structure violates the stationarity assumption of most spatial analysis methods because the expected value, given by the first three terms on the right-hand side of model (7), varies from place to place as a function of the geographic coordinates. It should be removed from the data before proceeding, for instance by trend surface analysis (see above).

In a "false" gradient on the other hand, there is no change in expected value (given by b_0) throughout the surface, although the value observed at each locality is partly determined by neighboring values:

$$z_{ij} = b_0 + \sum f\,(z_{i\pm d,j\pm d}) + \varepsilon_{ij} \qquad (8)$$

In this model, d represents geographic distances away from the value z_{ij} that we are trying to describe. The summation is over the various distance classes, so that the value of interest is modeled as partly determined by some function f of all the other points on the surface. Assume for simplicity that the points sit on the nodes of a regular spatial grid. If a point is determined by its first neighbors only, then d concerns distance class 1 only and the process is called "autoregressive of order 1". In the case of positive autocorrelation, the surface looks like a gently wobbling landscape. Isolation-by-distance models that have been extensively studied by population geneticists pertain to this class of low-order autoregressive models. Now if the influence of data points on others carries a long way through geographic space (through several distance classes d), and in a more or less linear fashion (function f being, for instance, the inverse of the geographic distance times the value at this neighboring point), then the model might be

$$z_{ij} = b_0 + \sum (1/d) z_{i\pm d, j\pm d} + \varepsilon_{ij} \qquad (9)$$

and the surface will look more like a mountainous landscape. An ecologist who studies only one slope of such a landscape is well justified to retain the gradient in his analysis, instead of removing it as in the case of a true gradient, since this is the structure to be analyzed and explained.

The problem, of course, is to tell true gradients apart from false ones. Furthermore, real data may result from a combination of both. For instance, if one focuses on vegetation structure along a wetness gradient, then the vegetation at any one point is probably partly determined by the amount of water in the soil (which is in itself a physically autocorrelated process, but as far as vegetation is concerned can often be modeled as a pure geographic phenomenon), and partly by the species composition at neighboring sampling stations (reproduction and avoidance phenomena, etc.). So it is in his theory and hypotheses that an ecologist must look for guidance, when he tries to determine whether model (7) or (8) applies to his data. The difference is important only when tests of statistical hypotheses are involved, of course, and not for the simple description of spatial structures.

Table 3. The following programs are available to compute the various methods of spatial analysis mentioned in the text. Only those methods are listed that are not available in general-purpose statistical packages.

CANOCO	Canonical (i.e., constrained) ordination methods: CCA, RDA.
CLADAREA	Area cladistic analysis. Wagner tree reconstruction (parsimony)*.
COCOPAN	ANOVA for spatially autocorrelated regional data.
COMPONENT	Construction and comparison of area cladograms.
CONTOUR 81	Locally weighted polynomial interpolation. Contour mapping.
CORR2D	Two-dimensional correlogram.
GEO-EAS	Variogram, kriging. Contour mapping.
GEOLIN	Variogram, kriging. Contour mapping. Also GEOSREC for non-linear and BLUEPACK for non-stationary kriging.
GEOSTAT	Variogram, kriging. Contour mapping.
Kellogg's	Variogram, kriging. Contour mapping.
NTSYS-PC	Simple Mantel test; correspondence analysis.
"R"	Spatial autocorrelation, simple and partial Mantel tests, Mantel correlogram, clustering with space and time contiguity constraint. ANOVA for regional data. Connection networks.
SAAP	Spatial autocorrelograms (Moran's I and Geary's c).
SASP	Two-dimensional spectral analysis.
SURFER	Kriging from linear variogram only; other interpolation methods. Contour mapping.
SYMAP	Trend surface analysis; other interpolation methods. Contour mapping.
UNIMAP	Variogram, kriging; other interpolation methods. Contour mapping.

- CANOCO is available for MS-DOS and Macintosh microcomputers and for mainframes from Cajo J. F. ter Braak, Agricultural Mathematics Group, TNO Institute for Applied Computer Science, Box 100, NL-6700 AC Wageningen, Netherlands.
- CLADAREA is available from Willem N. Ellis, Instituut voor Taxonomische Zoologie, afd. Entomologie, Plantage Middenlaan 64, NL-1018 DH Amsterdam, Netherlands.
- COCOPAN, written by Alain Vaudor and Junhyong Kim, is available from P. Legendre's lab (see title page) for Macintosh microcomputers and IBM and VAX mainframes.
- COMPONENT is available from Roderic D. M. Page, Department of Zoology, University of Auckland, Private Bag, Auckland, New Zealand.
- CONTOUR 81 is available for Macintosh machines from Technical Software Systems, P.O. Box 56, Millburn, New Jersey 07041, USA.

- CORR2D, written by Geoffrey M. Jacquez, is available from Applied Biostatistics Inc., 100 North Country Road, Bldg. B, Setauket, New York 11733, USA.
- The GEO-EAS package, developed by EPA, is available for MS-DOS machines from ACOGS, P.O. Box 44247, Tucson, Arizona 85733-4247, USA.
- GEOLIN, GEOSREC and BLUEPACK are available from Geovariances International, 1 rue Charles-Meunier, F-77210 Avon-Fontainebleau, France.
- The GEOSTAT package is available from: Geostat Systems International Inc., 4385 rue Saint-Hubert, Suite 1, Montréal, Québec, Canada H2J 2X1.
- The Kellogg's programs are available from the Computer Laboratory, W.K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060, USA.
- The NTSYS package, developed by F. James Rohlf, is available in MS-DOS version from Exter Software Inc., 100 North Country Road, Bldg. B, Setauket, New York 11733, USA.
- "The R package for multivariate data analysis", developed by Alain Vaudor (P. Legendre's lab: see title page), is available for Macintosh microcomputers, VAX, and IBM mainframes.
- The SAAP package is available from Daniel Wartenberg, Department of Environmental and Community Medicine, Robert Wood Johnson Medical School, 675 Hoes Lane, Piscataway, New Jersey 08854, USA.
- The SASP program is available from E. Renshaw, Department of Statistics, University of Edinburgh, King's Buildings, Mayfield Road, Edinburgh EH9 3JZ, United Kingdom.
- SURFER is available from Golden Software Inc., P.O. Box 281, Golden, Colorado 80402, USA.
- SYMAP is not distributed any longer by Laboratory for Computer Graphics and Spatial Analysis, Harvard University, USA. It is however still available at many computing centers.
- UNIMAP is available from: European Software Contractors A/S, Nφrregade, DK-2800 Lyngby, Denmark.

*Other programs such as HENNIG 86, MacCLADE, PAUP and PHYLIP are available for parsimony analysis.

MODELLING LOBSTER RECRUITMENT USING LANDINGS, WATER MASS ADVECTION, AND ENVIRONMENTAL VARIABLES

Pierre Legendre

Département de sciences biologiques, Université de Montréal,
C.P. 6128, succursale A, Montréal, Québec, Canada H3C 3J7

ABSTRACT

NOAA satellite images taken over the northern portion of the Gulf of St. Lawrence reveal several large-scale hydrographic phenomena such as gyres and coastal upwelling zones. These phenomena maintain a thermal gradient from the Québec North Shore (cold) to the west coast of Newfoundland (warm) and may be related to specific climatic conditions, such as the direction and speed of prevailing winds. These observations suggest a mechanism by which climatic and hydrographic factors could exert a direct impact on the advection and survival of planktonic crustacean larvae, particularly lobster. The study reported here (Hudon et al., 1991) reexamines Sutcliffe's (1973) hypothesis as to the relation between physical factors (on which larval survival depends) and lobster landings.

In the first part of the study, we examined the implicit assumptions to this type of relation: 1) the use of annual landing statistics to evaluate recruitment into the fishery, 2) the loss of larvae via water mass advection, 3) the survival of larvae in the plankton, 4) the number of years of benthic growth prior to minimum legal size, 5) the existence of a stock-recruitment relationship.

In the second part of the paper, the potential mechanisms at the origin of such correlations are evaluated for the critical phase of the planktonic larval phase, using data for the northern Gulf of St. Lawrence. A first model of larval exchange among the different regions using a Markov transition matrix suggests that larval exports from the Québec North Shore and Anticosti Island could explain the stability of landings off the west coast of Newfoundland. The persistence of the effects of larval exchange until recruitment into the fishery is evaluated using historical physical data (temperature, wind, freshwater flow) in conjunction with detailed landing statistics for the west coast of Newfoundland, Anticosti Island, the Québec North Shore and Iles-de-la-Madeleine. The relationships between various physical *factors and lobster landings are described using statistical models (multiple regressions), explaining up to 70% of the variance of landings between 1953 and 1982, depending on the region. Validation of the models using the 1983-1988 landings shows that predicted values always underestimate recent observed landings. This study indicates that the definition of a conceptual framework, the reliability and homogeneity of landings and physical data, as well as the knowledge of the physiographic characteristics of each region, are critical to the success of modelling.*

REFERENCES

Hudon, C., P. Legendre, A. Lavoie, J.-M. Dubois et G. Vigeant. 1991 - Effets du climat et de l'hydrologie sur le recrutement du homard américain (Homarus americanus) dans le nord du golfe du Saint-Laurent. Pp. 161-177 in: Therriault, J.-C. [éd.] Le golfe du Saint-Laurent: petit océan ou grand estuaire? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Sutcliffe, W.H. Jr. 1973. Correlations between seasonal river discharge et local landings of american lobster (Homarus americanus) et Atlantic halibut (Hyppoglossus hyppoglossus) in the Gulf of St.Lawrence. J. Fish. Res. Bd. Can. 30: 856-859.

The use of simultaneous equation models to analyse time-series of interacting benthic species and environmental variables: halfway between statistical and dynamical modelling.

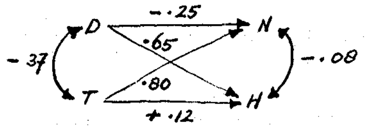
Jaap van der Meer
Netherlands Institute for Sea Research (N.I.O.Z.)
P.O. Box 59, 1790 AB Den Burg
The Netherlands

This abstract gives some prelimanary results of the application of simultaneous equation models to analyse time-series of several benthic species and a few environmental variables, which might effect the abundance of the animals. These models might be useful tools to examine this kind of data, where information on the underlying processes is sparse, if not to say almost not available.
The data used were gathered by Beukema (e.g. Beukema & Essink 1986, Beukema 1989) and concern late winter-early spring biomass data of the 13 most abundant benthic species of the Balgzand, a tidal flat area in the Dutch Waddensea. The environmental covariates used were average wintertemperature (December-February) and Diatoms densities averaged over the preceding growing season of the benthos (Beukema & Cadee 1990). The length of the series is 16 years (1974-1989).

An analysis of these data based on simple correlation coefficients suffer from two major problems: spurious correlation and auto-correlation. One way to deal with spurious correlation is to assume that some variables are dependent upon others. The accompanying regression model(s) can be represented in a path diagram (e.g. Sokal & Rohlf 1981). The table below shows a matrix of correlation coefficients, where the Diatoms are measured in the year before and the logarithm of Nepthys and Heteromastus biomasses are taken:

	Diatoms	Temperature	Nephthys	Heteromastus
Diatoms	1			
Temperature	-0.37	1		
Nephthys	-0.55	0.89	1	
Heteromastus	0.60	-0.12	-0.31	1

If the benthic species Nephthys and Heteromastus are assumed to be dependent upon Diatoms density and winter Temperature, the path diagram looks like:



Both analyses can easily lead to apparently different conclusions. For example, the path coefficient, which is equivalent to the standardized partial regression coefficient, between Temperature and Heteromastus is positive (+0.12), whereas the correlation coefficient (-0.12) appeared to be negative. Note that the latter can easily be derived from the path diagram (0.12-0.37*0.65). So given the assumptions about the causal relationships are true, the path diagram is far more informative than the matrix of correlation coefficients. Examples of path analysis in biology, in which more complex path models are examined, are few, but see Schwinghamer (1983), Trousselier et al. (1986) and De Leeuw (1989). Auto-correlation occurs because the abundances of the benthic species in successive years are not independent. If there are many animals in year i, presumably there will be many animals in year i+1 as well, due to survival and to reproduction being dependent upon the number of adults. A linear logistic model (Haldane 1953, Reddingius 1971, Reddingius & De Boer 1989) might be assumed:

$$N_t / \mu = (N_{t-1} / \mu)^{\beta} . \eta \qquad (1),$$

where Nt is the number of animals on time t, μ and β are parameters and η is the error. Defining

$$y_t = \log (N_t / \mu) \qquad (2),$$

the model can be written as

$$y_t = \beta \; y_{t-1} + \varepsilon \qquad (3).$$

The model behaves in a similar way as the well-known logistic growth model, but is mathematically more tractable. The parameter β governs the behaviour of the model: $\beta=0$ gives white noise; $0<\beta<1$ results in stationary time-series, $\beta=1$ in random walk, and $\beta>1$ leads to non-stationary time-series, i.e. the variance increases with time.

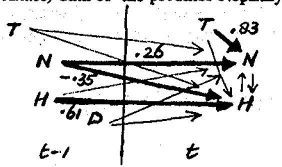
Combining the regression (or path) models, with the linear logistic model leads to the model:

$$y_t = \beta \; y_{t-1} + \gamma \; x_t + \delta \; x_{t-1} + \varepsilon \qquad (4),$$

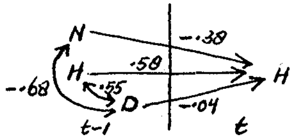
where the x indicate the environmental variable(s). Note that equation (4) is a member from a much broader class of time-series models, related to the ARIMA models (Box and Jenkins 1971). Tools like the auto-correlation function, the partial auto-correlation function and the cross-correlation function, all borrowed from the Box-Jenkins model identification, and the method of stepwise regression can be helpful in the model choice procedure. Equation 4 is a univariate model and can be used for each species seperately, but in fact the species also interact with each other. Incorporating such interaction leads to the following multivariate simultaneous equation model:

$$\Phi Y_t = B \; Y_{t-1} + \Gamma \; x_t + \Delta \; x_{t-1} + \varepsilon \qquad (5),$$

where Φ, B, Γ and Δ are matrices of unknown parameters. The matrix Φ contains ones on the diagonal. However, serious estimation problems will arise with such an oversaturated model. There are simply too many parameters. Note that with 13 species and 2 environmental variates, there are 377 parameters. With bivariate data, as in the example below, stepwise least-square regressions for both univariate models derived from equation 5, proved to be helpful in model identification. Y_t gives the log(biomass) data of the predator Nephthys and the prey Heteromastus:



So, diatoms seem to play no important role in the explanation of the abundance of Heteromastus, contrary to the suggestion raised by looking at the simple correlationmatrix presented at the beginning of this paper. The following path diagram shows the origin of the positive correlation between Diatoms_{t-1} and Heteromastus_t:



The correlations between Nephthys and Heteromastus biomasses and the successive Diatoms density must be spurious. Both species contribute to only a minor part of the total benthic biomass.
Here the need for the full simultaneous equation models turns up. In order to circumvent the estimation problems with the full simultaneous equation model, the model was applied not to the 13 species abundances, but just to the first three principal components of the species correlation matrix. These components explain about 75 % of the total variance. Again, a strong positive relationship was found between the first component and the successive Diatoms density. A possible explanation is the regeneration of nutrients by the benthos, which stimulates diatom blooming.

In conclusion, we can say that the use of simulataneous equation models seems to be a promising tool for an exploratory analysis of long-term biological data. Particularly when information on the underlying processes is almost absent.

ENVIRONMENTAL FACTORS CONTROLLING SPATIAL AND TEMPORAL VARIATIONS IN THE BENTHOS OF COASTAL LAGOONS

A.Nicolaidou, N.Simboura and S.Vamvakopoulou

Zoological Laboratory, University of Athens, Panepistimiopolis,
GR-15784 Athens, Greece

INTRODUCTION

Coastal lagoons are well defined ecosystems which may, for many purposes, be considered as self contained units. Consequently, they present themselves as a microcosm where variability should be largely predictable and capable of being defined by a relatively simple hydrodynamic model.

The present work is essentially a feasibility study with a view to successfully modelling the major processes which make up these lagoon systems. It describes the spatial and temporal variations of the benthic fauna in such a lagoon in Amvrakikos Bay. For a better understanding of the observed variations, the results of single benthic surveys in three other lagoons are also presented.

MATERIAL AND METHODS

The spatial and temporal variations throughout a year were studied in the brackish water lagoon Mazoma of Amvrakikos Bay on the west coast of Greece (Fig.1a, 1d). The lagoon communicated with the Bay through two narrow openings approximately 30 m wide. The depth ranged from 1.0 m to 1.4 m except for a "trench " dug in the NW which was 2.0 m deep. The bottom of the lagoon was muddy and covered in places by the eelgrass *Zostera noltii* and the green alga Chaetomorpha. The vegetation was dense in the eastern section closer to the sea, decreasing toward the west and disappearing almost completely in the innermost parts of the lagoon.

In the same Bay two other lagoons were studied. Pogonitsa at the entrance of the Bay also had two narrow openings to the sea (Fig.1a, 1b). Its depth ranged from

0.2 to 1.3 m and the bottom was muddy with patches of *Zostera*. Tsopeli, was further inside Amvrakikos Bay Fig.1a, 1c). At the time of sampling it had only one opening to the Bay. The depth ranged from 0.2 to 1.5 m. The bottom in most places was covered by eelgrass and green algae but some bare areas also existed especially in the deeper parts. Finally, the lagoon Vivari (Fig.1e), in a completely different area, on the east coast of the Peloponnese was also studied. It had a single opening to the open sea, bare muddy bottom and depth ranging from 0.5 to 1 m.

Sampling in Mazoma was carried out at approximately two-month intervals from June to June. In the other lagoons it took place in November. The samples were taken with a 0.05 m^2 Ponar grab, sieved through a 1mm mesh sieve and stained with Rose Bengal. The plants contained in each sample were kept separately and weighed after drying at 60 °C.

For the multivariate analyses, the computer programmes PRIMER developed in Plymouth Marine Laboratories and DECORANA (Hill, 1979) were used.

ENVIRONMENTAL PARAMETERS

During the study period the temperature in Mazoma lagoon ranged from 8° C in January, to 27^0 C in June. The salinity ranged from 14‰ in January to 37‰ in July and September. Dissolved oxygen concentration was lowest (2.11 ml/l) in July and highest (7.65 ml/l) in January. There were no considerable differences between the 10 stations in the values of the above parameters.

At the time of sampling in Pogonitsa the temperature ranged from 13^0 C at stations 1 and 2, to 14^0 C at station 4. The salinity ranged from 27‰ at station 3, to 29.9‰ at station 4. Dissolved oxygen concentration varied between 9.4 ml/l at stations 1 and 4 and 9.8 ml/l at stations 2 and 3. In Tsopeli, the temperature ranged from 19.5^0 C at stations 4 and 5 to 20.8^0 C at station 1, while the salinity varied between 26‰ at station 5 and 31.5‰ at station 3.

Dissolved oxygen concentration in Tsopeli was lowest (5.4 ml/l) at station 5 and highest (11.4 ml/l) at station 2. Finally in Vivari , the temperature ranged from 16^0 C at station 1 to 17.5 ^{0} C at stations 3 and 4. The salinity varied between 26‰ at station 2 and 37.5‰ at station 4. Dissolved oxygen concentration was lowest (8.2 ml/l) at station 3 and highest (9.2 ml/l) at station 1.

THE BENTHIC FAUNA IN THE LAGOON MAZOMA

The distribution, population dynamics and life histories of the most abundant species were studied. In most cases the vegetation seemed responsible for the distribution of the species. Among the Amphipods, for example, Gammarus insensibilis and Dexamine spinosa were most abundant at the eastern stations where the vegetation was denser (Nicolaidou & Karakiri, 1989), while they were practically absent from the bare western stations. From the polychaetes, Nereis diversicolor and Platynereis dumerilii were present over the whole lagoon but P.dumerilii was more abundant at the eastern stations and N.diversicolor at the western. Conversely, Nephthys hombergi was most abundant at the western stations. Where the distribution of two species coincided they reached their maximum population densities at different times of the year. For instance the maximum density of G.insensibilis was observed in January and of D.spinosa in June. The maximum density of N.diversicolor was in January and of P.dumerilii in June '81.

When the community was examined as a whole no clear pattern emerged. In the dendrogram of Fig.2 only the different monthly samples of station 10 in the trench formed a distinct group at similarity 50‰. There was also a tendency for stations sampled in the same month to appear together, as for example the samples of November. All the samples at all the stations, however, seem quite similar, the lowest similarity observed being approximately 40‰. The same result was given by the MDS plot in Fig.3a. The distribution of the stations in this diagram matches the distribution of plant biomass, superimposed on the MDS diagram of the stations in Fig.3b.

TABLE 1: Spearman Rank Correlation Coefficient and Significance Level (P) between environmental variables and Decorana Axis I values.

	Spearman coefficient	probability
SALINITY	0.813	0.0000
TEMPERATURE	0.575	0.0040
OXYGEN	0.619	0.0020
PLANT BIOMASS	-0.684	0.0006

When the benthic data from all the lagoons were analysed together, including the November samples from Mazoma, a very clear picture appeared. As the dendrogram in Fig.4 shows, the stations in each lagoon were clearly separated from the rest. The lagoons Pogonitsa and Vivari which have better communication with the open sea were more similar to each other than to the other two lagoons. The same was obvious from the MDS plot in Fig.5. Fig.6 shows the results of the detrended correspondence analysis applied to the same data. The scores on Axis I correlated strongly with salinity, temperature, oxygen and plant biomass, as shown in Table 1. All these are factors related directly or indirectly to water circulation. Consequently, as might be expected water circulation appears to be the major controlling factor in the lagoon ecosystem.

It is hoped that in the future this apparently simple relationship will lend itself to the application of a physical model, also capable of predicting changes in biological parameters related to prevailing environmental conditions.

REFERENCES

HILL, M.O., 1979. Decorana - A fortran program for detrended correspondence analysis and reciprocal averaging. Cornell Univ., Ithaca, New York. 30 pp.

NICOLAIDOU, A. and M. KARAKIRI, 1989. The distribution of Amphipoda in a brakish-water lagoon in Greece. Marine Ecology, 10(2): 131-139.

Fig. 1. (a) Map of Amvrakikos Gulf with the lagoons studied.
(b) Pogonitsa lagoon.
(c) Tsopeli lagoon.
(d) Map of Mazoma lagoon
(e) Vivari lagoon.

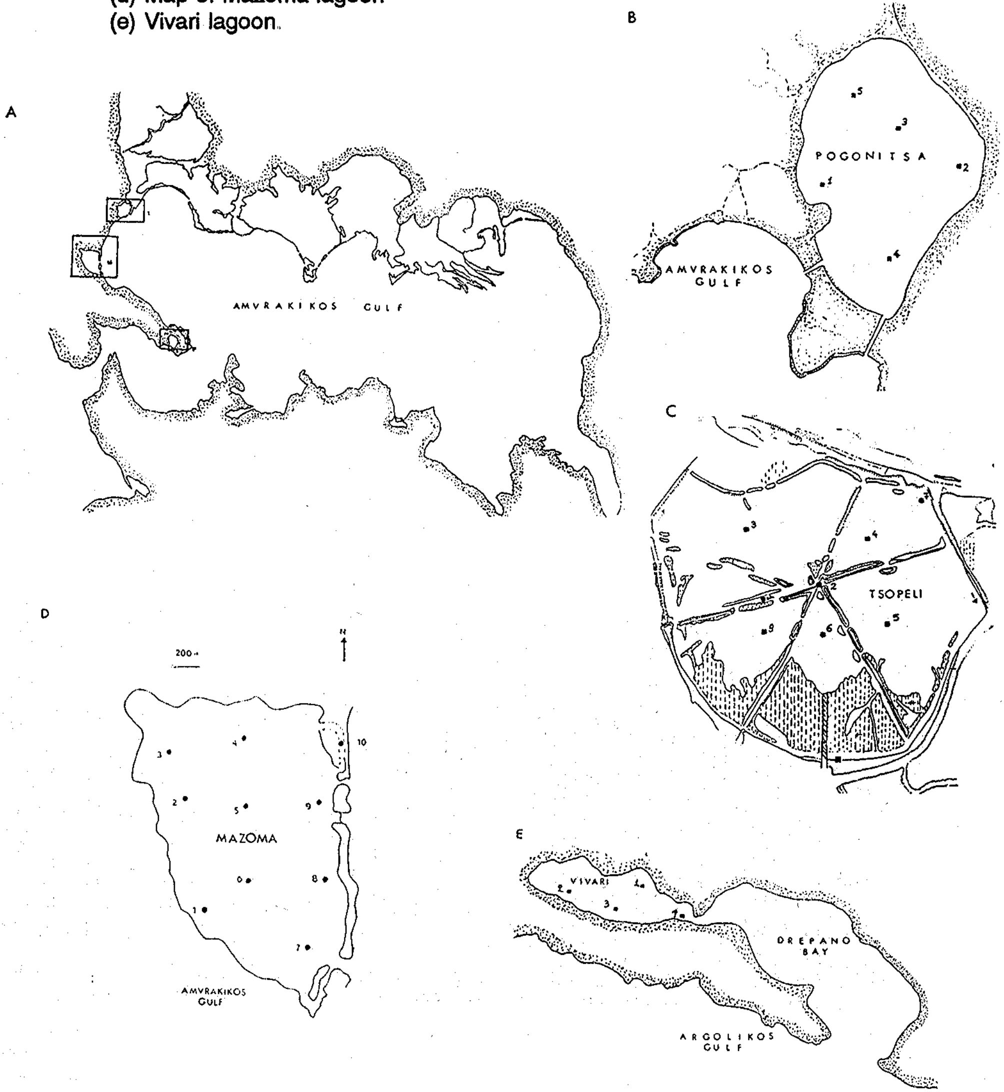


Fig. 2. Similarity between the ten stations of Mazoma at the different sampling times. J:June 81, A:August, S:September, N:November, I:January, M:May, U:June 82

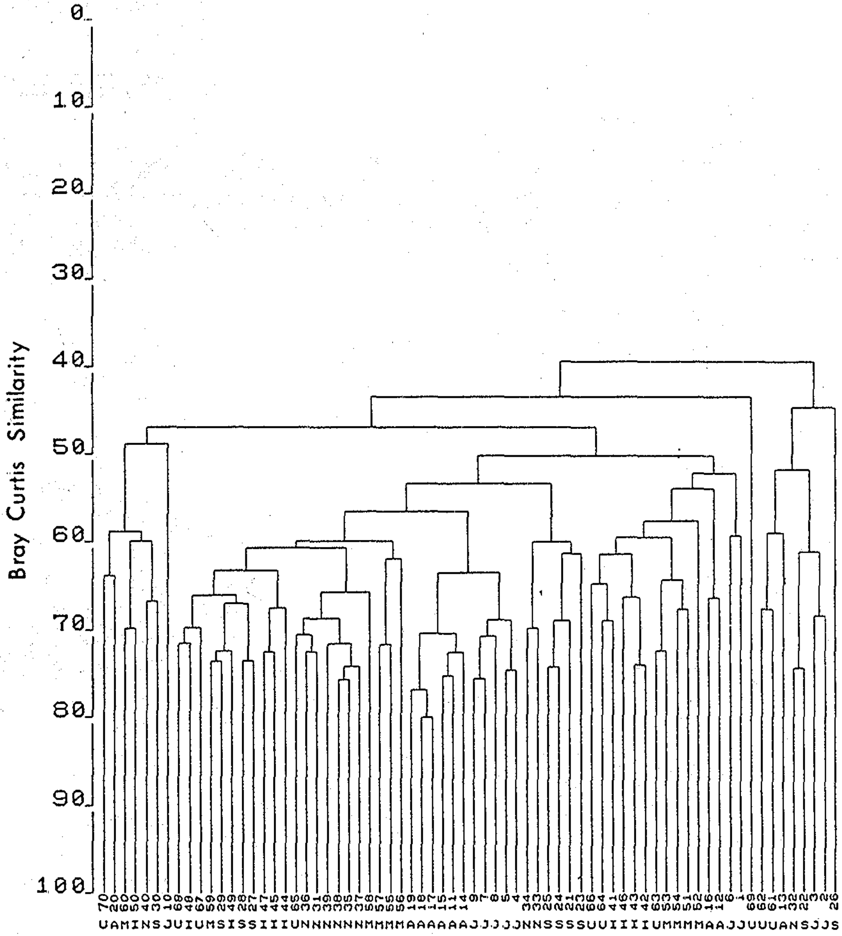


Fig. 3. (a) MDS plot of all stations of Mazoma at all sampling times.
(b) Plant biomass (expressed in dry weight) superimposed on previous MDS diagram .

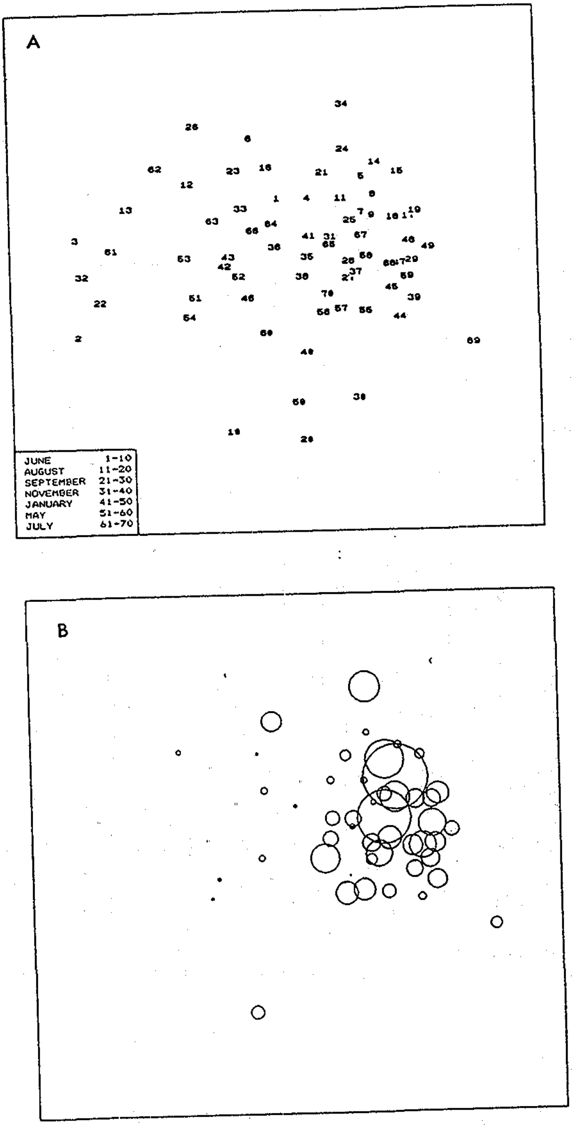


Fig. 4. Similarity between the stations of the four lagoons studied.

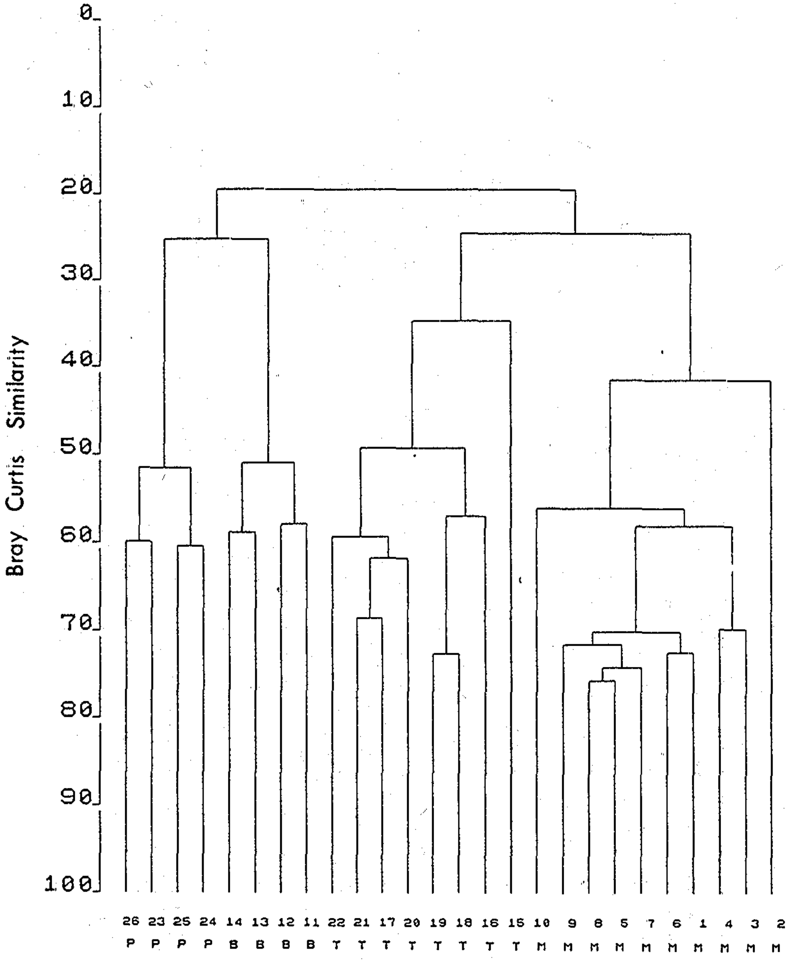


Fig. 5. MDS plot of all stations of the four lagoons.

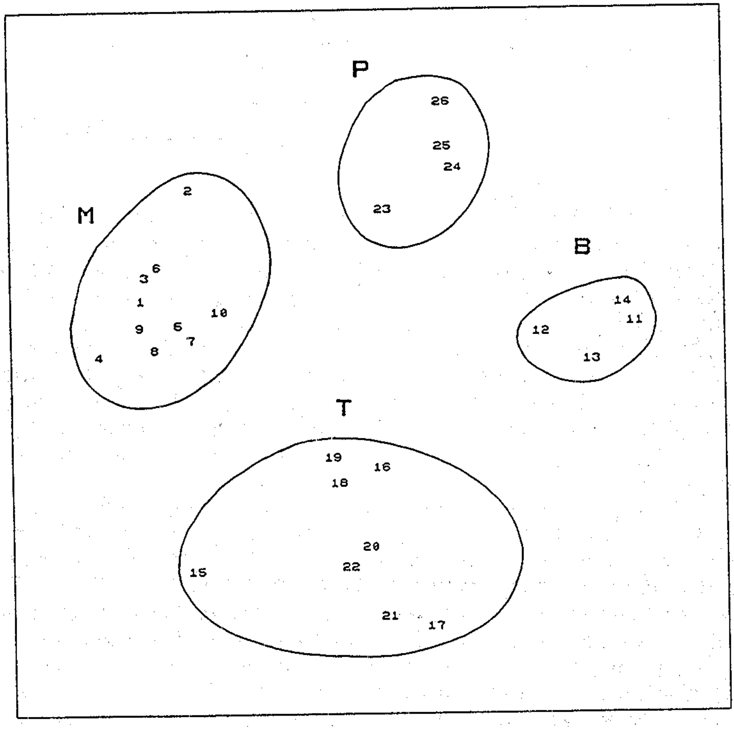
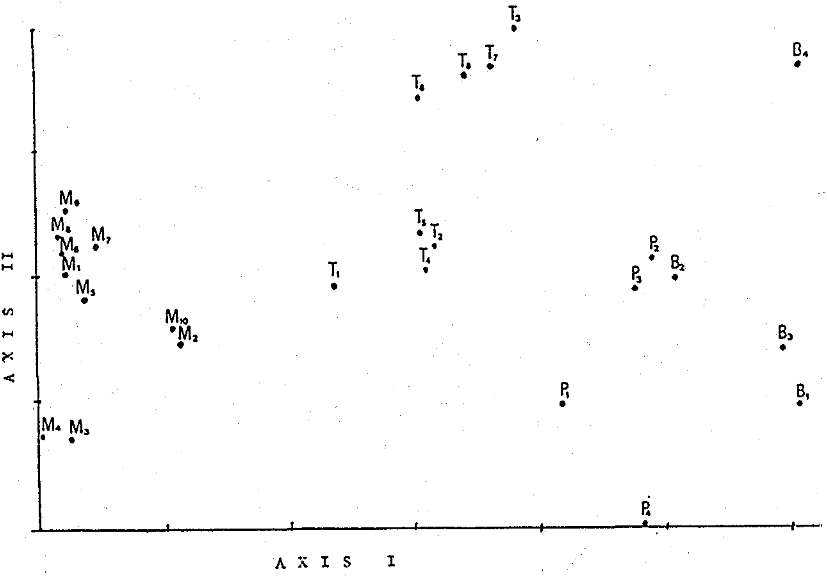


Fig. 6. Ordination of all stations of the four lagoons, produced by DECORANA.



THE USE OF HYDRODYNAMIC MATHEMATICAL MODELS IN PREDICTING TYPES OF SUBTIDAL MACROFAUNAL COMMUNITIES.

Brendan O'Connor

Aqua-Fact International Services
Innovation Centre, Newcastle, Galway, Ireland

INTRODUCTION

The use of mathematical models for predicting current speeds and directions and for determining dispersion and dilution of pollutants has become common place in assessing the environmental impact of many maritime activities. For example, when new harbours or piers are being contemplated, such models are developed to examine the local effects of such structures on the hydrodynamic regime. Similarly, during the planning process for the setting up of salmonid farms this approach has been used to locate the most suitable site for such an activity not only in terms of the dispersion and dilution of wastes but also in terms of the health of the environment and the safety of the fish. It is clear that the output from such models has significant uses for marine ecologists.

Some attempts have been made at relating physical oceanography to the distributions of benthic macrofaunal associations e.g. Warwick and Uncles (1980), while other workers e.g. Tyler (1977), Tyler and Banner (1977) and O'Connor *et al.* (1987), relate the occurrence of certain assemblages to physical oceanographic processes. Gerdes (1977) comments on the importance of local hydrographic regimes in regulating the re-establishment of benthic communities in the German Bight and Warwick and Uncles (1980) suggest the possibility of predicting distributions of benthic assemblages from hydrodynamic models while Warwick (1984) makes predictions based on output from a model on the spatial extent of different communities following the building of a tidal barrage.

This paper presents the results of a large scale benthic mapping exercise in Galway Bay giving data on sediment and assemblage distributions. Output from a two dimensional depth-integrated mathematical model on the residual flow pattern in Galway Bay is given which show where maximum current speeds can be found an where such features as gyres are predicted. These results are compared and demonstrate the predictive possibilities of such models in broadly outlining where different macrobenthic communities may be found.

MATERIAL AND METHODS

Biological and sedimentological sampling

Sampling stations were chosen where the main DECCA navigation lines intersect (Fig. 1) and positions were located using DECCA navigation. Samples were collected during 1975/1977 from r.v. Coruna using a Rallier du Baty dredge and the sedimentary or other material collected was subjectively described and recorded. The dredge contents were then washed through a 2 mm sieving table and the remains were picked over for animals which were later identified in the lab. No attempt was made to quantify the species present.

Prior to classificatory analysis of the animal assemblages, faunal data were reduced by including only those specimens which were identified to species level and by omitting those species which occurred at 5 % or less of the stations sampled. The Bray and Curtis measure of similarity was used to generate a similarity matrix for all stations, based on binary data. Similarity indices were subsequently classified by a monothetic agglomerative hierarchical method using group average sorting.

Computer model

A finite element model of the circulation of water in Galway Bay was developed and follows methods outlined in Brebbia and Partridge (1975), Connor and Brebbia (1976) and Withum *et al.* (1979). To do this the Bay was triangulated giving a total of 389 triangles and 250 nodal points with these points being carefully positioned so as to obtain the best match with bathymetry. Ocean boundaries were established as straight lines to the west and south of the Aran Islands. The amplitude of neap tides at the Aran islands (0.99 m) were used as input data at these boundaries. The other specified boundary conditions were the inflow of fresh water at Galway City (46.5 $m^3 s^{-1}$) and wind speed and direction (4.426 $m s^{-1}$, 21.2 ° west of south). Allowances were also made in the model for bottom and wind friction and the Coriolis effect.

After the input of all elements, nodal and boundary data, the situation represents that of a flat calm water mass with a level given by the Admiralty Chart (no. 2173). The input tidal amplitude data and freshwater inflow from Galway City were initiated and a periodic effect was achieved after 3 periods of semi-diurnal tides. Computed values for current speeds were very close to field data. Fig. 5 shows the dominant net flow of current flow in the bay. A full report on this study can be found in Harte *et al.* (1982).

RESULTS

Sediments

Fig. 2 represents the distribution of the sediments as determined by the subjective on-board analyses. As can be seen from this figure the north western and south western sectors of the study area are dominated by sands and muddy sands while the remaining bottom types are characterized by coarser substrates with extensive areas of maerl, gravel and bedrock. Along the north shore, a band of bedrock extends from the shore line and gives way to a narrow strip of gravel. This rocky mantle is also present around the Aran Islands. The inner part of Galway Bay is a mosaic of finer sediments to the north east and coarser deposits in the south east. Some rocky outcrops occur in the central portion while the outer section is comprised of sands an muddy sands.

From the data, broad statements on the nature of the sea-bed in Galway Bay can be made: 65% of the sea bed in the study area is characterized by a silty-sand/-sand substrate. It occurs over a large part of Inner Galway Bay and divides into two sections in Mid Galway Bay, i.e. one following the North Shore, the other, the Clare Coast. This sediment type extends over most of the area to the south-west of the Aran Islands. Gravels, either shell or stone, are best represented in South Bay, Inner Galway Bay and in localized patches throughout the rest of the study area, while maerl beds occur in North and South Bay, Inner Galway Bay, at the mouth of Casla Bay and in a large area north-east of Inishmean and Inisheer. Rocky patches occur in the Inner Bay (Henry Ledges, Margaretta Shoals) and Mid Bay (Curran Banks, Inverin, Killa and Craigmore Patches), while exposed bed rock from the land and islands extends into the sea to a greater or lesser extent along the coastline. Such rock is frequently flanked by a strip of mixed substrates, e.g. stones, gravel, shell debris, coarse sand, before giving way to the sands or silty-sands.

Faunal assemblages

Fig. 3 presents the distribution of the assemblages defined by the classificatory methods outlined. The inner parts of Galway Bay are characterized by a mosaic of assemblages typified by the *Venus fasciata* grouping (as mixed coarse substrates, sheltered rock and mixed coarse substrates and maerl in Fig. 3) while a patch to the north of this area falls within the *Abra alba* community (as Variation B in Fig. 3). Moving westward, the coastal strips have a community which has similarities to the *V. fasciata* community but present also on some sections is an epifaunal grouping. These same community types characterize the benthos in the immediate vicinity of the three Aran Islands. In the central portion of Galway Bay and in deeper water to the south west, softer substrate communities occur which, in the case of the section inside the Islands is referable to either the *Amphiura filiformis* assemblage (*sensu* Buchanan, 1963) or the Thorson (1957) *Venus striatula* grouping (as Variation A in Fig. 3). The communities recorded in the deeper water outside the Islands to the south and southwest, although similar in some respects to the *A. chiajei* community of Buchanan (1963), are somewhat different in faunal composition.

Computer model output

The computer model of currents and directions shows that maximum speeds occur in the sounds between Inishmore and Inisheer and Inisheer and Inishmean (Aran Islands) and to a lesser extent in the eastern parts of Inner Galway Bay (Fig. 4). computed velocities are in the range of 0.5 - 1 m s^{-1}. Looking next at the residual current, gyres are predicted in the central sector and in the north eastern corner of Inner Galway Bay (Fig. 5) with net speeds being in the range of 0.05 - 0.1 cm s^{-1}. In other parts of the Inner Bay, residuals are low being in the range of 0.01 - 0.03 m s^{-1}. These residuals show the general pattern that water enters the Bay from the south and leaves via the North Sound.

DISCUSSION

The relationship between the sedimentological, faunal and computer model output data are to a large extent in agreement : where lowest current speeds are predicted by the model, field data show that depositional sediments and infaunal communities occur. With regard to the presence of the predicted gyre in the Inner Bay, a well developed *Amphiura filiformis* dominated community has been in existence at least for the last 20 years (O'Connor *et al.*, 1987). O'Connor *et al.* (1987) have suggested that such a community is a manifestation of such a hydrographic phenomenon whereby the gyre acts to concentrate primary production and detritus over the area providing not only a greater supply of food to the sea floor but also creating physical conditions which give rise to a soft, loosely bound sediment which is favored by *Amphiura.*

With regard to the distribution of the coarse/epifaunal communities, the picture is less clear : even though maximum current speeds do occur where field data described such communities, these types of communities also occur where low current speeds are predicted by the model. This can be explained by the fact that such locations e.g. along the northern shore of the bay, are in very exposed areas where wind and wave effects produce localized areas of turbulence.

The output from such models can be further interrogated to pin-point areas of possible localized increased primary productivity since the current strength determines the nature and quality of the food supply for benthic organisms and therefore the trophic structure of the community. As food availability is one of the main factors governing the structure of benthic communities, further hypotheses could be built on the predictions of the model. It may prove possible in the future to make predictions on the sediment structure in different locations which in turn is another important factor governing benthic community structure.

Such two dimensional models do have their limitations as current speeds and directions are integrated throughout the water column. Output from them therefore is only of use in coastal, well mixed water bodies. However this section of the marine environment has been most often modelled since it receives large amounts of waste material and nutrients from land run-off and is used for large scale engineering projects e.g. oil and gas extraction, tidal barrages, tunnels, piers, breakwaters and dams.

ACKNOWLEDGEMENTS

Thanks to Pat. Dinneen and Dave McGrath for discussions and reviews.

REFERENCES

Brebbia, C.A. and Partridge, P. 1975. Finite element models for circulation studies. *In*: Mathematical models for environmental problems. Pentech Press, London.

Buchanan, J. 1963. the bottom fauna communities and their relationship off the coast of Northumberland. Oikos, 14 : 154-173.

Connor, J.J. and Brebbia, C.A. 1976. Finite element techniques for fluid flow. Newnes-Butterworth, London.

Gerdes, D. 1977. The re-establishment of an *Amphiura filiformis* population in the inner part of the German Bight. *In*: The biology of benthic organisms (eds. B. Keegan, P.O'Ceidigh and P. Boaden), pps. 277-284. Pergammon Press, Oxford.

Harte, A.M., Gilroy, J.P. and McNamara, S.F. 1982. A computer simulation of water circulation in Galway Bay. Engineering Journal of Ireland, 35 : 6-8.

O'Connor, B., Keegan, B. and McGrath, D. 1987. Demographic equilibrium ? the case of an *Amphiura filiformis* community in Galway Bay, west coast of Ireland.

Hydrobiologia, 142: 151-158.

Thorson, G. 1957. bottom Communities (sublittoral or shallow-shelf). *In*: Treatise on Marine Ecology and Paleoecology (Ed. J. Hedgepeth). Memoires of the Geological Society of America 67:461-534.

Tyler, P.A. 1977. Sub-littoral community structure of Oxwich Bay, South Wales in relation to sedimentological, physical oceanographic and biological parameters. *In*: The biology of benthic organisms (eds. B. Keegan, P.O'Ceidigh and P. Boaden), pps. 277-284. Pergammon Press, Oxford.

Tyler, P.A. and Banner, F.T. 1977. The effect of coastal hydrodynamics on the echinoderm distribution in the sublittoral of Oxwich Bay, Bristol Channel. Estuarine and Coastal Marine Science 5: 293-308.

Tyler, P.A. and Shackley, S.E. 1980. The benthic ecology of linear sandbanks: a modified *Spisula* sub-community. In : Industrialised embayments and their environmental problems, 539-551. Pergammon Press, Oxford.

Warwick, R.M. 1984. The benthic ecology of the Bristol Channel. Marine Pollution Bulletin. 15: 70-76.

Warwick, R.M. and Uncles, R.J. 1980. Distributions of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. Marine Ecology Progress Series 3: 97-103.

Withum, D., Holz, K.P. and Meissner, U. 1979. Finite element formulations for tidal wave analysis. Computer methods in Applied Mechanics and Engineering 17/18 : 699-716.

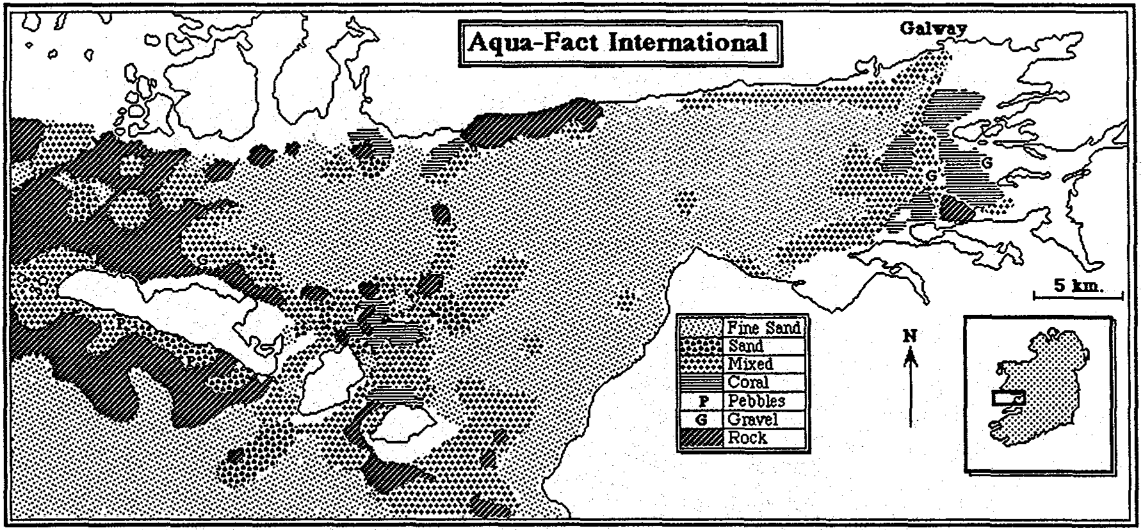


Figure 2. Distribution of bottom types in Galway Bay.

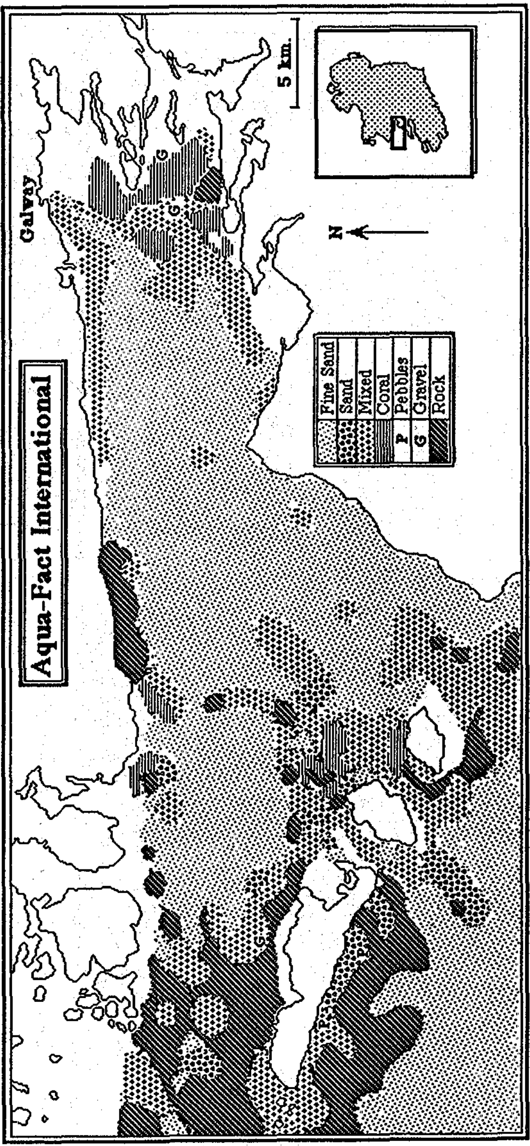


Figure 2. Distribution of bottom types in Galway Bay.

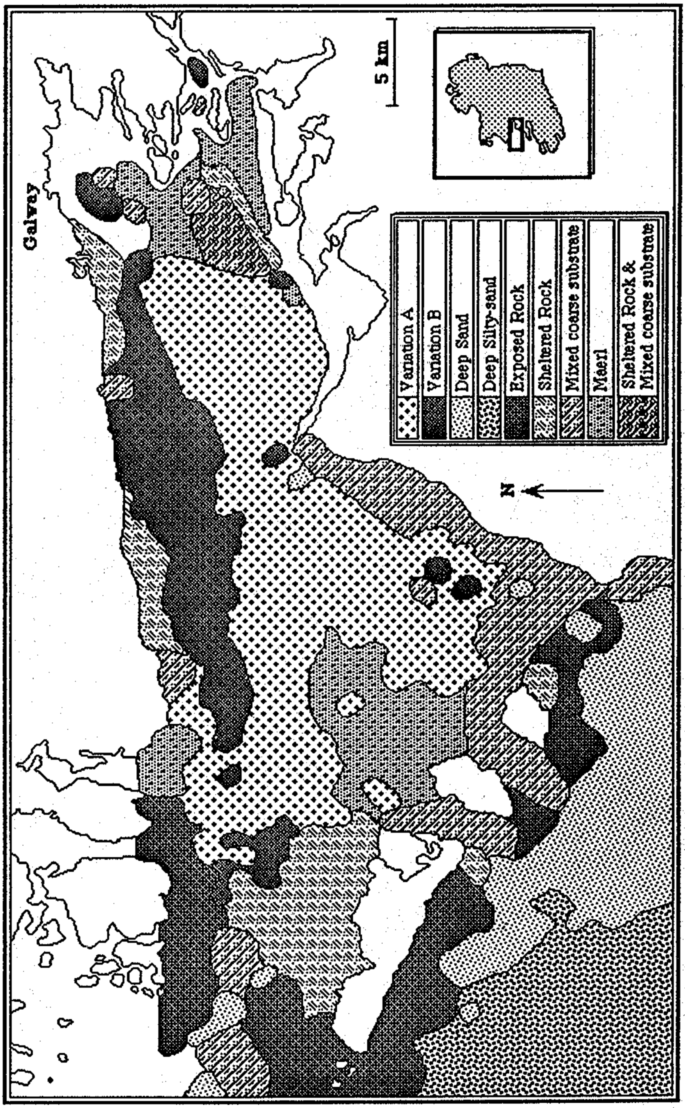


Figure 3. Distribution of macrofaunal benthic assemblages in Galway Bay.

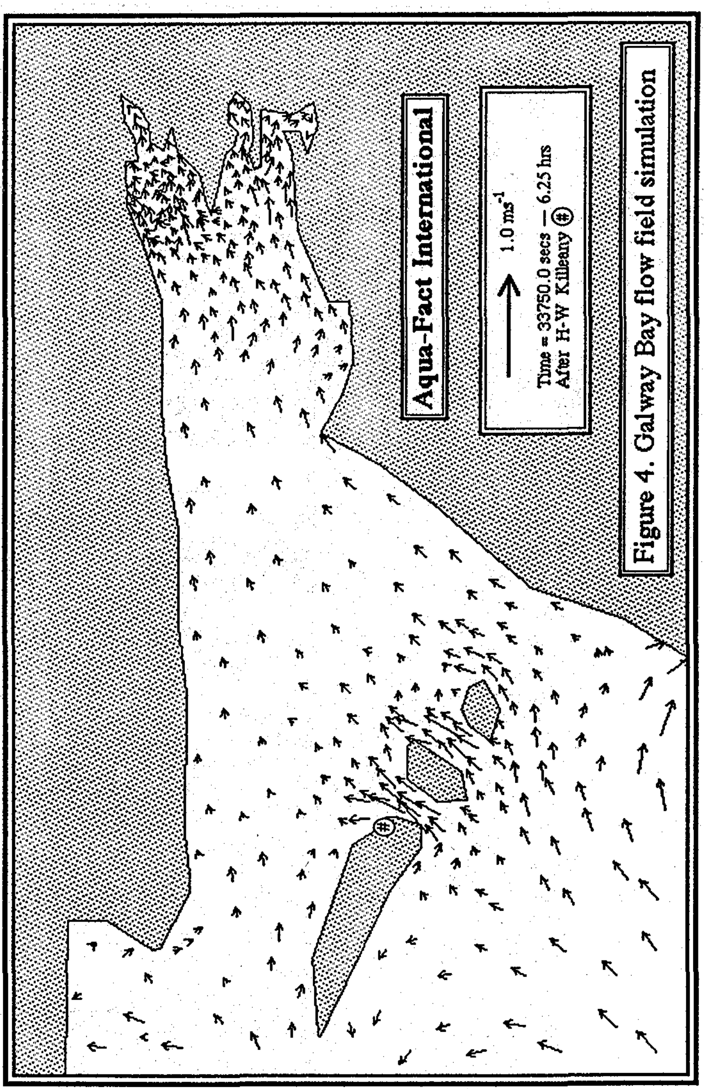


Figure 4. Galway Bay flow field simulation

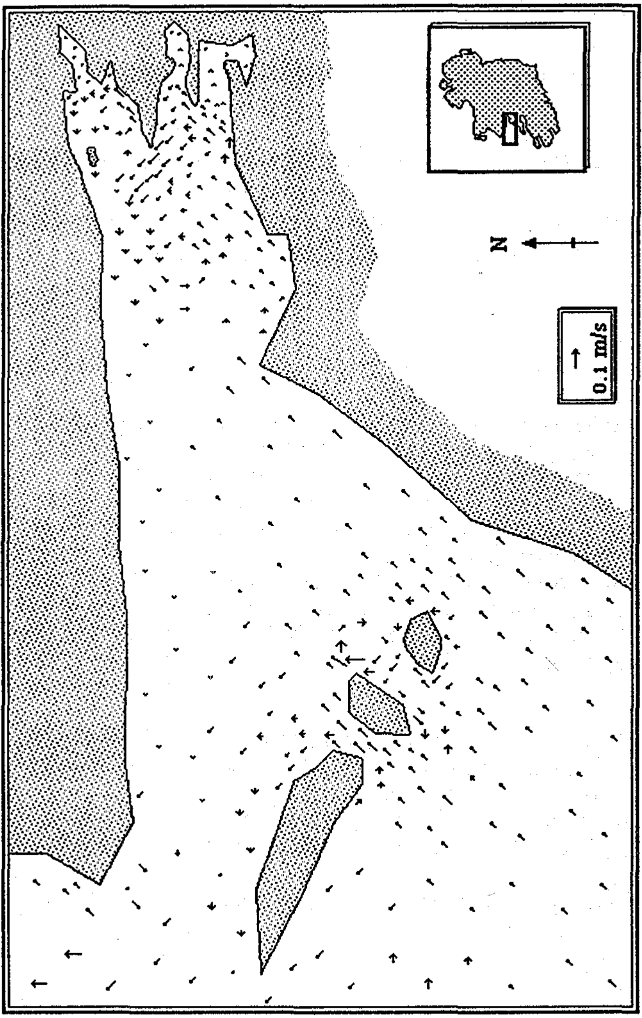


Figure 5. Residual Currents in Galway Bay.
(From Harte *et al.*, 1982).

Aqua-Fact International

THE MUSSEL BED BIOCOENOSE AS A DRIVING FORCE IN THE ESTUARINE NUTRIENT TURNOVER

T. Prins[1], A.C. Smaal[2] and M.W.M. van der Tol[2]

[1] Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA Yerseke, The Netherlands
[2] Ministry of Public Transport, Tidal Waters Division, P.O. Box 439, 4330 AK Middelburg, The Netherlands

ABSTRACT

Bivalve filter feeders may play an important role in the uptake of phytoplankton and the regeneration of nutrients in estuarine and coastal ecosystems. In situ measurements on mussel beds in the Oosterschelde by use of the benthic ecosystem tunnel show a large filtration capacity. In situ clearance rates and laboratory measurements show comparable values, allowing extrapolation of laboratory data to the field situation. The export of dissolved nutrients from the mussel bed was much higher than the laboratory values of individual excretion rates of N and P. This is attributed to mineralization of pseudofaeces and faeces, biodeposited on the mussel bed. It is hypothesized that the biocoenose of a mussel bed, consisting of biodeposition and associated micro and macrofauna is the key in the nutrient regenerating capacity of a mussel bank.

Filtration and mineralization are important state variables in the simulation model of the Oosterschelde ecosystem (SMOES). It is shown that the mussels and cockles can filter the total volume of the estuary every 5 days. Nutrient regeneration is modelled as the result of detritus breakdown. The driving force in the regeneration of nutrients in the Oosterschelde is the filtration activity of the benthos.

In our presentation especially the question concerning major processes will be adressed.

BENTHIC SUB-MODULES OF ECOSYSTEM MODELS

P.J. Radford

Plymouth Marine Laboratory
Prospect Place, The Hoe, Plymouth Devon PL1 3DH

ABSTRACT

Benthic populations are difficult to model because their presence or absence depends on the interactions of substratum characteristics with bed stress caused by tidal currents, which individually are extremely heterogeneous in time and space. Intertidal areas present further problems because of the variable impact of exposure to the atmosphere, and predation by birds. Also the production of pelagic spawn and the larval stages which form the meroplankton make the successful prediction of colonisation or re-colonisation problematical. These issues have been addressed by ecosystem modellers in very simplistic ways which produce quite convincing predictions. However the lack of time series biomass estimates of benthic functional groups makes it impossible to objectively assess the degree of success of such models.

The substance of this paper has been taken from the following publications :

Radford, P.J., Burkill, P.H., Collins, N.R., and Williams, R. 1988. The validation and scientific assessment of an ecosystem model of the Bristol Channel. In: "*State-of-the-Art in Ecological Modelling*" (Eds. A. Marani). Proceedings of the ISEM conference on ecological modelling, Italy, 1987. Elsevier, p. 427-442.

Radford, P.J. 1990. Pre and Post barrage scenarios of the relative productivity of benthic and pelagic sub-systems. In: *Evolution and change in the Bristol Channel and Severn Estuary.* (Ed. J. Crothers). The Biological Journal of the Linnean Society. (*In Press*).

THE VALIDATION AND SCIENTIFIC ASSESSMENT OF AN ECOSYSTEM MODEL OF THE BRISTOL CHANNEL

P.J. Radford, P.H. Burkill, N.R. Collins and R. Williams

Institute for Marine Environmental Research
Prospect Place, The Hoe, Plymouth Devon PL1 3DH

ABSTRACT

The General Ecosystem Model of the Bristol Channel and Severn Estuary (GEMBASE) was developed in the 70's and calibrated against three years contemporaneous survey data. In the early 80's this model was validated against a further five years of independent monitoring data. A comparison of the model and data revealed both the weaknesses and strengths of the data and the model. Unrealistic model output was observed for many different state variables but ultimately these problems pointed to one root cause. The omission from the model of process involving the production and recycling of benthic and pelagic reproductive products caused excessive growth of simulated adults, and inadequate food for zooplankton. The inclusion of these energy pathways resulted in much more satisfactory agreement between model and data without the need for any parameter adjustment. Control chart theory as been use to assess, with a degree of objectivity, the precision and consistency of the validated model. The goodness of fit of model to data is shown to be consistent over the nine year simulation for each of the six geographical compartments and across trophic levels even though precision of measurement is highly variable.

INTRODUCTION

Large ecosystem models may not take too long to formulate, but their validation must often be delayed until the results of extensive surveys, conducted over a number of years have been suitably analysed. The General Ecosystem Model of the Bristol Channel and Severn Estuary (GEMBASE), which was developed in the mid 1970's (Radford 1979) was no exception to this rule. The model was initially calibrated against three years baseline survey data obtained over the period 1973-1975 (Radford & Joint 1980). Verification of the model against these data was satisfactory, and the experience gained enabled the efficient design of a series of monitoring surveys over a subsequent five year period (1977-1981). Details of the design of the sampling methods which were used are given by Morris (1983) and subsequent data analyses are explained by Radford (1983). After the raw data had been corrected to represent its mean tidal position it was fitted to a response surface using an automated contouring package and finally integrated to yield average concentrations of pelagic components over the six geographical regions shown in figure 1. This was done for measurements of salinity, temperature, chlorophyll a (phytoplankton), carnivorous and omnivorous zooplankton, nitrate and dissolved organic matter (Williams and Collins, 1985). For the first five of these variables data were available for 40-50 points in time over a nine year period, but the organic and inorganic nutrients were only measured on 15-20 occasions over a three year period (no time series data were available for the benthic variables). In order to validate GEMBASE against these data it was necessary to simulate a ten year period starting on the 1 November 1972, a date for which estimates of all state variables were available. The parameters of the model for this run were maintained at the values judged to be correct at the end of the three year verification run (Radford & Joint, 1980). The state variables and their interrelationships are shown in Figure 2.

PRIMARY SIMULATION RESULTS

The Plankton

The discontinuous lines in Figure 3 and Figure 4 show the nine year simulations for phytoplankton and zooplankton respectively. Phytoplankton results are shown for all of the six geographical regions recognised by the model. In general the simulations represent the average concentration of phytoplankton and its broad seasonal cycle with some realism, bur certain inconsistencies become evident. For example in the Outer Estuary, where the turbidity of the water is very high (> 300 g.dray wt.m^{-3}) the overall phytoplankton estimates are too high. This is probably due to the method of measuring chlorophyll a by a spectro photometric technique which does not discern between estuarine and terrigenous chlorophyll. The simulation also makes it clear that the measurements taken during the baseline surveys yield results which are consistently lower than those of the monitoring cruises for this region. This identifies a distinct change in the sampling methods which affected results in the Outer Estuary only. For the other five regions, but especially in the Outer Channel North the simulated overwintering levels of phytoplankton were far lower than those actually measured. A reason for this discrepancy was needed.

Simulation results and measurements of both omnivorous and carnivorous zooplankton are given in Figure 4 for the two regions where the agreement was best for the Outer Channel North were agreement was the worst of all. The model can be seen to simulate mean levels and seasonal cycles reasonably well, clearly distinguishing the order of magnitude differences between these functional groups of organisms. The discontinuous lines of the simulations are consistently below the measurements particularly in the Outer Channel North where the simulated over-wintering stock is two orders of magnitude below measured values. Again a reason for the discrepancy was needed.

Planktonic Heterotrophs

Although no time series data were available to validate the performance of planktonic heterotrophs the nine year simulations for this variable (Figure 5a) are informative in as much as they fail to show a reasonably consistent seasonal cycle. In particular their average simulated biomass increases over the first three years and then declines over the next six years in all geographical regions (In Figure 5 results for regions 4 and 7 have been omitted simply because they are so similar to those for regions 5 and 6 respectively). It is very unlikely that such a fundamental state variable would behave in this way over a ten year period and one is therefore led to the conclusion that it is the result of unrealistic behaviour originating in some other part of the model.

Zoobenthos

The simulated benthic suspension (Figure 5b) and deposit feeders (Figure 5c) both showed continuous trends over the time. The suspension feeders followed a distinctive seasonal cycle which reflected the pelagic primary and secondary productivity but demonstrated a consistent increase in biomass over the nine year period. The deposit feeders similarly followed a distinctive seasonal cycle which reflected changes in their benthic food supply but they showed a consistent decline in biomass over the same period. All of these anomalies required some explanation but the fundamental cause was not obvious.

PROBLEM DIAGNOSIS

Careful consideration of all of the long term discrepancies between model and data eventually led to the discovery of a major error in the model structure. Unfortunately there is no objective or fool-prof method of making the necessary logical jump which could reveal this type of error. In retrospect it seemed that the model was demonstrating a consistent ratio between the biomass of carnivorous and omnivorous zooplankton across all six regions whereas the data indicated rather more omnivores than would be expected for the measured biomass of carnivores in some regions. A probable explanation could be found by considering the role of the meroplankton viz. those organisms which are only planktonic for a fraction of their life cycles as opposed to the permanent holoplankton (Williams and Collins, 1986). The meroplankton consists of the early larval stages of benthic invertebrates including deposit feeders and suspension feeders. In this biomass-oriented model, products of reproduction had not been explicitly included since in general it simply represents a particular form belonging to its own functional group, but in the case of these invertebrates its most distinctive characteristic is that it transports benthic biomass to the pelagic system where it interacts with the holoplankton providing food for and feeding on zooplankton and fish. These energy pathways were therefore included in the model (Figure 2). At the appropriate time of the year, for each functional group of zoobenthos benthic invertebrates and fish, one third of their biomass was distributed, over a period of one month, into the pelagic system where it became part of the omnivorous zooplankton biomass.

MODIFIED SIMULATION RESULTS

Zoobenthos

After modifying the representation of zoobenthos and fish to allow for energy pathways representing reproduction (Figure 2), the model was re-run for the same nine year period (1973-1981). The immediate effect on benthic suspension feeders (Figure 5b) was to reduce their average biomass and prevent an ever increasing biomass over time. The seasonal cycle followed a rather similar pattern to previous simulations except for a distinct biomass decline each year, during the period of spawning. On the other hand, under the new regime the benthic deposit feeders were competing for food with a smaller biomass of suspension feeders. This prevented the previously simulated decline in their biomass (Figure 5b) and for most regions a very stable seasonal cycle was attainable over the whole period. The form of the biomass cycle looks very different to that of the earlier simulations because its smooth sinusoidal growth pattern is severely truncated due to the loss of one third of its biomass in reproduction each year. The upward trend for region 2 is probably due to an unrealistic initial value for that variable.

Planktonic Heterotrophs

The bacteria in the pelagic region of the model form part of the food source for suspension feeders. Having stabilised the predator biomass it can been seen (Figure 5a) that the prey biomass is also stabilised. There is now no observable trend with time and the seasonal cycles are as regular as one would expect given the annual changes in the environmental forcing functions (solar radiation and river run-off).

The Plankton

Simulations of phytoplankton and zooplankton in the modified model are shown as continuous lines in Figure 3 and Figure 4 whereas the primary simulation results are shown as discontinuous lines. Transfer of reproductive products from zoobenthos and fish to the omnivorous zooplankton state variable (Figure 4) has had the immediate effect of elevating their simulated biomass in all regions especially enhancing the over-wintering stock, the lines becoming much closer to the measured values. This effect is even more pronounced in the case of the carnivorous zooplankton where the changed shape of the seasonal cycle agrees more closely with that of the data points (see validation section). The model is still far from perfect for the Outer Channel North region but the modification was in the right direction for all regions. The enhanced food supply provided by the reproductive products also reduces the grazing pressure of the omnivorous zooplankton on phytoplankton (Figure 3). Again the overwintering biomass of phytoplankton is increased in all regions bringing the simulations more into line with the measurements.

Nutrients

No nutrient data were available for the period of the verification runs (1973-1976) but nitrate measurements were made on some twelve occasions between 1977-1980. There were insufficient data to fully validate the model but when the available data are plotted against the modified simulation results the agreement is reasonable (Figure 6). The mean nutrient concentration for each of the six regions is well reproduced and the amplitude of the seasonal oscillation is satisfactory in each case. (In Figure 6 results for regions 4 and 7 have been omitted simply because they are so similar to those for regions 5 and 6 respectively). Both model and data indicate that severe nutrient limitation occurs only in region 6 (and 7).

OBJECTIVE VALIDATION

The model validation procedure described above is purely subjective but valid in so far as the improvements attained are large and would hardly be in dispute. Once the model has been demonstrated to be a reasonable fir to the data it is important to adopt some objective criteria to give confidence to the validation attained. This has been achieved by the use of a system of Control Charts developed by Page (1961) for problems of process control in the manufacturing industry. Briefly the technique depends on the computation of the cumulative sum of a time series of deviations (d_i) of the measured values from the model data. A test has been devised to detect significantly large changes in this cumulative sum (S_n) for a given probability level. The method is suitable for detecting either large individual deviations or a small but consistent bias in model or data. An explanation of its application has been given by Radford and West (1986) using a simple water quality model as an example. However the technique is of particular value in the validation of ecosystem models where, for example, the precision of fit of model to data shows a tendency to decrease with increasing trophic level. For the GEMBASE model the correlation coefficients relating simulation results to measured values are given in Table 1.

For salinity alone the correlations change considerably from region to region. This is due to a number of factors, the most important of which are beyond the control of the data gatherer. In particular the seasonal variance of salinity tends to

Table 1. Correlations between observed and simulated values of four state variables for six geographical regions. Each was computed from about forty pairs of values. The letters NS indicate that no significant correlation was found at the 95 % confidence level.

	State Variables			
Regions	Salinity	Phytoplankton	Omnivores	Carnivores
Outer Estuary	0.90	0.31	0.35	0.26
Inner Channel	0.88	0.56	0.49	0.45
Central North	0.72	0.57	NS	NS
Central South	0.62	0.47	0.62	0.59
Outer North	0.70	0.33	NS	NS
Outer South	0.41	0.77	NS	NS

decrease with increasing salinity, due to the decreasing impact of river run-off. So also does the residual variance, (i.e. variance of d_i) simply because the more oceanic the water, the more homogenous it tends to be. The cumulative sum technique enables each region and each variable to be objectively validated in relation to its inherent degree of fit. It tests the models' consistency in simulating each variable without bias, and highlights individual anomalies which may be traced to specific unpredicted events in the system or errors in measurements made on the system. In each case a control chart is plotted of deviation (d_i) of measured values from simulated data, and a cumulative sum chart of these deviations summed ($\Sigma d_i = S$) as a time series against sample number. For control charts one would not expect deviations to exceed ± two standard deviations ($\pm 2\ \sigma$) more than about once in twenty samples (95% confidence level) if model and measurements are consistent).

A similar test which utilises the cusum chart defines a "V" shaped envelope within which the cumulative sum line should lie if no consistent bias is present in data or model. If the cusum line crosses either arm of the "V" then either an unexpectedly large individual deviation has occurred or a small but consistent bias has been detected. Details of the construction of the "V" test are given by Radford and West (1986).

Validation for regions of different salinity

If a good validation for salinity can be established this would indicate that the modelled dispersive and advective processes are providing a reliable basis for the computation of inter-regional transfers of dissolved and planktonic components of the system. Graphs giving observed and simulated salinities as generated by GEMBASE, for all six geographical regions have been published by Uncles (1983). Examples of their objective validation using control charts and cusum charts are shown in Figure 7 for four regions, and in Figure 8a for the Central Channel South Region. Taking the Outer Estuary Region as an example, the control chart, (Figure 7a) indicates anomalies at samples 32 and 43 and this is confirmed by the "V" tests cumulative sum chart. These deviations are not excessive and certainly within three standard deviations of zero and so do not indicate a significant departure of model and data in the context of a run of forty-five samples. Although there are more -ve deviations than +ve deviations the "V" tests applied to all forty-five samples do not indicate a significant consistent bias. The same conclusions can be reached for the Central Channel North and the Outer Channel North and South. The most striking feature of these results is the overall consistency of model and data for all regions. This is in spite of the rather different correlation for the different regions (Table 1).

Validation at different trophic levels

Salinity

The control charts in Figure 8 represent state variables from different trophic levels in the same geographical region viz. Central Channel South.In the case of salinity none of the individual points deviate by more than three standard deviations from zero although one sample (No. 18), does not just fail the "V" test (95% confidence level). This is an acceptable failure rate among 40 samples.

Phytoplankton

Again there is only one anomalous phytoplankton deviation and this is so great (exceeding the 3 σ limit) that its cause merits investigation. Referring back to the original data (Figure 3) it can be seen that this measurement was taken in 1979, a year when the simulated levels of phytoplankton are greater for a longer period of time than any other year. This effect is probably due to a simulation error in that year which could be due to an incorrect model structure, process of forcing function. The objective test has therefore been useful in highlighting an individual anomaly in an otherwise consistent simulation.

Omnivorous zooplankton

Although there is a higher correlation between observed and measured values for omnivorous zooplankton than for phytoplankton (0.62 and 0.47 respectively) the cusum chart (Figure 8d) reveals more weaknesses in the goodness of fit for the zooplankton. There is a clear and consistent decline in the cusum line indicating a strong tendency for the model to overestimate the omnivore biomass. This becomes significant, as shown by the "V" test at sample 32 although this event also coincides with a deviation which is more than three standard deviations below zero. The downward trend of the cusum line also continues until the last sample. The model is therefore producing a good representation of the general seasonal cycle of omnivores but its estimate of the mean value is consistently high. This could well be due to an error in a parameter of the model which was not evident until the more serious omission of the reproduction pathways had been rectified.

Carnivorous zooplankton

The cusum chart for carnivores is very stable (Figure 8c) and the deviations between observations and simulation data are very consistent. The thirty fourth sample yields a much higher biomass than would have been predicted by the model. This is an isolated point but it is of interest in that it coincides with the largest negative deviation on the omnivore plot (N.B. It does not have the same sample number because not all state variables are available for each occasion. The actual data points can be judged (from Figure 4).. These anomalies might be explained in terms of incompatible classifications in the model between the two functional groups. In reality the meroplankton are taxonomically heterogeneous and include carnivorous as well as omnivorous taxa. Examples of the former include medusae such as *Aurelia* which consumes zooplankton, eggs and other meroplankton (Raymont, 1983), and fish larvae whose diet is carnivorous following absorption of the yolk sac (Lebour, 1921). It would be better, therefore, to classify some of the hatched larval stages of the benthos as carnivores rather than omnivores (Williams and Collins 1986) as a further refinement of the model for future simulations.

Other regions

Cusum tests have been applied to all the variables for which sufficient data are available but there is insufficient space in a publication of this nature to present it all. One particular series of tests which proved interesting related to the various trophic levels for the Inner Channel Region where the correlations decline with increasing trophic level (Table 1). The results for salinity have been published by Radford (in press). For the other variables, phytoplankton, carnivores and omnivores, although the goodness of fit was not as good as for the Central Channel South, the overall conclusions drawn from the cusum tests were very similar. This strengthened the arguments to investigate specific aspects of the data and the model along the lines described in the previous paragraphs although, in general, model results were satisfactory and consistent with measurements.

CONCLUSIONS

Control chart theory and cumulative sum techniques are very suitable for the objective assessment of simulation models. They are particularly valuable in that they detect significant departures of model and measurements caused by consistent bias or by individual anomalies. Also they test these deviations against the general precision of fit as measured, for example, by the correlation coefficient. This is an important attribute to the ecosystem modeller who invariably finds that his model fits with varying precision for state variables from different trophic levels and for different geographical locations due to causes beyond the data gatherers control.

These techniques have the added advantage that they can be used to decide the level of future monitoring of the system, if this should be required (Radford & West 1986). Also they can form part of the monitoring scheme, for detecting significant changes in the system or for exposing the impact of individual pollution events.

ACKNOWLEDGEMENTS

The work reported in this paper involved the use of models developed by the Estuarine Systems Ecology Group of IMER, NERC. The authors are particularly indebted to those who provided field measurements namely Dr. I.R. Joint (phytoplankton) and Dr. A. Morris (nutrients and salinity). Partial financial support for this programme was given by the UK Department of the Environment (contract number DGR 480/48).

REFERENCES

Lebour, M.V., 1921. The food of young clupeoids. J. Mar. biol. Ass. UK 12: 458-467.

Morris, A.W., (1983) Practical Procedures for Estuarine Studies (ed. A.W. Morris) publ. Natural Environment Research Council pp 262.

Page, E.S., (1961) Cumulative Sum Charts. Technometrics 3, 1-9.

Radford, P.J., 1979. Some aspects of an estuarine ecosystem model - GEMBASE. In "State-of-the-art in Ecological Modelling" (Ed. S.E. Jorgensen). Proceedings of the ISEM conference on ecological modelling, Copenhagen, 1978. International Society for Ecological Modelling, pub. p. 301-322.

Radford, P.J., and Joint, I.R., 1980. The application of an ecosystem model to the Bristol Channel and Severn Estuary. Institute of Water Pollution Control. Annual Conference. Water Pollution Control, 79, 244-254.

Radford, P.J., 1983. Systems Modelling of Estuaries. In "Practical Procedures for Estuarine Studies". (Ed. A.W. Morris). Natural Environment Research Council. 239-262.

Radford, P.J. and West, J.A., (1986). Models to Minimise Monitoring. Water Research, 20, 8, 1059-1066.

Radford, P.J. (In press), Model monitoring relationships. In Pollution of the North

Sea; an assessment". (Eds. W. Salomons, B. Bayne, E. Duursma and U. Foerstner). Springer Publ. Co. New York.

Raymont, J.E.G., 1983. Plankton and productivity in the Ocean. Vol. 2. Zooplankton. Pergamon Press. Oxford pp 824.

Uncles, R.J. (1983). Modelling tidal stress, circulation and mixing in the Bristol Channel as a prerequisite for ecosystem studies. Canadian Journal of Fisheries and Aquatic Sciences Sci. 40, 8-18.

Williams, R. and Collins, N.R. (1985), Zooplankton atlas of the British Channel and Severn Estuary. Publ. Natural Environment Research Council, Institute for Marine Environmental Research pp 169.

Williams, R. and Collins, N.R. (1986), Seasonal composition of meroplankton and holoplankton in the Bristol Channel. Mar. Biol. 92, 93-101.

Fig. 1. Chart showing the six geographical regions (2-7) recognised by GEMBASE together with the boundary regions of the Inner Estuary and the Celtic Sea. The double headed arrows represent the transfer of material between adjacent regions.

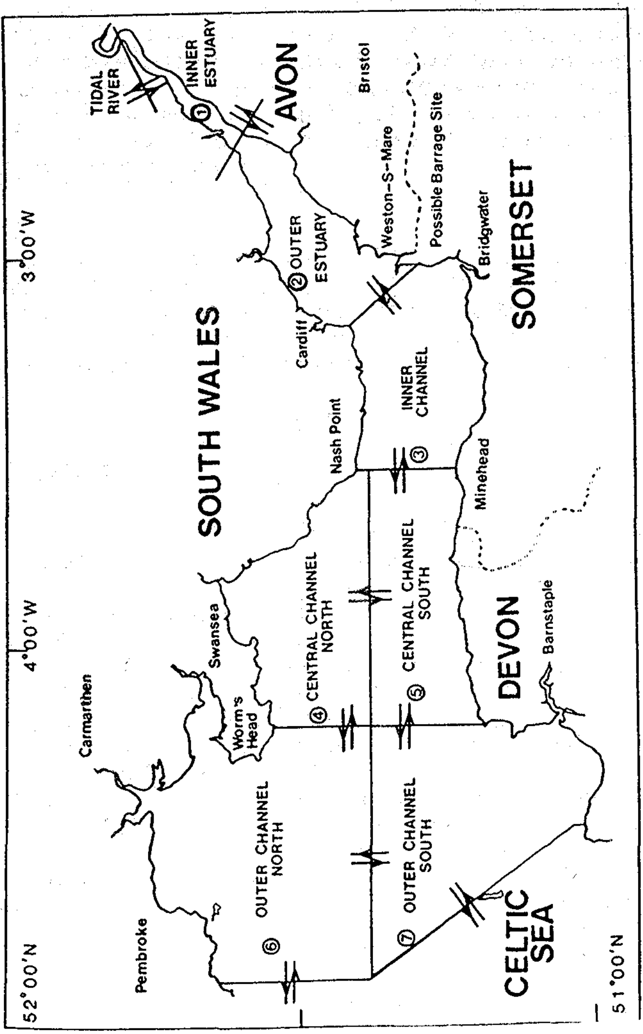


Fig. 2. System flow diagram for GEMBASE giving the groups of state variables (rectangles) and Processes (lines) recognised by the model. The two dashed lines which represent the reproductive pathways for zoobenthos and fish (spawning) were not included in the primary simulations.

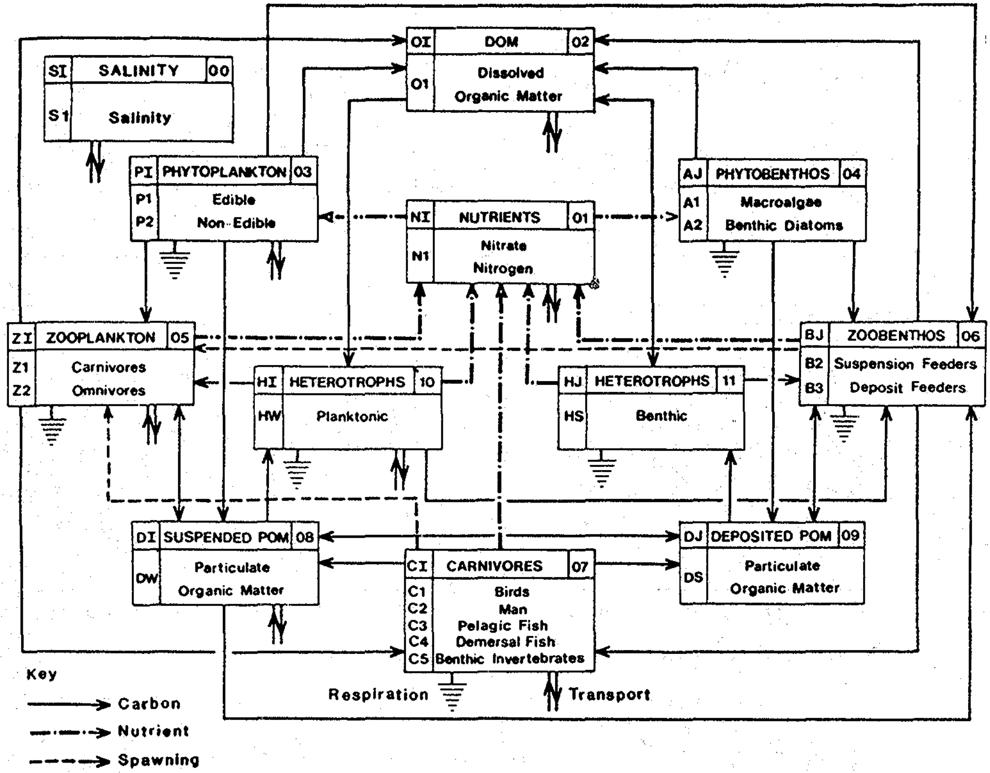


Fig. 3. The continuous lines are 9-year GEMBASE simulations of phytoplankton biomass, and the points are measured concentrations taken over the same time period. The discontinuous lines are the results of the primary simulations before the reproductive pathways for zoobenthos and fish were included in the model. For each of the six geographical regions the concentrations are expressed in terms of $\log_{10}$ (g C.m^{-3}).

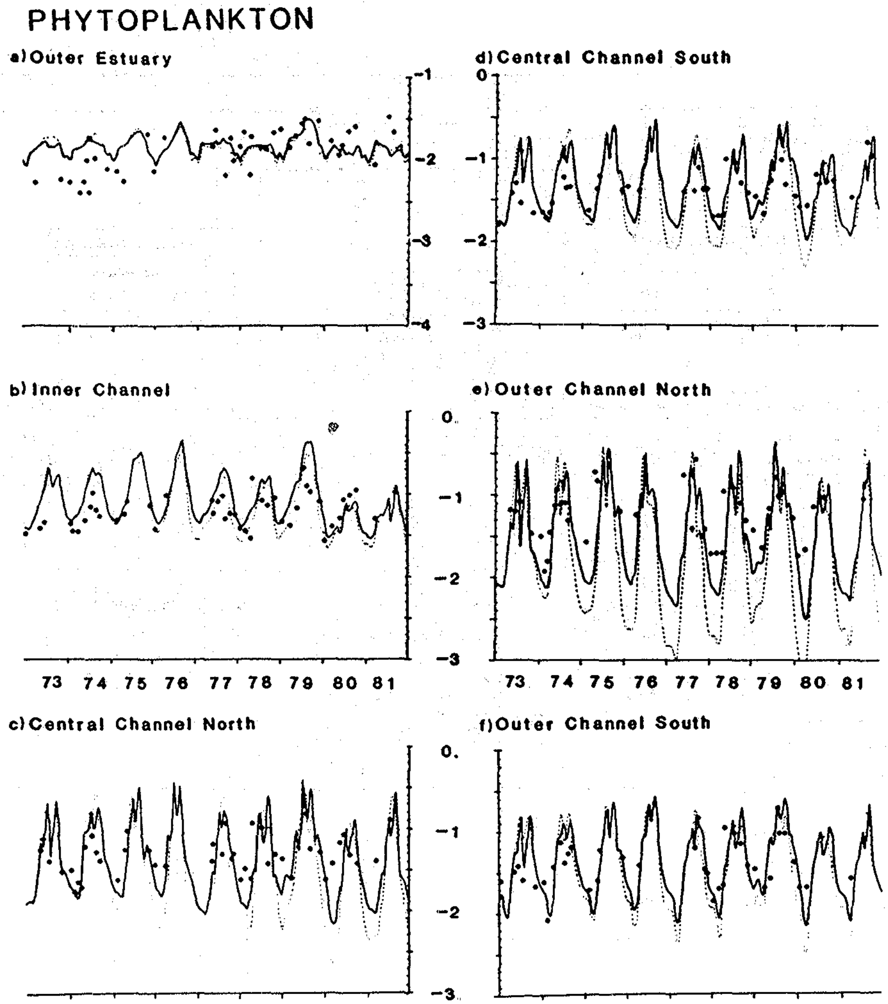


Fig. 4. The continuous lines are 9 year GEMBASE simulations of zooplankton biomass, and the points are measured concentrations taken over the same time period. The discontinuous lines are the results of the primary simulations before the reproductive pathways for zoobenthos and fish were included in the model. Results are given for both carnivorous (a, b & c) and omnivorous (d, e & f) zooplankton for three geographical regions; in each case the concentrations are expressed in terms of $\log_{10}$ (g C.m^{-3}).

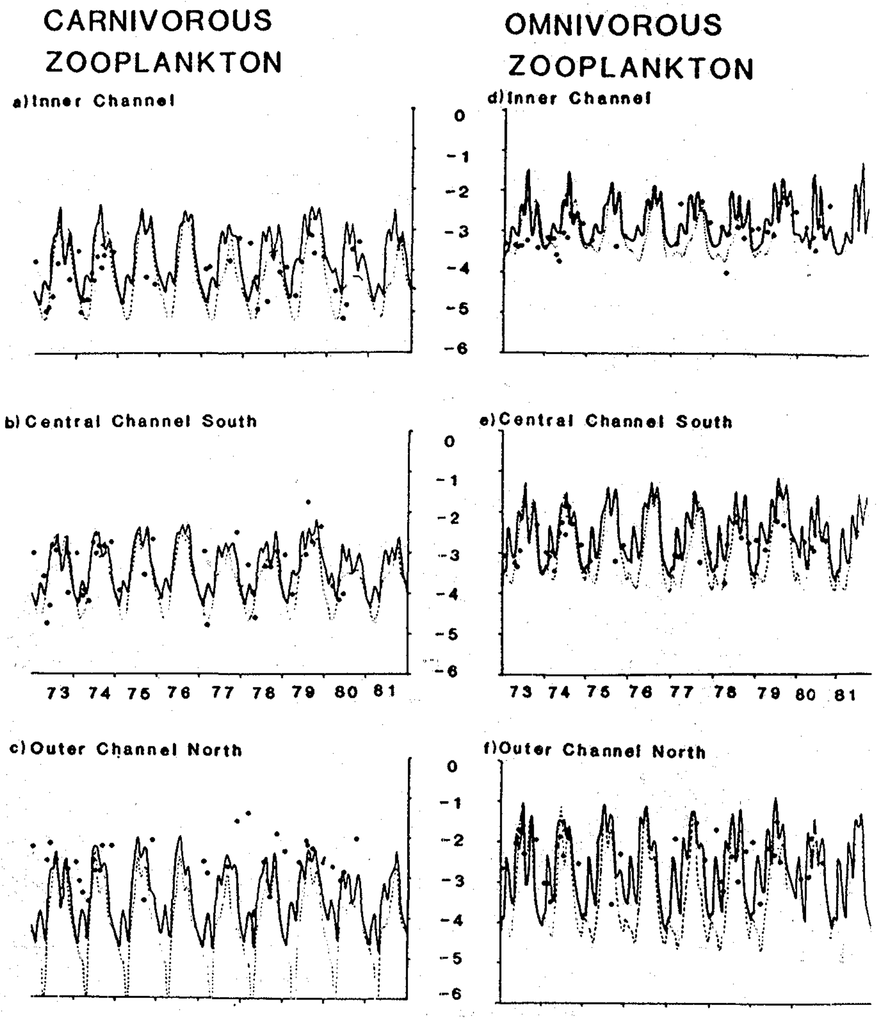
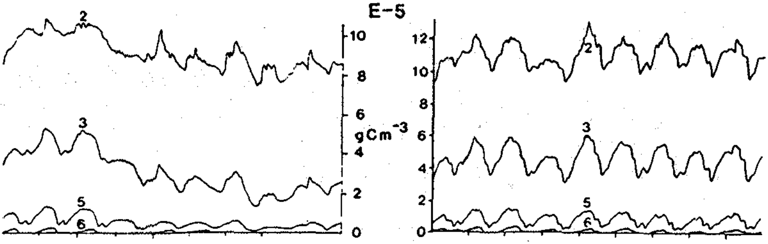


Fig. 5. The left hand graphs show the results of the primary simulation before the reproductive pathways for zoobenthos and fish were included in the model. The modified simulation which included these energy transfers improved the simulation for all three variables (a, b & c) for all regions of the estuary. Improvements were also evident in the simulations of phytoplankton (Fig. 3) and zooplankton (Fig. 4).

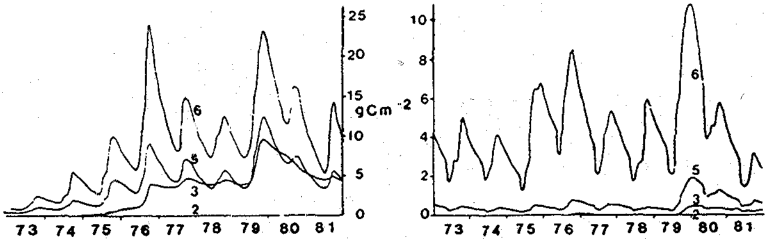
PRIMARY SIMULATION

MODIFIED SIMULATION

a) Planktonic Heterotrophs



b) Suspension Feeders



c) Deposit Feeders

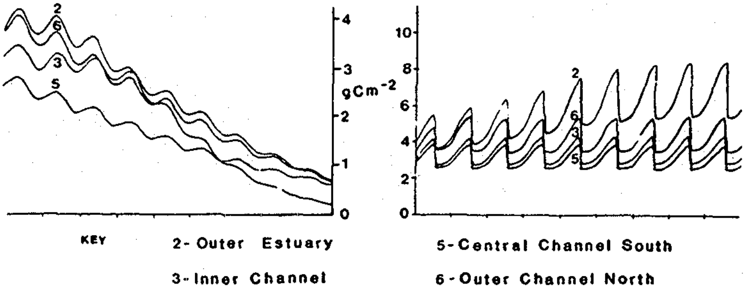


Fig. 6. Simulated nitrate concentrations are shown as lines and measured values (gNm^{-3}) are shown as points for four geographical regions of the Severn estuary and Bristol Channel.

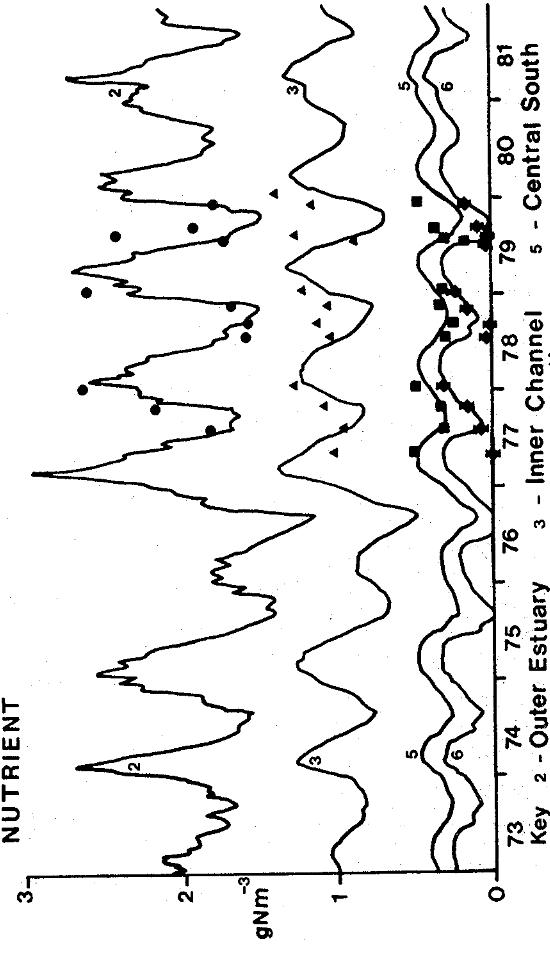


Fig. 7. Control charts and cumulative sum charts for the deviations of simulated from observed salinities, for four geographical regions. The frequency of individual deviations of more than plus or minus two standard deviations (± 2 σ) is no greater than could occur by chance. The "V" tests confirm that there is no significant systematic deviation between model and measurement.

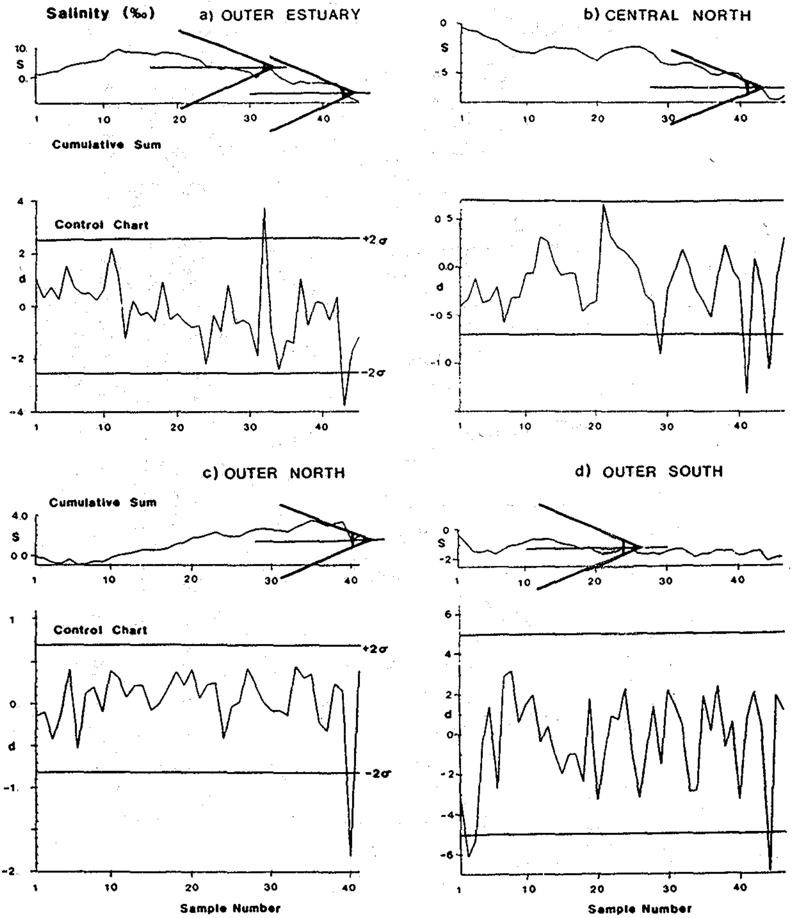
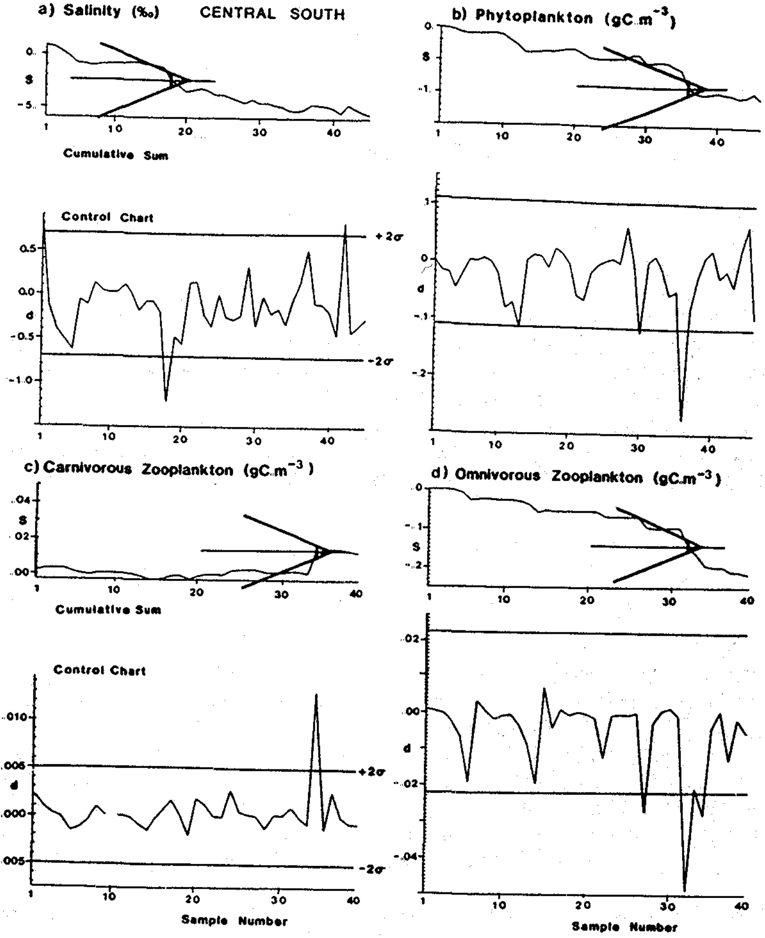


Fig. 8. Control charts and cumulative sum charts for the deviations of simulated from observed values of a) salinity, b) phytoplankton, c) carnivores, d) omnivores in the central Channel South Region. The frequency of individual deviations of more than plus or minus standard deviations (± 2 σ) is no greater than could occur by chance. The "V" tests confirm that there is no significant systematic deviation between model and measurements except for omnivorous zooplankton (see text).



EVOLUTION AND CHANGE IN THE BRISTOL CHANNEL AND SEVERN ESTUARY :

Pre- and post barrage scenarios of the relative productivity of benthic and pelagic subsystems

P.J. Radford

Plymouth Marine Laboratory
Prospect Place, West Hoe, Plymouth, PL1 3DH

ABSTRACT

The relative importance of benthic and pelagic production within the ecosystem energy cycle, varies considerably for different regions of the Bristol Channel and Severn Estuary. In regions of high turbidity pelagic primary production is negligible whereas in the clearer waters of the Outer Channel the much higher pelagic production contributes to both benthic and pelagic secondary production. The construction of a tidal power scheme would most probably reduce turbidity, so increasing the overall productivity of the enclosed estuary. A range of scenarios and their implications id discussed.

INTRODUCTION

The majority of papers presented at this meeting have been concerned with littoral areas, local effects and selected species or communities. I would like to present a broader brush view of the Estuary as a whole in order to set these local issues into their broader perspective. It is important is grasp the geographical scale of the Estuary and the implicit large and significant changes that the presence of a barrage might induce. For convenience we may divide the whole of the Bristol Channel and Severn Estuary into six sub-regions and consider the cubic capacity, average depth, surface area and littoral areas, as given in Table 1.

The impact of a Barrage will not be restricted to these relatively small littoral areas

Table 1. Volumes, depths, areas, littoral areas and mean turbidities of the six regions of the Bristol Channel/Severn Estuary used in the PML study (Radford et al., 1988).

BOUNDARIES	NAME OF REGION	VOLUME km^3	DEPTH m	AREA km^2	LITTORAL %	TURBIDITY g m^{-3}
to Holm Island	Outer Estuary	5	9	513	24	300
to Nash Point	Inner Channel	14	18	756	7	40
to Worms Head	Central North	20	24	857	3	12
	Central South	25	32	789	1	11
to Lundy Island	Outer North	53	33	1602	7	5
	Outer South	52	41	1250	1	4

but will extend throughout the whole estuary, length, breadth and depth (water column) and impinge upon all the sub-tidal benthos as well. Whole communities of organisms will be affected, comprising many individual species. For a broad and comprehensive view it is only possible to consider biota in terms of functional groups because if only fifteen of such groups are modelled this implies the need to model about 150 individual biological processes (e.g. feeding, respiration and mortality). Plymouth Marine Laboratory has developed and validated such a model (Radford *et al.*, 1988) which reproduces the broad features of the Severn Ecosystem. The model simulates the annual cycles of salinity, nitrate, phytoplankton and zooplankton over a ten year period without significant bias and in phase with measurements made at monthly intervals in most years. It reproduces the essential differences between the six regions of Table 1 caused by the varying hydrodynamic regimes and subsequent water column turbidities. The good measure of agreement between the observed and modelled time series enables a comparison to be made between the simulated pre- and post barrage scenarios, with some confidence.

The most obvious regional differences are caused by the high water column turbidities of the Outer Estuary (Table 1) which result in consistently low background levels of phytoplankton and zooplankton compared to the vigorous seasonal cycles observed in the Central and Outer Bristol Channel, where turbidities are much lower (Table 1).

In Table 2 the fifteen organic state variables of the model are first listed followed by the processes which represent the transfers of carbon between components. The six columns headed "Unmodified System" represent the six geographical compartments of the Bristol Channel and Severn Estuary as defined in Table 1. The data in each row has been scaled by a power of ten to ensure that the greatest number in any cell is between one and ten. The scaling factor (exponent) used is given in the final column of Table 2. This facilitates comparisons between different regions for any single variable. For an idea of the relative magnitude of the different variables it is useful to scan the exponent column. The code names for the processes are four character strings, composed of the departure and destination state variable codes of carbon transfer (e.g. N1P1 represents the uptake of nitrates, N1, by phytoplankton, P1). The loss of carbon by respiration is coded 00 (e.g. P100 represents phytoplankton respiration), and groups of related variables are code I (e.g. A1 + A2: Benthic algae = macro algae + diatoms). The code TR represents the net transfer of material by advection and diffusion from a given region (e.g. N1TR is net transport of nitrate).

SIMULATED PRE-BARRAGE PRODUCTIVITY

Pelagic Production

Phytoplankton biomass (P1 in Table 2) is a very poor indicator of primary production in the water column although annual mean levels (Table 2) do tend to increase with decreasing turbidity (Table 1) i.e. increasing photic depth (Table 1). This is evidenced by measurements (Radford *et al.*, 1988), and also by simulation results (Table 2), except the phytoplankton (P1) in the very turbulent water of the Outer Estuary is influenced much more by transport (P1TR REGIONAL TRANSFER) from the tidal river than by *in situ* primary production (N1P1). The ecosystem model computes primary production directly, using a sub model which integrates the effects of solar radiation, turbidity, and nutrient availability. These results (Table 2), expressed in terms of g C m^{-2} d^{-1}, illustrate the overriding effect of turbidity which restricts primary production (N1P1) in the Outer Estuary and Inner Channel to very low levels (.002 and .01 g C m^{-2} d^{-1}) compared to the much higher levels of the remainder of the Bristol Channel (.10 → .17 g C m^{-2} d^{-1}). The slight differences between the Northern and Southern Regions are mainly due to the higher nutrient levels in the Bays (North) compared to the lower nutrients of the Southern, more saline regions. The primary production per unit volume (i.e. N1P1 data divided by depth) further emphasises these differences because the bays are, in general, more shallow than the Southern regions.

Secondary production in the water column reflects primary production resulting in an average omnivorous zooplankton biomass (Z2) which ranges from 0.01 g C m^{-2} in the Outer Estuary to 0.14 g C m^{-2} in the North Outer Channel. Carnivorous zooplankton (Z1) tend to be correlated with their prey biomass but are fewer by an order of magnitude.

Benthic Production

Benthic suspension (B2) feeders are virtually absent from the Outer Estuary (.00039 g C m^{-2}) because they depend upon filtering food from the water column. In this region the high suspended particulates which average 300 g C m^{-3} would clog their filtering mechanisms and prevent them from ingesting sufficient food for normal growth. Similarly their growth is severely limited in the Inner Channel where the water column turbidity averages 40 g m^{-3} and their predicted average biomass is only 0.017 g C m^{-2} compared to that in the North Outer Channel of 5.425 g C m^{-2}. Benthic community studies (Warwick and Price, 1975; Warwick *et al.*, 1978; Warwick and George, 1980 and George and Warwick, 1985) which relate to the Bristol Channel have shown that for specific communities the Production: Biomass ratios (P/B's) of suspension and deposit feeders are constant. The PB's, given in Table 3, have been estimated by Warwick (personal communication) and from these the annual production figures have been deduced.

Table 3. Estimated benthic production based on simulated average biomass (B2 and B3 Table 2) and empirical production/biomass ratios measured by Warwick (see text). The substrate areas represent the percentage of the sublittoral area which potentially could provide a niche for the existing functional groups.

REGION	SUSPENSION FEEDERS		COMMUNI	DEPOSIT FEEDERS	
	Suitable Substrate % AREA	Estimated Production gC $m^{-2}y^{-1}$	Production/ biomass RATIO	Suitable Substrate % AREA	Estimated Production gC $m^{-2}y^{-1}$
Outer Estuary	61	0.00039	1.0	27.	1.02
Inner Estuary	84	0.024	1.2	36.	1.30
Central North	97	2.31	1.3	32.	1.55
Central South	99	0.88	1.4	18.	0.60
Outer North	94	3.25	0.6	77.	1.66
Outer South	99	1.31	0.6	47.	0.85

These data confirm that suspension feeders thrive in the nutrient rich bays to the north of the Bristol Channel but that their production is lower in the more oceanic waters of the Southern Channel. However the greatest impact on suspension feeder production is caused by the high turbidities of the Outer Estuary and Inner Channel. The effect is accentuated by the mobile bottom sediments of these two regions which do not provide suitable substrates for communities to develop and which reduce potential sites to only 61% and 84% of the total area respectively.

Benthic Deposit Feeders (B3) are not inhibited by high turbidities in the same way as suspension feeders. Even within the turbid Outer Estuary, in those areas where communities exist, their production is very high (3.8 g C m^{-2} y^{-1}), and on average exceeds that of Carmarthen Bay (2.15 g C m^{-2} y^{-1}). It is because the harsh hydrodynamic regime of the Outer Estuary reduces the areas suitable for colonisation to only 72% that mean biomass over the whole area is only 1.02 g c m^{-2} (Table 3). Applying Warwick's P/B ratios to the biomass estimates given in Table 2 (B3) we find that mean production of deposit feeders averaged over the whole of each region is very uniform (Table 3) varying only between 0.60 g C m^{-2} y^{-1} for the Central Channel South to 1.66 g C m^{-2} y^{-1} for the Outer Channel North. The Outer Estuary (1.02 g C m^{-2} y^{-1}) and the Inner Channel (1.30 g C m^{-2} y^{-1}) both permit average production of deposit feeders in spite of the high turbidities and high tidal currents and the associated benthic areas of relatively barren rocks.

Total System Productivity

The totality of the data presented in Table 2 is rather difficult to assimilate and understand. One method of presenting it is in the form of a flow diagram for each region of the Bristol Channel and Severn Estuary. Fig. 1 gives a summary of the information for the unmodified Outer Estuary. The width of the squares and the width of the pathways, representing the state and process variables respectively, have been drawn in proportion to the logarithm of their annual mean magnitude (mg Cm^{-2} and g Cm^{-2} d^{-1}) and the pathways labelled with their truncated exponent (eg. $5.3.10^{-3}$ as -3). The relative productivity of two regions may be compared by visual impressions of the different pathway widths and state variable areas. It should be noted that state variables with average biomass of less than .3g Cm^{-2} have not been drawn strictly to scale and the numerical values have not been included in the diagrams due to lack of space. Different shading has been used to distinguish between respiration, food, waste products and inter-regional transfer pathways. Fig. 2 presents a similar flow diagram of the Central Channel North for the unmodified Estuary. Comparing Fig. 1 with Fig. 2 the important differences between these two regions are clearly visible. On of the most striking features concerns the respiration pathways which are much broader for the Central Channel North than the Outer Estuary. Similarly the food pathways from phytoplankton (Pl) and particulate carbon (DW) are much greater in the Central Channel due to the larger biomass of suspension and deposit feeders (B2 & B3) to be found there. Other features which are prominent include the much smaller biomass of phytoplankton (Pl) in the Outer Estuary and the much higher concentration of suspended organic carbon there due to its continual resuspension into the turbid water column. Concentrating on the process pathways it becomes evident that the Central Channel North is far more productive in every way that the Outer Estuary region.

The clue to these differences is to be found in its larger average biomass of phytoplankton and the concomitant greatly increased primary production rate in this Northern Region.

SIMULATED POST-BARRAGE PRODUCTIVITY

Physical Environment

It has been assumed that a tidal power scheme would be build on a line across the Holm Islands from Brean Down to Lavernock Point. It would enclose a volume of water which, on average, would be the same as that presently attained at high water on an average neap tide and littoral areas would be reduced by half. The depth of this water would be consistent with this volume and its dispersion coefficients would be reduced to one quarter of existing values. Undoubtedly the reduced tidal range behind the barrage would reduce tidal resuspension of deposited sediments leading to reduced turbidities. The magnitude to this effect is unknown but early predictions (Miles, 1982) suggest that fine mobile sediments could be reduced by any order of magnitude. The model was therefore executed substituting into the Outer Estuary (annual mean 300 gm^{-3}) the turbidities experienced in the Central Channel North (annual mean 40 $g\ m^{-3}$). No other assumptions were made and the immediate post barrage simulations started with the same initial conditions for all state variables as for the unmodified estuary. The model predicts that after a period of ecological adjustment the modified system would settle down to its new dynamic equilibrium. The most important changes are predicted to occur in the enclosed Outer Estuary so, for simplicity, only these are reported here (Table 2 first column headed "BARRAGE").

Pelagic Production

The mean phytoplankton biomass (P1) would double from 0.28 $g\ C\ m^{-2}$ to 0.56 $g\ C\ m^{-2}$ due to the reduced turbidity in the water column. This effect is small compared to the great increase in primary production (N1P1) from 0.0023 to 0.121 $g\ C\ m^{-2}\ d^{-1}$ that makes it possible. Thus productivity in the Outer Estuary is predicted to rise to levels not very different from those currently attained in the remainder of the North Central Channel.

Secondary production in the water column does not show a corresponding response to the increased primary production. In particular the mean biomass of omnivorous zooplankton (Z2) only increases by about 10% and carnivorous zooplankton (Z1) are predicted to halve their average biomass. This leads one to ask about the fate of this large increase in primary production in the water column. The answer is to be found in the ability of suspension feeders (B2) to exploit this new resource, in the absence of the pre barrage heavy turbidity load.

Benthic Production

The model predicts that the post-barrage equilibrium biomass of benthic suspension feeders (B2) would average 11.89 gCm^{-2}. This is greater than the average biomass (B2) currently predicted for the unmodified North Outer Channel (5.42 g Cm^{-2}) but is of the same order of magnitude as measured populations in that region (10.32g Cm^{-2}, Warwick, personal communication). There are reasons to believe that the computer prediction is slightly greater than it should be, but in qualitative terms one would confidently predict that in the post-barrage Outer Estuary benthic biomass would exceed levels currently found in the unmodified system. It has already been established that benthic biomass is a good indicator of benthic production (Warwick and Price, 1975; Warwick *et al* 1978; Warwick and George, 1980; George and Warwick, 1985), thus we may deduce that the predicted increased biomass indicate increased production of suspension feeders.

Benthic deposit feeders (B3, Table 2) are not inhibited by the high turbidity of the water column neither do they need new primary production as an essential food source since they thrive on detritus. This is evidenced by the high population densities in the Outer Estuary and simulated by the model (B3 in Table 2). However, the model predicts that the cleaner and more productive waters of the post barrage Outer Estuary do cause an increase in population of about 20% (1.025 → 1.219 g Cm^{-2}). This effect is probably due to the increased supply of detritus from dead phytoplankton cells and from pseudo faeces deposited by suspension feeders.

Higher Trophic Levels

The biomass of the Higher Carnivores including birds (C1), demersal fish (C4), and benthic invertebrates (C5), for any specific region is primarily controlled by immigration and emigration. These processes were not explicitly modelled but estimated monthly biomasses were imposed upon the model system which allowed for the calculation of the food which these organisms take from the system and the organic detritus which they contribute. The same annual biomass cycle was imposed for each year but the specific gains and losses to the system depended upon the *in situ* availability of food. The biomass of birds (C1) is very small when averaged over the whole area of the estuary (.0005 g Cm^{-2}) but it is assumed that the majority of these birds feed on the benthos in the small littoral zone.

The quantity of food consumed by birds is given in Table 2 (B3C1 and B2C1 PREDATION) and it represents intake by birds (C1) of benthic suspension (B2) and deposit feeders (B3). Although in the unmodified system the birds consumed enough food to survive, the same biomass of birds increased their intake by an order of magnitude in the simulated post-barrage situation. This was possible in spite of the fact that the littoral area was assumed to be reduced to 50% of the existing area. Thus in the post barrage situation the same biomass of birds would be able to be supported on a smaller area because the prey species would become more productive. In Practice this increased prey density could lead to an increased influx of birds but such a prediction is beyond the scope of the model.

Total System Productivity

The impact of a barrage on the totality of the estuarine ecosystem may be judged by comparison of Fig. 1 with Fig. 3. These represent the flow of carbon through the Outer Estuary as predicted by the model for the unmodified system and for the post-barrage conditions respectively. The most distinguishing feature is the increased respiration pathway for the post barrage scenario. This is indicative of the overall increase in productivity of the estuary caused by the reduced turbidity of the water column and its concomitant increased photic zone. Food pathways are similarly increased as enhanced primary production is utilised by a greatly increased population of benthic suspension and deposit feeders. Although photosynthesis has greatly increased this does not manifest itself in greatly increased biomass of phytoplankton (Pl) but rather by a large contribution to secondary production. The amount of particulate carbon in the water column (DW) is greatly decreased in the post barrage scenario because it is no longer resuspended by the lower tidal velocities and because much more of it is utilised by the larger population of suspension feeders. In general terms it can be seen that the post barrage system is far more productive than that of the present unmodified estuary. It is useful to compare the post barrage scenario for the Outer Estuary (Fig. 3) with the unmodified Central Channel North (Fig. 2). In terms of general productivity these two systems appear very similar i.e. the energetic pathways are of similar order of magnitude and the average levels of the state variables are much the same. Both systems are strikingly different from the Outer Estuary for the unmodified estuary (Fig. 1).

CONCLUSIONS

In effect the imposition of a barrage releases the potential of the Outer-Estuary ecosystem to perform in a more typical estuarine mode; not inhibited by excessive water column turbidity. It seems unlikely that the modified estuary would be unable to support the existing populations of birds and fish. It is probable that the more productive system caused by the imposition of a barrage would attract and sustain greater populations of higher carnivores than the present unmodified system. The reduced littoral areas would be far more productive than the existing mud flats and should enable birds to obtain adequate prey even if their feeding grounds were exposed for a shorter time periods.

ACKNOWLEDGEMENTS

The work reported in this paper involved the use of models developed by the Estuarine Systems Ecology Group of IMER (now Plymouth Marine Laboratory) NERC. The author is particularly indebted to Dr. R.M. Warwick who provided field measurements of benthic populations in the Bristol Channel and Severn Estuary. Partial financial support for this programme was given by the UK Department of the Environment (Contract No. DGR 480/48).

REFERENCES

George, C.L. and Warwick, R.M. 1985. Annual Macrofauna production in a hard-bottom reef community. J. Mar. Biol. Ass UK, 65: 713-735.

Miles, G.V. 1982. Impact on currents and transport processes. In: "Severn Barrage", proc. symp. on the Severn Barrage. Institution of Civil Engineers, Thomas Telford Ltd., publ. London. p. 203-216.

Radford, P.J., Burkill, P.H., Collins, N.R. and Williams, R. 1988. The validation and scientific assessment of an ecosystem model of the Bristol Channel. In advances in environmental modelling. (Ed. A. Marani). Proceedings of the ISEM conference on ecological modelling, Italy, 1987. International Society for Ecological Modelling, Elsevier, Amsterdam. 427-442.

Warwick, R.M. and Price, R. 1975. Macrofauna production in an estuarine mud-flat. J. Mar. Biol. Ass. UK 55: 1-18.

Warwick, R.M., George, C.L. and Davies, J.R. 1978. Annual macrofauna production in a *Venus* community. Est Cstl. Mar Sci. 7: 215-241

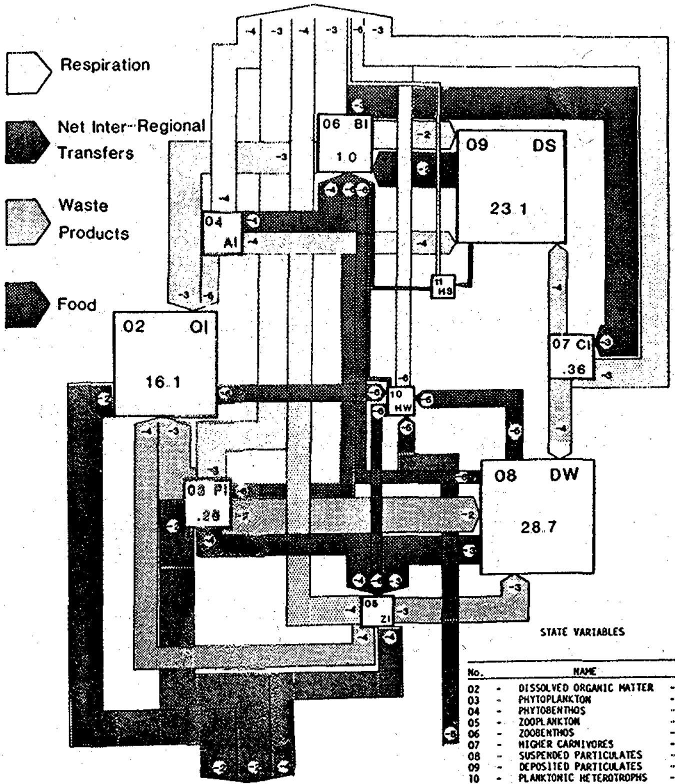
Warwick, R.M. and George, C.L. 1980. Annual macrofauna production in an *Abra* community. pp 517-538. In: Collins, M.B. *et al* (eds.). Industrial embayments and their environmental problems. A case study of Swansea Bay. Pergamon, Oxford.

Table 2. Simulated annual mean values for the 15 state variables (gC.m^{-2}) and the 40 groups of processes (gC.m^{-2}d^{-1}) for each of the six regions of the Bristol Channel and Severn Estuary. The first column of data, headed "BARRAGE" gives the predicted results assuming that a tidal power scheme had been built near the Holm Islands some two years previously.

CODE	VARIABLE/PROCESS \ REGION	BARRAGE OUTER ESTUARY	UNMODIFIED SYSTEM						EXPONENT
			OUTER ESTUARY	INNER CHANNEL	NORTH CENTRAL	SOUTH CENTRAL	NORTH OUTER	SOUTH OUTER	
O1	DISSOLVED ORGANICS	2.071	1.608	2.079	1.959	2.518	2.296	2.427	1E+01
P1	PHYTOPLANKTON	0.5616	0.2849	0.2263	1.518	1.726	1.805	2.079	1E+00
A1	MACRO ALGAE	0.0002932	0.00937	0.006274	0.0937	0.2795	1.373	3.452	1E+00
A2	DIATOMS	9.123	8.712	0.674	1.323	0.5233	2.504	0.5863	1E-02
Z1	CARNIVORES	0.01556	0.04521	0.1712	0.5342	0.8767	1.567	2.532	1E-02
Z2	OMNIVORES	0.1121	0.1033	0.1364	1.06	1.033	1.447	1.063	1E-01
B2	SUSPENSION FEEDERS	1.189	0.0000391	0.00171	0.1781	0.06274	0.5425	0.2189	1E+01
B3	DEPOSIT FEEDERS	1.219	1.025	1.085	1.195	0.4274	2.767	1.419	1E+00
DW	PARTICULATES WATER	0.006082	2.877	3.041	1.474	1.964	0.7397	0.7973	1E+01
DS	PARTICULATES (SUBSTRATE)	5.26	2.312	3.397	3.233	2.071	7.507	5.014	1E+01
HW	BACTERIA (WATER)	0.07123	1.389	1.285	0.3507	0.5781	0.05041	0.131	1E-03
HS	BACTERIA (SUBSTRATE)	3.205	1.238	0.6932	3.041	3.89	8.274	7.918	1E-05
C1	BIRDS	5.123	5.123	3.178	0.5863	0.1748	0.4493	0.3041	1E-04
C4	DEMERSAL FISH	0.3562	0.3562	0.2795	2.178	1.795	2.233	2.055	1E-01
C5	BENTHIC INVERTEBRATES	3.288	3.288	0.2904	2.189	3.397	3.288	3.397	1E-01
N1P1	PRIMARY PRODUCTION	1.219	0.02381	0.111	1.23	1.085	1.726	1.477	1E-01
N1AI	PRIMARY PROD. LIT.	0.1412	0.101	0.009765	0.07663	0.2007	1.877	4.085	1E-02
O1HW	FEEDING HETEROTROPHS	0.4466	8.822	2.822	1.011	1.674	0.1192	0.2822	1E-06
P100	RESPIRATION PHYTO.	1.523	0.6822	0.6849	4.575	5.123	5.233	5.973	1E-02
P101	EXUDATION PHYTO	6.082	8.63	5.068	6.164	5.425	8.63	7.233	1E-03
P1Z2	GRAZING OMNIVORES	0.1373	0.04082	0.05945	3.945	3.534	5.068	3.068	1E-02
P1B2	FILTERING SUS. FEED.	1.195	0.0000013	0.1918	0.2192	0.1118	0.7123	0.3753	1E-01
P1DW	MORTALITY PHYTO.	0	3.397	1.811	0	0	0	0	1E-02
AI00	RESPIRATION ALGAE	1.359	0.7362	0.06734	0.3025	0.6186	3.138	7.391	1E-03
AI01	EXUDATION ALGAE	0.8932	0.07288	0.02104	0.2767	0.8027	5.562	10.52	1E-03
A2B3	FEEDING DEPOSIT FEED.	3.562	3.479	0.3781	0.3507	0.07233	0.5918	0.09671	1E-04
AIDS	MORTALITY ALGAE	0.1723	0.01608	0.004411	0.05397	0.1542	1.027	1.89	1E-02
Z100	RESPIRATION ZOO.	0.1245	0.0991	0.1595	2.074	1.935	2.828	1.964	1E-02
Z101	EXUDATION ZOO.	0.1186	0.4274	0.4411	3.89	3.664	5.135	3.205	1E-03
Z1DW	MORTALITY ZOO.	0.02447	0.1584	0.1586	0.8247	0.8027	1.118	0.6767	1E-02
B200	RESPIRATION SUS.FEED.	5.58904	0.108	0.0108	0.981	0.3562	2.37	1.093	1E-02
B300	RESPIRATION DEP. FEED.	0.767	0.6246	0.0108	0.77	0.2821	1.808	0.9407	1E-02
BI01	EXUDATION BI	2.249	0.5315	0.4493	1.282	0.4932	2.682	1.334	1E-02
BIC1	PREDATION BY BIRDS	1.415	0.1598	0.03598	0.4668	0.2049	1.468	0.6959	1E-02
BIDS	MORTALITY BI	5.041	1.063	0.9507	3.014	1.134	5.342	2.644	1E-02
CI00	RESPIRATION CI	4.407	1.703	0.4293	2.302	3.01	4.421	3.776	1E-03
CIDW	MORTALITY TO WATER	2.82	0.3205	0.07205	0.9836	0.4466	2.986	1.149	1E-03
CIDS	MORTALITY TO SUBS.	0.4793	0.4793	0.502	3.673	1.721	9.05	5.112	1E-04
DWZ2	GRAZING OMNIVORES	0.005151	2.063	1.973	0.7726	1.614	0.7863	0.5178	1E-03
DWB2	FILTERING SUS.FEED.	0.3068	0.0003233	0.1104	1.455	0.7397	1.2	0.8137	1E-02
DWHW	FEEDING HETEROS.	0.00013	1.633	0.4274	0.07616	0.1323	0.003781	0.009205	1E-05
DSB3	FEEDING DEP. FEED.	0.0000227	2.321	1.915	3.014	1.118	7.123	3.753	1E-02
DSHS	FEEDING HETEROS.	2.279	0.3644	0.2225	1.099	1.649	2.877	3.096	1E-07
HW00	RESPIRATION HETEROS.	0.1342	7.534	2.129	0.5315	0.8986	0.04712	0.1126	1E-06
HWZ2	GRAZING OMNIVORES	0.0707	2.011	1.559	1.896	3.288	0.3674	0.8795	1E-06
HWB2	FILTERING SUS.FEED.	1.26	0.0000635	0.02049	0.411	0.1978	0.1268	0.1238	1E-05
HS00	RESPIRATION HETEROS.	6.85	1.09	0.6685	3.288	4.959	8.658	9.26	1E-08
HSB3	FEEDING DEP. FEED.	1.249	0.4959	0.389	0.811	0.5397	1.959	1.304	1E-07
N1TR	REGIONAL TRANSPORT	3.222	1.169	0.8926	1.38	1.232	1.863	1.721	1E-02
O1TR	REGIONAL TRANSPORT	0.03107	0.01346	0.008727	0.6602	0.8739	0.9043	1.132	1E+00
P1TR	REGIONAL TRANSPORT	2.011	4.763	1.959	0.9904	0.9876	0.2035	2.581	1E-02
Z1TR	REGIONAL TRANSPORT	0.0000555	0.0001335	0.0005554	6.602	8.739	9.043	0.0113	1E-01
Z2TR	REGIONAL TRANSPORT	0.2218	0.5179	0.9967	1.373	0.3365	0.454	2.411	1E-03
DWTR	REGIONAL TRANSPORT	0	2.602	4.958	0.3354	0.3802	0.1149	0.1574	1E-01
HWTR	REGIONAL TRANSPORT	1.208	1.471	0.1944	0.513	0.3811	0.1565	0.1992	1E-05

Fig. 1. Mean annual levels of state variable and processes during 1974, predicted for the unmodified Outer Estuary. The Width of the squares and the width of the arrows, representing the state variables and processes respectively, have been drawn in proportion to the logarithms of their magnitude ($gC.m^{-2}d^{-1}$) and are labelled with the truncated exponent (e.g. 5.3 10^{-3} as -3).

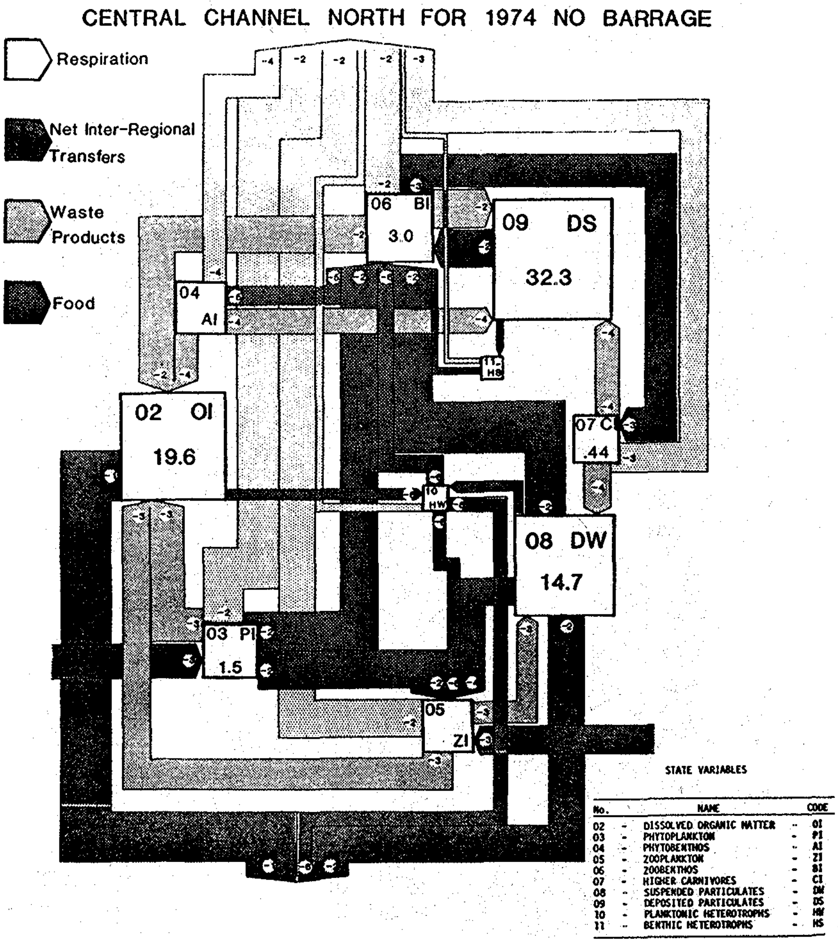
OUTER ESTUARY FOR 1974 WITHOUT BARRAGE



STATE VARIABLES

No.		NAME		CODE
02	-	DISSOLVED ORGANIC MATTER	-	OI
03	-	PHYTOPLANKTON	-	PI
04	-	PHYTOBENTHOS	-	AI
05	-	ZOOPLANKTON	-	ZI
06	-	ZOOBENTHOS	-	BI
07	-	HIGHER CARNIVORES	-	CI
08	-	SUSPENDED PARTICULATES	-	DW
09	-	DEPOSITED PARTICULATES	-	DS
10	-	PLANKTONIC HETEROTROPHS	-	HW
11	-	BENTHIC HETEROTROPHS	-	HS

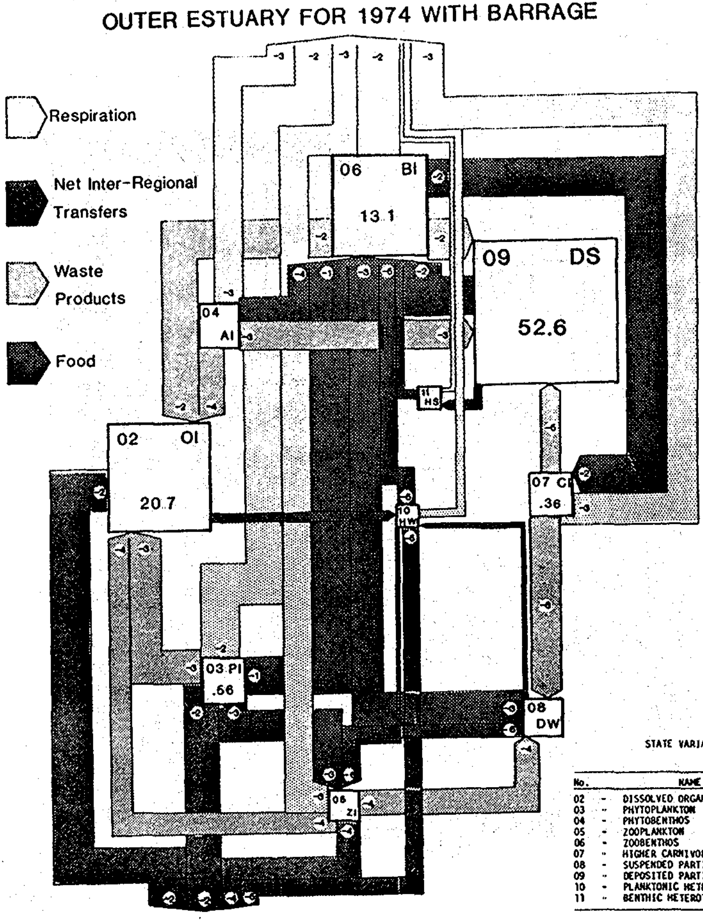
Fig. 2. Mean annual levels of state variable and processes during 1974, predicted for the unmodified Central Channel North. The width of the squares and the width of the arrows, representing the state variables and processes respectively, have been drawn in proportion to the logarithms of their magnitude ($gC.m^{-2}d^{-1}$) and are labelled with the truncated exponent (e.g. $5.3\ 10^{-3}$ as -3).



STATE VARIABLES

No.		NAME		CODE
02	-	DISSOLVED ORGANIC MATTER	-	OI
03	-	PHYTOPLANKTON	-	PI
04	-	PHYTOBENTHOS	-	AI
05	-	ZOOPLANKTON	-	ZI
06	-	ZOOBENTHOS	-	BI
07	-	HIGHER CARNIVORES	-	CI
08	-	SUSPENDED PARTICULATES	-	DW
09	-	DEPOSITED PARTICULATES	-	DS
10	-	PLANKTONIC HETEROTROPHS	-	HW
11	-	BENTHIC HETEROTROPHS	-	HS

Fig. 3. Mean annual levels of state variables and processes during 1974, predicted for the Outer Estuary assuming that a barrage had been introduced 2 years before. The width of the squares and the width of the arrows, representing the state variables and processes respectively have been drawn in proportion to the logarithm of their magnitude ($gC.m^{-2}d^{-1}$) and are labelled with the truncated exponent (e.g. $5.3\ 10^{-3}$ as -3).



STATE VARIABLES

No.		NAME		CODE
02	-	DISSOLVED ORGANIC MATTER	-	OI
03	-	PHYTOPLANKTON	-	PI
04	-	PHYTOBENTHOS	-	AI
05	-	ZOOPLANKTON	-	ZI
06	-	ZOOBENTHOS	-	BI
07	-	HIGHER CARNIVORES	-	CI
08	-	SUSPENDED PARTICULATES	-	DW
09	-	DEPOSITED PARTICULATES	-	DS
10	-	PLANKTONIC HETEROTROPHS	-	HW
11	-	BENTHIC HETEROTROPHS	-	HS

EXPERIMENTS IN BENTHIC MODELLING

William Silvert

Department of Fisheries and Oceans, Habitat Ecology Division,
Bedford Institute of Oceanography
P. O. Box 1006, Dartmouth, Nova Scotia, CANADA B2Y 4A2

ABSTRACT

A wide variety of different approaches has been used for modelling the benthic component of estuarine and continental shelf ecosystems, including various combinations of size-structured and functionally based representations. Best results have been obtained with a highly aggregated approach based on functional groups which reflect organism size, and continental shelf models have been developed which use this type of benthic submodel coupled to a size-structured model of the pelagic subsystem. Unfortunately it has proved far more difficult to quantify feeding rates for benthic organisms than for pelagic grazers, so there are large uncertainties in the energy budgets and in the benthic-pelagic coupling rates. Because of this, conclusions drawn from our current models are very tentative, but simulation studies indicate that there appears to be a mechanism for dynamic instability in continental shelf ecosystems which is manifested by dramatic shifts in both pelagic and benthic community structure.

INTRODUCTION

The Bedford Institute of Oceanography has had an active ecological modelling program for approximately fifteen years, and for the past ten years this program has relied heavily on computer simulation modelling of energy and nutrient flows. This has led to the development of progressively more complex and comprehensive models with increased attention to the role of the benthic subsystem. Development of benthic submodels has been hindered by lack of adequate quantitative information on benthic organisms, complicated by the strong dependence of the benthic community on properties of the local substrate. In order to deal with these difficulties a variety of approaches has been investigated. None of these has proved totally satisfactory, but several interesting patterns have emerged. One of the most interesting results has been that in many cases relatively gradual changes in the pelagic community seem to be associated with dramatic and virtually discontinuous changes in benthic community structure. These simulation results are obtained with highly aggregated and generalized models; whether they are realistic is not yet known, but they suggest that the structure of benthic communities is very sensitive to external factors and that the modelling of benthic subsystems may reveal some interesting surprises.

BACKGROUND

Our simulation modelling program grew out of a collaboration with the BOEDE group at the Netherlands Institute for Sea Research (NIOZ). I worked on the benthic submodel for their original modelling of the Ems-Dollard estuary in 1981 (Ruardij and Baretta 1982), and subsequently several colleagues from the former Marine Ecology Laboratory visited NIOZ and used the Ems-Dollard model as the basis of a simulation model of the Cumberland Basin in the Bay of Fundy (Gordon and Baretta 1982, Gordon *et al.* 1986, Keizer *et al.* 1987). The original Ems-Dollard model identified four classes of benthic organisms, namely bacteria, plants, meiobenthos and macrobenthos (Ruardij and Baretta 1982). The Cumberland Basin model retained this basic structure, but differentiated between intertidal and subtidal organisms and split the macrobenthos into several functional groups (Keizer *et al.* 1987). By comparison, the Ems-Dollard benthic submodel became very sophisticated, with a much more detailed representation of bottom chemistry and structure involving almost 30 parameters; there is also a separate epibenthic submodel (Baretta and Ruardij 1988). Clearly there is room for a wide divergence of opinion on how to model the benthos even in similar systems.

We have continued to study and model the benthos of estuaries, currently in the context of attempting to determine the capacity of the bottom to assimilate waste products from mariculture, but the balance of this paper will focus on modelling the benthos in continental shelf ecosystems. Although this is a much simpler problem, since factors such as plant growth, bird predation, and tides can generally be omitted, there remain many important issues which are difficult to resolve. Much of our recent modelling effort has been directed at finding a general approach to incorporation of the benthos in continental shelf models and understanding at least the gross features of benthic community dynamics.

This stage of the work started in 1983 with the initiation of a project to develop a trophodynamic ecosystem model of the Grand Banks of Newfoundland that could be used to assess the potential impacts of petroleum exploration and development. After completion of this project in 1986, a generic model of continental shelf ecosystems was developed for further investigation of the dynamics of continental shelves. This model, called the Theoretical Macrocosm (TM), consists of a single compartment based on common features of the compartments in the Grand Banks model. Physical transport, which is so strong on the Grand Banks that it frequently dominates the biological processes, is represented by import and export terms which can be reduced to a level that makes it possible to study the biological effects in isolation. This has made it possible to refine the modelling work in several ways, particularly by developing much better models of nutrient dynamics and, of particular relevance for this paper, by experimenting with different approaches to modelling the benthos.

ALTERNATIVE STRATEGIES FOR BENTHIC MODELLING

The Grand Banks project was hindered by a severe lack of benthic data, and by a virtual absence of information about benthic bacteria and meiofauna. It became evident at an early stage that our inability to obtain adequate information about the benthos would lead to serious modelling difficulties. However we also knew that the benthos is a very important part of the system, with mean annual production estimated at approximately 500 $g/m^2/y$ (dry weight) and standing stocks of several kg/m^2 recorded in some areas (Hutcheson *et al.* 1981). The approach taken was motivated both by a lack of adequate data on which to base a detailed benthic submodel and by the strong vertical mixing found over most of the Grand Banks, which indicates a high level of benthic-pelagic coupling. We chose simply to integrate the benthic community with the rest of the water column and to define general classes of organisms which include both pelagic and benthic populations. For example, one of the biological compartments in the model consists mainly of small pelagic fish, and benthic macrofauna are included in this category.

This vertically aggregated approach obviously does not provide any information about the dynamics of the benthos, since the benthic organisms are only a small part of the total biomass in each biological grouping, but it was surprisingly well accepted by biologists who evaluated the model. Meiobenthos specialists were the ones most unhappy about this approach, but acknowledged that there was not enough information about the Grand Banks meiofauna to enable us to treat them separately. The major predators on the pelagic fish/macrobenthos compartment are midwater and bottom feeders, and the absence of detailed feeding preferences for many of these fish species provided further justification for the aggregation in the model. There was some concern about whether the high biomasses of the hard-shelled clam *Mesodesma deauratum* were dealt with adequately, but because these clams appear to play a minor role in the ecosystem this was not a major concern.

With the development of the TM (Theoretical Macrocosm) model it was felt essential to incorporate a more realistic benthic submodel. Two basic approaches were investigated. One was to treat the benthos in terms of functional groups distinguished by size, feeding behaviour, and mobility. The other was to use a classification based primarily on organism size. This latter approach has been used with great success in the pelagic submodel of both the Grand Banks model and the TM, and it has a strong theoretical basis (Silvert 1984, 1988). Particle size has been used very effectively to characterize benthic communities (Schwinghamer 1981, Warwick 1984), and the study of particle size distributions has been a focus of research at the Bedford Institute of Oceanography for over twenty years (*e. g.*, Sheldon *et al.* 1972 and 1977). However, we experienced serious difficulties in trying to develop a benthic submodel based primarily on size, and consequently chose instead to deal with functional groups rather than size classes. The reasons for this are complicated, but two factors proved decisive:

- Feeding relationships in pelagic marine ecosystems are for the most part size-structured, with animals of a given size feeding mainly on a restricted size range of smaller organisms (Kerr 1974). The effectiveness of the size-structured approach derives to a great extent from the resulting food chain structure (Silvert and Platt 1978). Size is a much poorer predictor of feeding behaviour in the benthos, as large deposit feeders compete with meiofauna for microscopic detrital particles while suspension feeders of the same size scavenge algal cells and other suspended particulates from the water column.

- The size structure of the benthos is strongly determined by grain size of the sediment, an external factor which is difficult to relate to other ecological factors.

We agreed that a size-structured benthic submodel would have to incorporate at least five size classes in order to represent the W-shaped size spectrum described by Schwinghamer (1981), but concerns about our ability to quantify the trophic fluxes of benthic organisms forced us to conclude that any attempt to obtain reasonable values for anything more than an extremely simple two-compartment model (meiofauna and macrofauna) would be impractical. Some work was done with this representation, but it was felt that the flux of sinking algal cells to the benthos could not be modelled adequately unless a distinction was made between suspension feeders, which can feed on living cells in the water column, and detritivores. Consequently we felt that functional groupings were necessary at this stage of the modelling work. The TM model currently divides benthic fauna into four functional groups: meiofauna, large detritus feeders, suspension feeders, and epibenthic carnivores. In addition, benthic detritus and bacteria are included in the model (benthic primary production is not considered important on the continental shelves of the Northwest Atlantic). The metabolic rates for these highly aggregated groups were taken to be somewhat less that those calculated for pelagic organisms of the same size on the basis of allometric relationships (Platt and Silvert 1981).

Even this very simple characterization of the benthic fauna has been difficult to quantify, and there is a great deal of uncertainty as to how to model and parametrize benthic feeding. Currently the feeding relations are as follows:

> Meiofauna eat benthic detritus and bacteria. Although some meiofauna are carnivorous and eat other members of this group, this process is not explicitly modelled (it is however treated as a metabolic loss by the aggregated meiofauna).
>
> Large detritus feeders also consume benthic detritus and bacteria, and they consume meiofauna. They thus compete for food with one of their prey groups. This tends to be destabilizing and may account for dramatic swings in the relative abundance of meio- and macrofauna that are observed in some simulations.
>
> Suspension feeders consume the same prey as the large detritus feeders, but the prey resource is partitioned between a fraction that is resuspended, and thus available to suspension feeders, and the remainder which is available to detritus feeders.
>
> Epibenthic carnivores eat the other macrofauna, namely large detritus feeders and suspension feeders.
>
> All three macrobenthic groups are subject to grazing by demersal fish, and both the suspension feeders and epibenthic carnivores are exploited by the fishery.

These feeding relations incorporate numerous assumptions, some of which are temporary ones taken to simplify the modelling process. For example, although it is clear that suspension feeders can graze on living algal cells that are mixed into the lower part of the water column, modelling direct predation on phytoplankton would require better vertical resolution than was felt practical at the present stage of the modelling work. Consequently consumption of phytoplankton is treated by reclassifying cells which fall below the pycnocline as benthic detritus (which means that they are permanently lost to the phytoplankton population and cannot reappear in the euphotic zone). This makes them available to both detritus feeders and suspension feeders. We feel that this treatment is acceptable at the present state of the work for the systems we are studying, since in most cases the bottom is well below the compensation depth and the fraction of algal cells which will survive being mixed to the bottom is probably small. We would however caution against using this approach in well-mixed or shallow environments; in the Cumberland Basin model for example the suspension feeders consume phytoplankton directly (Keizer *et al.* 1987).

Despite these concerns, we feel that the partitioning of food between suspension and detritus feeders is reasonable and consistent with evidence from estuarine studies (Wildish and Peer 1983). The major implication is that suspension feeders should dominate the macrobenthos in areas with high currents, and during storm events and other periods of high resuspension the resource available to suspension feeders increases at the expense of detritus feeders (although disturbance of the bottom may lead to a net increase in the total particulate loading). For continental shelf ecosystems with lower bottom currents we expect detritus feeders to dominate, as is the case in our simulations (*c. f.* Figure 2).

It has proved very difficult to arrive at a robust partitioning of the food resource between meiofauna and larger deposit feeders, and we are concerned that the high degree of competition between the meiofauna and their principal predators may have a tendency to destabilize the model. By highly aggregating the model we may be artificially creating an instance of the competitive exclusion principle (Gauss 1934, MacArthur and Levins 1967).

The difficulty of parametrizing even this simple model is well represented by the following basic question: Given a known density of a food resource on the bottom (*e. g.,* so many grams of bacterial biomass per square metre), how much will a given detritivore consume per day? For pelagic grazers this type of question is relatively easy to answer, since food can be assumed isotropically distributed and filtering volumes are generally known or can be calculated, but the corresponding values for benthic grazing rates are not available. Suspension feeders represent an intermediate case, since filtering volumes are known at least for commercial species like *Mytilus edulis,* but because of the strong vertical gradients of resuspended food particles near the bottom this information is not of as much value as it is for pelagic feeders. The feeding rate parameters we are using at the present time were estimated after extensive consultation with benthic ecologists, but there is a consensus that the best values we have been able to obtain are not very reliable.

SIMULATION RESULTS

Although extensive simulation "experiments" have been carried out with the TM model, we are not confident that the behaviour of the benthic variables is realistic. We therefore present the results of only one simulation run which exhibits a very interesting transition in the benthic community and which, if valid, raises some very important questions about the long-term dynamics of continental shelf ecosystems.

The simulation shown in Figures 1 and 2 correspond to the recovery of a heavily exploited stock of large fish over a period of ten years. The overall pattern of biomass shifts between size classes superposed on annual oscillations which are larger for the smaller size classes is consistent with theoretical studies of particle size dynamics (Silvert and Platt 1980). These stocks build up over the first six years, and during most of this period the biomass of smaller pelagic fish remain high. However, the increased predation by the larger fish eventually causes these stocks to decline. Since the smaller fish are planktivorous, this causes an increase in the zooplankton biomass toward the end of the simulation; extended simulations beyond the ten year period show damped oscillations similar to those generated by Lotka-Volterra models (Goel *et al.* 1971).

The dynamics of the benthic community are similar but the changes are more pronounced. During the initial part of the simulation when the biomass of the larger fish, which include demersal species which feed on benthos, is low, virtually all of the benthic biomass is in the macrobenthos. Most of this biomass is in the large deposit feeders which are consuming detritus and bacteria as well as grazing down the meiobenthos, with a smaller density of suspension feeders and a growing biomass of carnivorous epifauna. As the biomass of large fish nears its peak value the grazing pressure on the macrobenthos causes it to collapse, particularly the epifauna which loses its food resource as well. This is consistent with the analysis by Persson (1981) of macrobenthic changes in the Baltic associated with fishing. The result of this decline in macrobenthos is a dramatic increase in the meiofauna, which are ungrazed during the last few years of the simulation.

While grazing alone is probably enough to suppress the macrobenthic populations, the increase in zooplankton abundance reduces the amount of primary production reaching the benthos, and this competitive effect also has an effect on the benthic community. However, the simulations indicate that the fifth year is when the large fish biomass reaches a critical level marked by simultaneous crashes in the pelagic fish biomass and macrobenthos, but it takes another year or two before the zooplankton levels become much higher. We therefore conclude that grazing is more important than food limitation in causing the dramatic drop in macrobenthos.

These strong fluctuations in the benthos, clearly associated with fish predation, determine whether the large deposit feeders remain numerous enough to suppress the meiobenthos. Because of the competitive interaction between these two groups of detritivores we do not find in any of our simulations that meiofauna and large deposit feeders are simultaneously abundant. Whether predation is generally the controlling factor for benthic populations is an underlying question which we have not been able to answer. Certainly at this stage of the modelling work we have made no allowance for substrate type and other environmental factors that might affect the benthos, particularly the availability of refugia that might buffer the predation pressure by fish and lessen the possibility of drastic collapse such as that shown in Figures 1 and 2.

OMISSIONS

The modelling work for the TM model described above is not site-specific, but the approach is strongly biassed by the Northwest Atlantic context in which the work was done. Any attempt to transplant models from one context to another must include a careful inventory of all assumptions underlying the model and an evaluation of whether these assumptions have to be modified.

For example, the omission of benthic plants from the TM model would clearly not be acceptable in modelling a macrotidal estuary. A more critical area in which major changes would have to be made is in the development of models for which bottom chemistry is critical, as in areas where anoxic conditions are prevalent or where pollution impacts are significant, and inclusion of a more detailed chemical submodel of the benthos is a priority for future development of the TM model.

A major problem in benthic modelling is the treatment of sediment transport. Detritus accumulation on the bottom is virtually impossible to predict, and the role of burial as a carbon sink consequently has to be derived from a mass balance calculation. Given the well-known difficulties of hydrological engineers at predicting sedimentation, this is likely to remain one of the major limitations on our ability to develop predictive models of benthic dynamics.

ALTERNATE APPROACHES

The simulation modelling approach we have used in developing the TM model is fairly orthodox, although the benthic submodel is highly aggregated and the use of size structure to characterize pelagic organisms is not common. We have also been exploring alternative ways to visualize and model the benthos, and we think that some of these may prove more effective in understanding some aspects of benthic community structure.

The size-structured analysis of benthic communities pioneered by Schwinghamer (1981) is difficult to integrate into a trophodynamic simulation model because of uncertainty about how much of the size structure is due to energetic factors (both feeding and predation) and how much reflects substrate size and other environmental factors. Despite this we feel that particle size analysis is a valuable methodology in benthic ecology, and we feel that understanding how benthic biomass spectra arise will provide an important contribution to our ability to model benthic dynamics.

One approach that may prove productive is the analysis of fractal properties of the benthic substrate. It is well known that the biomass spectra of terrestrial ecosystems are markedly different from those of pelagic aquatic systems (Elton 1927), and there are reasons to believe that this may reflect the difference between two-dimensional growth on a substrate and three-dimensional growth in an isotropic medium (Silvert 1984). For example, macrophytes and terrestrial plants require a surface on which to grow, while the primary producers in open water are single-celled phytoplankters. Predation is similarly affected by dimensionality, as evidenced by the fact that major terrestrial predators often are able to bring down larger prey, while equivalent aquatic predators, lacking a surface on which to pin their prey, generally feed by engulfing smaller prey. There are of course other factors; in particular, hydrodynamics dictates that the speed of fish is likely to be correlated with size, so small predators are unlikely to be able to catch up with larger prey. However, the dimensionality of the environment is certain to play an important role in shaping ecological roles.

The benthos offers an interesting pattern of change in fractal dimension as a function of body size. Large organisms generally perceive the bottom as a two-dimensional substrate, although large polychaetes and other burrowing organisms can move through it in three dimensions. However, for organisms of a size comparable to the interstitial spacing of the sediment grains the bottom becomes a three-dimensional matrix of pores through which movement in any direction is possible. The smallest organisms experience an environment in which the three-dimensional domain of pore water is bounded by the surfaces of individual grains, which is a literal microcosm of the entire ecosystem with both free-swimming and surface bound components. This recursive relationship between the microbenthos and the entire ecosystem suggests that the application of scaling relations to benthic ecology, of which fractal analysis is one of many promising techniques, may be an effective way to enhance our understanding of benthic ecology.

We can refine these ideas by more careful analysis, and it should be possible to calculate the fractal dimension of the environment seen by different organisms as a continuous function of their body size. We might therefore expect the size structure of the benthos to reflect an Eltonian pyramid at the upper end linked to a relatively flat intermediate region characteristic of the three-dimensional biomass spectrum found in pelagic marine environments, and a lower end which reflects the size structure of the entire ecosystem. I believe that this idea is worth pursuing, but there are a number of fundamental issues about the relationship between ecology and dimension that will have to be resolved before we know whether fractal analysis is an effective way to study benthic ecosystems (Abbott 1952).

DISCUSSION

Most benthic modelling relies on computer simulation, and the work described in this paper shows that even very simple models can be more difficult to implement and parametrize than models of pelagic ecosystems. The situation is made worse by the structure of the benthic food web, which can lead to sudden shifts in benthic community structure due to instabilities induced by coupling to pelagic predators. At this stage it is not clear whether these effects are real, or whether they are artifacts caused by incorrect assumptions about benthic interactions.

Given the uncertainties expressed above about the reliability of our benthic submodel, it would be rash to claim that this simulation model provides plausible evidence for instabilities in the dynamics of marine ecosystems arising from the structure of the benthos. However, the source of instability appears to be the competitive interaction between meiofauna and large detritus feeders, with a switch point determined by the magnitude of fish predation on the macrofauna relative to the grazing pressure which they exert on the meiofauna (the different turnover times of the two groups enter as a weighting factor). It therefore seems worthwhile to examine data on relative abundance of different size classes of detritivores over time in order to establish whether there is any evidence for the kind of switching behaviour found in our simulations. Such an analysis would play an important role in clarifying the role of predation in benthic dynamics and would indicate how detailed a study of feeding rates is needed in order to model the benthos adequately.

Finally, we should seriously consider the development of alternate approaches to benthic modelling that might clarify the relative importance of physical environment (especially substrate) and biological factors in determining benthic community structure. Fractal analysis is one such approach, but others may also be fruitful.

Acknowledgements

Many of my colleagues contributed to the modelling work reported here, among them Don Gordon, Barry Hargrave, Paul Keizer and Don Peer of the Habitat Ecology Division. Several foreign colleagues have also contributed to this work, and I am indebted to Job Baretta and his coworkers at the Netherlands Institute for Sea Research, Wolfgang Ebenhöh at the University of Oldenburg, and Wulf Greve of the Biological Station on Helgoland for their hospitality and cooperation over the past decade.

REFERENCES

Abbott, E. A. 1952. *Flatland.* Dover, N. Y.

Baretta, J., and P. Ruardij (Eds.). 1988. *Tidal Flat Estuaries.* Springer-Verlag.

Elton, C. 1927. *Animal Ecology.* MacMillan, N. Y.

Gause, G. F. 1934. *The Struggle for Existence.* Williams and Wilkins, Baltimore.

Goel, N. S., S. C. Maitra and E. W. Montroll. 1971. On the Volterra and other nonlinear models of interacting populations. Rev. Mod. Phys. 43:231-276.

Gordon, D. C. Jr., and J. W. Baretta. 1982. A preliminary comparison of two turbid coastal ecosystems: the Dollard (Netherlands-FRG) and the Cumberland Basin (Canada). Hydrobiol. Bull. 16: 255-267.

Gordon, D. C. Jr., P. D. Keizer, G. R. Daborn, P. Schwinghamer and W. L. Silvert. 1986. Adventures in holistic ecosystem modelling: the Cumberland Basin ecosystem model. Neth. J. Sea Res. 20:325-335.

Hutcheson, M. S., P. L. Stewart and J. M. Spry. 1981. *The Biology of Benthic Communities of the Grand Banks of Newfoundland (Including the Hibernia Area).* Grand Banks Oceanographic Study, Mobil Oil Canada.

Keizer, P. D., D. C. Gordon, Jr., P. Schwinghamer, G. R. Daborn and W. Ebenhöh. 1987. *Cumberland Basin Ecosystem Model: Structure, Performance and Evaluation.* Can. Tech. Report Fish. Aquat. Sci. No. 1547.

Kerr, S. R. 1974. Theory of size distribution in ecological communities. J. Fish. Res. Board Can. 31:1859-1862.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101:377-385.

Persson, L.-E. 1981. Were macrobenthic changes induced by thinning out of flatfish stocks in the Baltic proper? Ophelia 20:137-152.

Platt, T., and W. Silvert. 1981. Ecology, physiology, allometry and dimensionality. J. Theor. Biol. 93:855-860.

Ruardij, P., and J. W. Baretta. 1982. *The Ems-Dollart Ecosystem Modelling Workshop.* BOEDE Publ. en Versl. No. 2, Texel.

Schwinghamer, P. 1981. Characteristic size distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. 38:1255-1263.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe, Jr. 1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17:327-340.

Sheldon, R. W., W. H. Sutcliffe, Jr., and M. A. Paranjape. 1977. The structure of the pelagic food chain and the relationship between plankton and fish production. J. Fish. Res. Bd. Canada 34:2344-2353.

Silvert, W., and T. Platt. 1978. Energy flux in the pelagic ecosystem: a time--dependent equation. Limnol. Oceangr. 23:813-816.

Silvert, W., and T. Platt. 1980. Dynamic energy-flow model of the particle size distribution in pelagic ecosystems. In *Evolution and Ecology of Zooplankton Communities*, pp. 754-763. W. C. Kerfoot, ed. Univ. Press of New England, Hanover, N. H.

Silvert, W. 1984. Particle size spectra in ecology. In *Mathematical Ecology*, pp. 154-162. S. A. Levin and T. G. Hallam, eds. Springer-Verlag Lecture Notes in Biomathematics 54.

Silvert, W. 1988. Generic models of continental shelf ecosystems. In *Ecodynamics: Contributions to Theoretical Ecology*, pp. 153-161. W. Wolff, C.-J. Soeder and F. R. Drepper, eds. Springer-Verlag.

Warwick, R. M. 1984. Species size distributions in marine benthic communities. Oecologia 61:32-41.

Wildish, D. J., and D. Peer. 1983. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. Can. J. Fish. Aquat. Sci. 40(Suppl. 1):309-321.

Fig. 1. Changes in zooplankton and fish biomasses over a 10-year simulation.

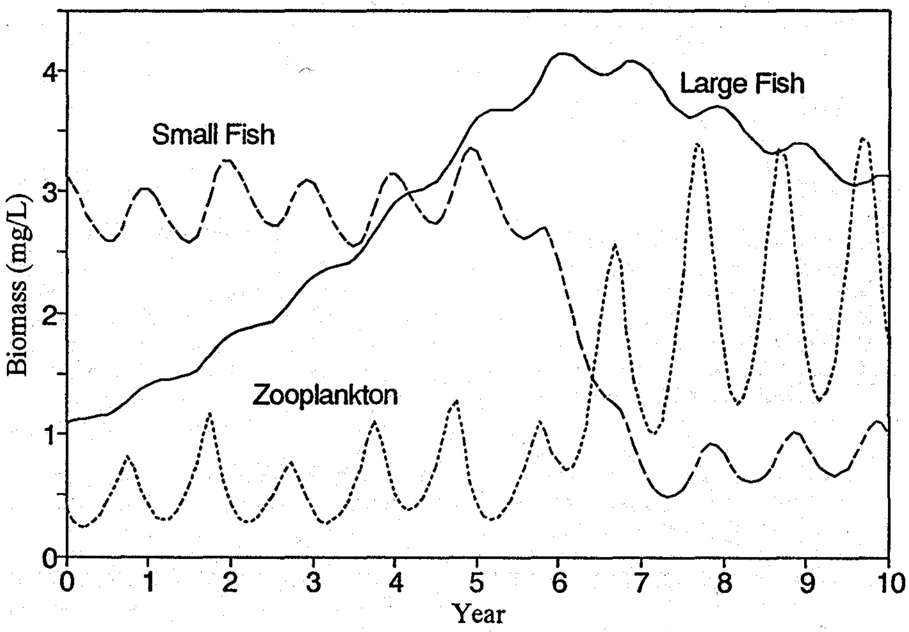
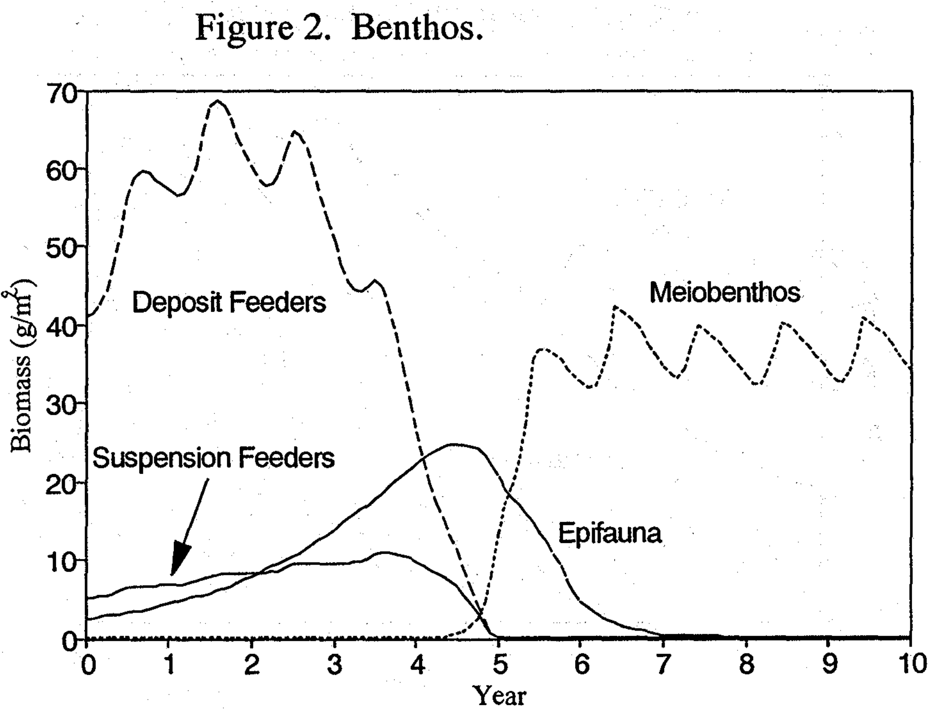


Figure 1. Zooplankton and Fish.

Fig. 2. Changes in benthic biomasses over a 10-year simulation.



MODELLING OF POPULATION DYNAMICS OF *OWENIA FUSIFORMIS* (ANNELIDA, POLYCHAETA) IN EASTERN BAY OF SEINE

E. Thiebaut[1] **and J.C. Dauvin**[2]

[1]Station biologique de Roscoff, BP 74, 29680 Roscoff Cedex
[2]Laboratoire de biologie des Invertébrés marins et Malacologie,
Museum National d'Histoire Naturelle, 57, Rue Cuvier, Paris

ABSTRACT

The Polychaete worm Owenia fusiformis, a polythelic species with a bentho-pelagic cycle, is one of the most common species in the Abra alba - Pectinaria koreni - isolated muddy fine sand-community in the eastern Bay of Seine. It was chosen for the study of interactions between physical processes and recruitment. This study is the contribution of the "GDR Manche" to the "Programme National du Déterminisme du Recrutement". Several previous studies reported information about different phases of the life cycle of Owenia fusiformis, i.e. demographic structure of the population, fecundity and mortality.

From available data collected at two stations A and B in front of the estuary of Seine, a model of population dynamics with a Leslie matrix was made. The population was structured in five age-classes from 0-year-old juveniles to adults 4 + year of age. The time increment was one year. The parameters were fecundity and probability of survivorship to age x from age x-1. Different demographic characteristics were calculated: (1) potential population growth rate, (2) intrinsic rate of increase in a population, (3) age-specific reproductive value, (4) sensitivity and (5) elacticity.

The resolution of constructed matrices in conditions of favourable recruitment and the calculation of demographic parameters revealed for the two stations a growth rate related to 1, suggesting a stable population or a population in slight growth. The analysis of sensibility showed the primary role of 2 or 3 year-old adults in population increase because of their importance in larval production.

Simulations based on one or several recruitments with no settling showed variations in densities and demographic structure of the population, and the necessary

time to a return to a balanced state.

However, even if such a model provides some data on population dynamics and its critical phases, it showed significant deficiencies concerning the study of processes of recruitment, mainly: (1) the impossibility to consider the space, (2) the constancy of the time increment which integrates larval phase into fecundities, (3) the rigidity of associated parameters at each age-class.

TEMPORAL DISTRIBUTION OF MEIOBENTHOS (NEMATODES) IN AN ESTUARY: A SUBMODEL FOR MEIOBENTHOS IS NEEDED

Magda Vincx & Jian Li

Marine Biology section, Zoology Institute, State University of Gent, Belgium

INTRODUCTION

Most models in marine ecology consider the meiobenthos either as one functional group (not submodel) or do not take the meiobenthic part (e.g. Steele, 1974 and Keizer *et al.*, 1987) into account. Recently, the importance of meiobenthos in benthic ecological system is well known (e.g. McIntyre, 1969, Heip *et al.*, 1985 and Higgins and Thiel, 1988). In this paper, we will discuss the feasibility of submodelling the meiobenthos from a view of a temporal study of the meiobenthos in the Westerscheldt estuary.

MATERIAL

The biannual meiobenthic sampling (Spring and Autumn) have been carried out over the period 1983-1989 at two fine sandy intertidal stations in the Westerscheldt estuary, which are exposed daily for more than one hour during each tidal cycle: station 1 is located at 15 km from the mouth of the Scheldt and station 2 is at 35 km from the mouth of the Scheldt (Fig. 1). They are situated at different salinity zones: marine tidal and brackish tidal zone (Hummel, 1988) The main meiobenthic group, the nematodes (> 95 % in total meiobenthic density) has been classified into four feeding types: A1=selective deposit-feeders, B1=non-selective deposit-feeders, A2=epigrowth-feeders and B2=predators (Wieser, 1953) and identified to the genus level. Simple multiplicative decomposition method (Bowerman and Richard, 1979) is used for calculating the trend and seasonal fluctuation of series. The macrobenthic data from the same two stations (Heip *et al.*, 1986 and Janssen *et al.*, 1988) were used. The biomass data of the nematodes were calculated by the method of Andrassy (1956).

RESULTS

The temporal fluctuation of nematode density

From densities distributions (Fig.2), we found that station 1 has higher density (average 3249 ind./10cm^2) than station 2 (average 2268 ind./10cm^2). But both stations show trends ($p < 0.05$ at year level by 3-level nested ANOVA test) as judged by positive Kendall's τ. The slopes of the trends are around 100 ind./10cm^2-/year in both stations, calculated out of the multiplicative decomposition method (Table 1).

Table 1: The slopes and seasonal change for nematode densities from multiplicative decomposition method.

items	station 1	station 2
slopes	106	120
seasonal change	± 0.8 %	± 0.2 %

The seasonal fluctuations between Spring and Autumn are not clear ($p > 0.1$ at month level by 3-level nested ANOVA test) There is a negative or near 0 auto-correlation variance (Fig. 3) with a period of one year and a low fluctuation volume (Table 1) which correspond with the results of multiplicative decomposition method.

The temporal fluctuation of the four feeding types

The average densities of the four feeding types follow the same order in the two stations: the non-selective deposit-feeders are the most dominant group followed by predators, epigrowth-feeders and selective deposit-feeders (Table 2). However, the fluctuation of the density of the four feeding types differs remarkably between the two stations, also when compared with the total nematode density. One non-selective deposit-feeders peak (1983) and one predators peak (1988) is present in Autumn from station 1 (Fig. 4). But for station 2 (Fig. 5), two non-selective deposit-feeders peaks (1987 and 1989) are present in Autumn, two predators peaks are present in Autumn (1988) and Spring (1983) and Epigrowth--feeders peaks are present in Spring (1986) and Autumn (1989), too. The consequent peaks of the feeding types (from 1986 onwards) in station 2 are as follows: epigrowth-feeders dominate in Spring 1986, followed by peak of non-selective deposit-feeders in Autumn 1987 and followed by predators peak in Spring and Autumn 1988. This sequence in density can be explained as follows: high primary production allows epigrowth-feeders to become dominant in Spring 1986, which probably also give rise to an increase in organic detritus that can be used by non-selective deposit-feeders (Autumn 1987). Last animals can serve as the food for the predators, which become dominant in 1988.

The temporal fluctuation of the main genera of nematodes

The temporal distribution of some dominant nematode genera (which represent maximum more than 20 % in each feeding type) follows the different feeding type peaks as described above are: Daptonema and Theristus (B1) in station 2 (Fig. 6), Enoploides and Onyx (B2) in station 1 (Fig. 7), Daptonema in station 1 (Fig. 8) and Dichromadora and Praeacanthonchus (A2) in station 2 (Fig. 9). Following genera peaks do not correspond with their feeding type peaks: Viscosia (B2) in station 2 (Fig 7), Chromadorita (A2) in station 2 (Fig. 9) and Enoploides (B2) in station 2 (Fig. 10).

Table 2: The comparison of four feeding types' mean densities (ind./10cm^2) and densities' range.

feeding types	station 1	station 2
selective deposit-feeders	187 (22-352)	211 (9-1271)
non-selective deposit-feeders	1301 (266-3038)	804 (23-3439)
epigrowth-feeders	450 (86-1001)	564 (29-2202)
predators	1221 (429-4026)	681 (119-2893)

CONCLUSIONS AND DISCUSSION

Following conclusions can be made out of the above mentioned results:

1. The distributions of the total nematode densities cannot give a good understanding of their 'dynamics'.
2. The density distribution of the nematode feeding types gives much more understanding of their 'dynamics'.
3. The dynamics of feeding types can stand for the dynamics on some genus level but not for all.

The trends in seasonal fluctuations of total densities is not found in the feeding type distributions; in last distributions, the trends and seasonal fluctuation calculated are mainly determined by the heterogeneous distribution of the feeding types (because only one or two peaks of each feeding type determines the trend).

Table 3: The correlation coefficient between nematode data and their feeding type data.

station	station 1		station 2	
items	nematode density	nematode biomass	nematode density	nematode biomass
A1 density	0.143		0.239	
B1 density	0.586		0.591	
A2 density	0.095		0.658	
B2 density	0.638		0.559	
A1 biomass		-0.277		0.361
B1 biomass		-0.087		0.215
A2 biomass		-0.249		0.249
B2 biomass		0.98		0.954

The phenomenon of peaks present in station 2 indicates that nematodes in the Westerschelde have an inside dynamics which is caused by the interaction of the feeding type groups. The total density of nematodes does not show the importance of the inside dynamics. The correlation coefficient (Table 3) show low level between total nematode data and the four feeding type data, except high correlation (0.98 in station 1 and 0.95 in station 2) between predators and total nematode from biomass' data, because the predators are very abundant in biomass (61 % in station 1 and 74 % in station 2). The correlation coefficient between macrobenthos (possible predators of nematodes) and the nematodes is very low (Table 4 and 5), except for non-selective deposit-feeders and polychaete density (0.82) and epigrowth-feeders and oligochaete (0.92) in station 1. Therefore, we think that nematodes constitutes a certain independent system within the benthos. The success of nematode in all marine environment (e.g. McIntyre, 1971; Nicholas, 1975 and Heip *et al.*, 1982) indicates the importance of this 'independent' system, from which the fluxes through the benthos are to be quantified.

From this study, it has been shown that feeding types or even dominant species are necessary to consider as functional groups in a submodel for meiobenthos.

Table 4: The correlation coefficient between nematode densities and macrobenthic densities.

station 1					
items	total nematode	A1	B1	A2	B2
total macrobenthos	0.72	0.32	0.77	0.13	0.14
polychaete	0.74	0.44	0.82	0.01	0.18
oligochaete	-0.11	-0.03	-0.02	0.38	-0.33
mollusc	0.44	0.32	0.52	0.20	-0.12
crustacean	0.65	0.62	0.78	0.06	0.04
station 2					
items	total nematode	A1	B1	A2	B2
total macrobenthos	-0.02	-0.34	0.41	0.25	-0.38
polychaete	0.38	-0.22	0.68	0.52	-0.25
oligochaete	0.25	-0.22	-0.08	0.92	-0.08
mollusc	0.29	0.02	0.57	-0.14	0.02
crustacean	-0.49	-0.27	0.02	-0.37	-0.36

Table 5: The correlation coefficient between nematode biomass and macrobenthic biomass.

station 1					
items	total nematode	A1	B1	A2	B2
total macrobenthos	0.32	-0.25	0.27	0.08	0.06
polychaete	-0.07	-0.07	0.43	-0.04	-0.49
oligochaete	-0.21	-0.33	0.18	0.01	-0.34
mollusc	0.16	-0.47	-0.25	0.36	0.33
crustacean	-0.21	-0.04	0.13	0.20	-0.4
station 2					
items	total nematode	A1	B1	A2	B2
total macrobenthos	-0.17	0.09	0.15	-0.004	-0.18
polychaete	-0.14	0.13	0.1	0.1	-0.16
oligochaete	0.01	-0.22	-0.13	0.29	-0.01
mollusc	-0.06	0.20	-0.01	-0.03	-0.06
crustacean	-0.30	-0.44	0.50	-0.08	-0.31

REFERENCES

Andrassy, I., 1956. The determination of volume and weight of nematodes. Acta. Zool., 2 (1-3): 1-15.

Bowerman, B. L. and Richard, T. O., 1979. Forecasting and time series. Miami Univ., pp. 1-481.

Heip, C., Herman, R. and Craeymeersch, J., 1986. Diversiteit en biomassa van het macrobenthos in de Westerschelde: 1978-1985. Rapport in Opdracht van de Dienst Getijdenwateren, RWS, Nederland.

Heip, C., Vincx, M., and Vranken, G., 1985. The ecology of marine nematodes. Oceanogr. Mar. Biol. Ann. Rev.,23: 399-489. Heip, C., Vincx, M., Smol, N. and Vranken, G., 1982. The systematics and ecology of free-living marine nematodes. Helminthological Abstracts Series B, Plant Nematology, 51 (1): 1-31.

Higgins, R. H. and Thiel, H. (editors), 1988. Introduction to the Study of meiofauna. Smithsonian Institution Press. Washington, D. C., London, pp. 1-488.

Hummel, H., Moerland, G. and Bakker, C., 1988. The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde Estuary. Hydrobiological Bulletin, 22(1): 35-41.

Janssen, C. R., Boel, E., Herman, R. and Vincx, M., 1988. Diversiteit, densiteit en biomassa van het macrobenthos in de Westerschelde: 1986-1988. Rapport in Opdracht van de Dienst Getijdenwateren, RWS, Nederland.

Keizer, P. D., Gordon, D. C. and Schwinghamer, J. P., 1987. Cumberland basin ecosystem model: structure, performance and evaluation. Canadian Technical Report of Fisheries and Aquatic Sciece. No. 1547.

McIntyre, A. D., 1961. Ecology of marine meiobenthos. Biol. Rev. 44:245-290.

McIntyre, A. D., 1971. Observations on the status of subtidal meiofauna research. Proceedings of the First International Conference on Meiofauna. Hulings, (Editor). Smithsonian Contributions to Zoology, 76: 149-154.

Nicholas, W. L., 1975. The biology of free-living nematodes. London & New York: Oxford University Press.

Steele, J. H., 1974. The structure of marine ecosystems. Harvard University Press Cambridge, Massachusetts, pp. 1-128.

Wieser, W., 1953. Die beziehung zwischen mundhohlengestalt, ernahrungsweise und vorkommen bei freilebenden marinen nematoden. Archives fur Zoologie, 4 (26): 439-484.

Fig. 1. Location of sampling stations in the Westerscheldt.

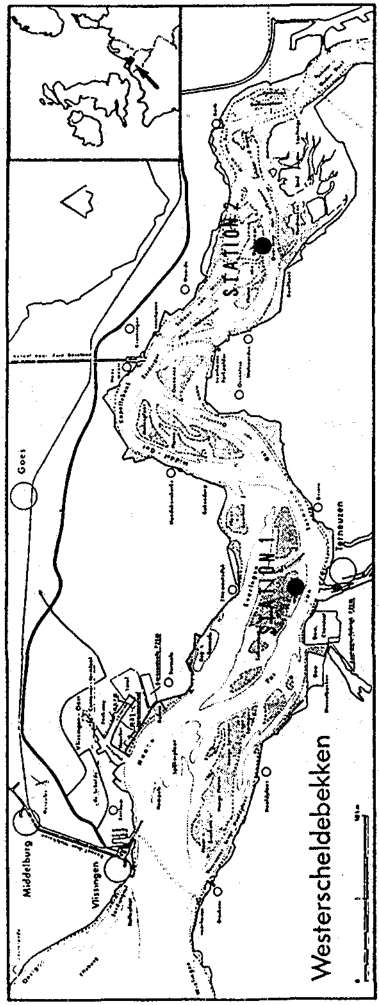


Fig. 2. The temporal distributions of nematode densities over seven years from two stations (densities=1000 ind./10cm²).

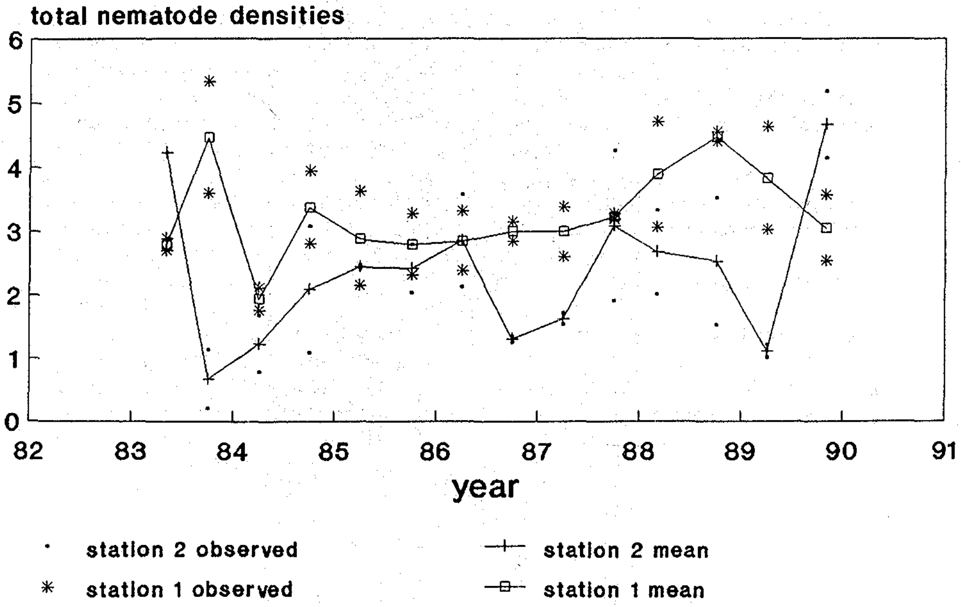


Fig. 3. Autocorrelogram of nematode densities after extraction of linear trends.

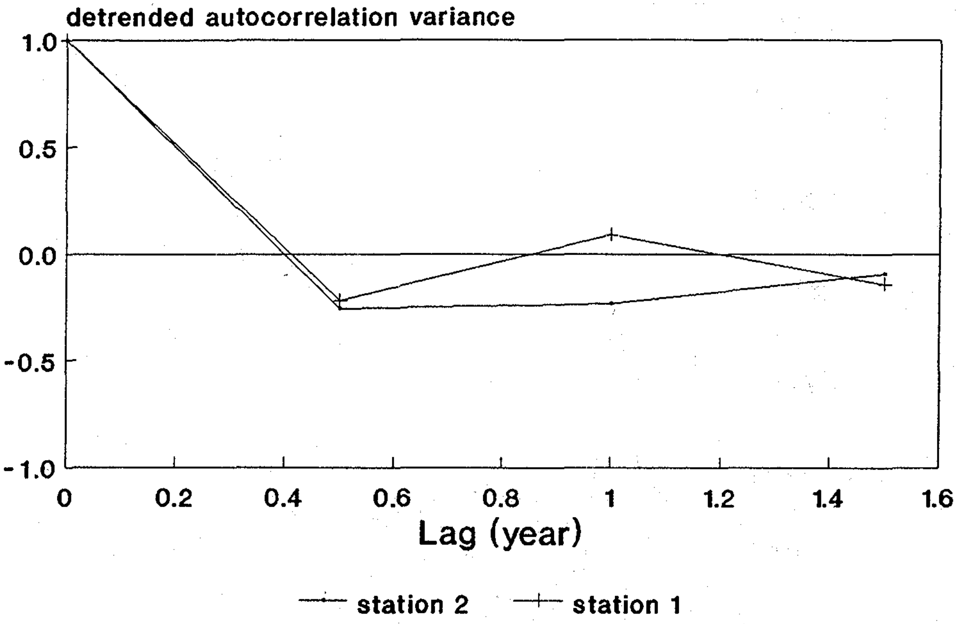


Fig. 4. The temporal distribution of four nematode feeding types over seven years from station 1 (densities=ind./10cm²; A1=selective deposit-feeders, B1=non-selective deposit-feeders, A2=epigrowth-feeders and B2=predators).

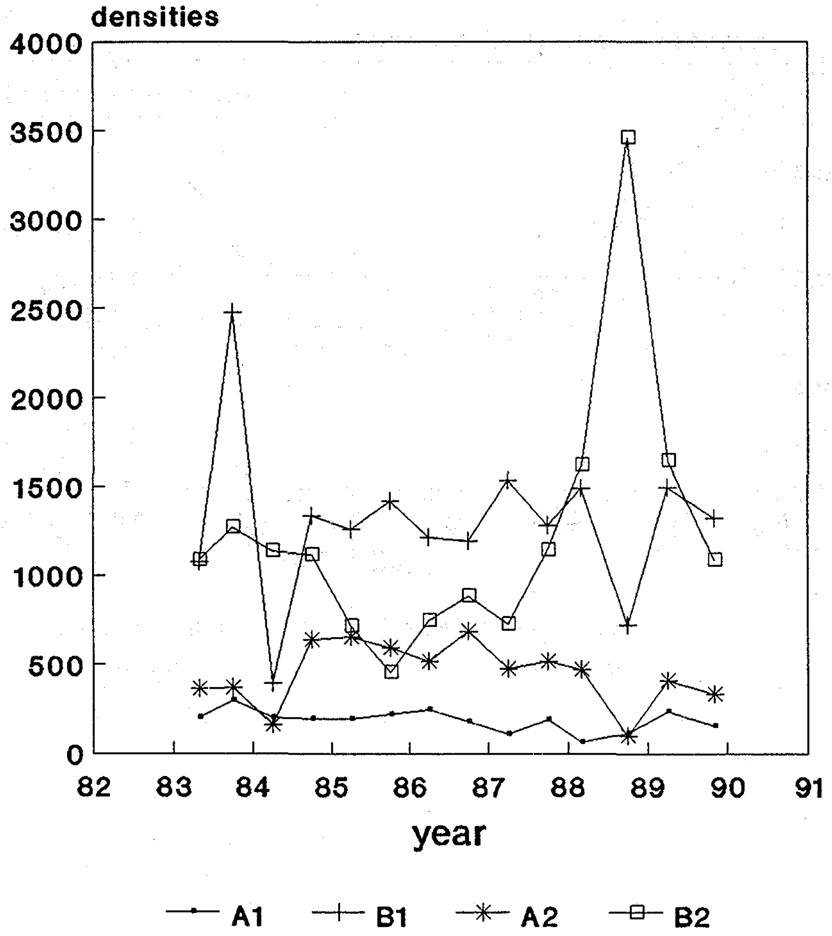


Fig. 5. The temporal distribution of four nematode feeding types over seven years from station 2 (densities=ind./10cm²).

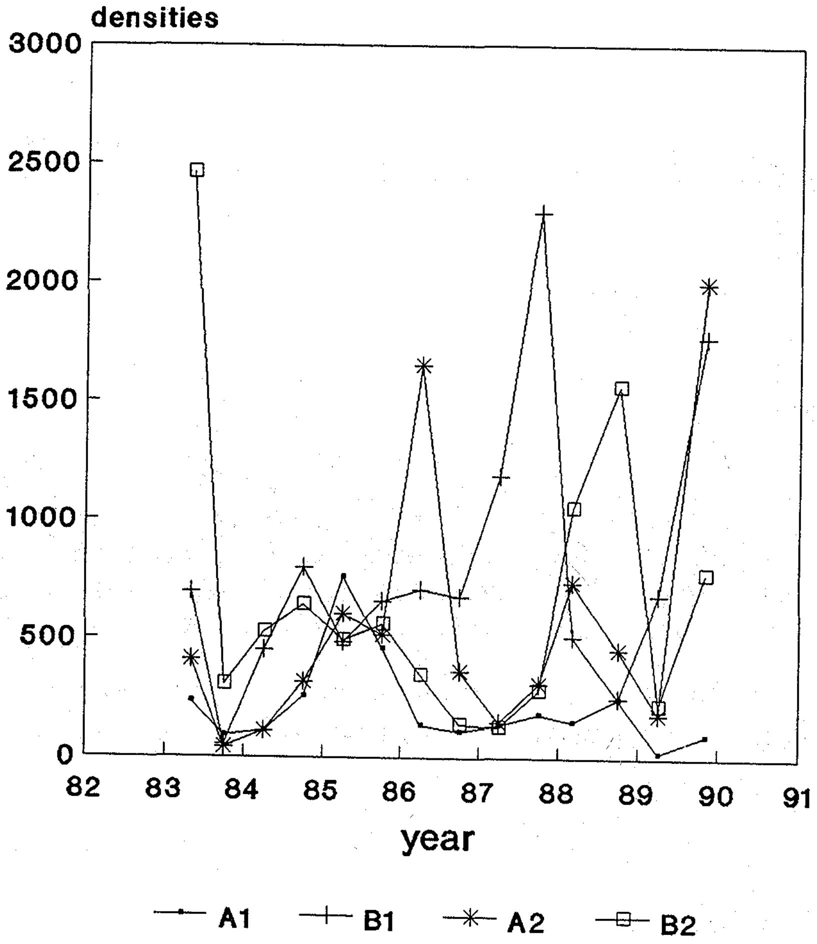


Fig. 6. The temporal distribution of non-selective deposit-feeders densities from station 2 (densities=ind./10cm²).

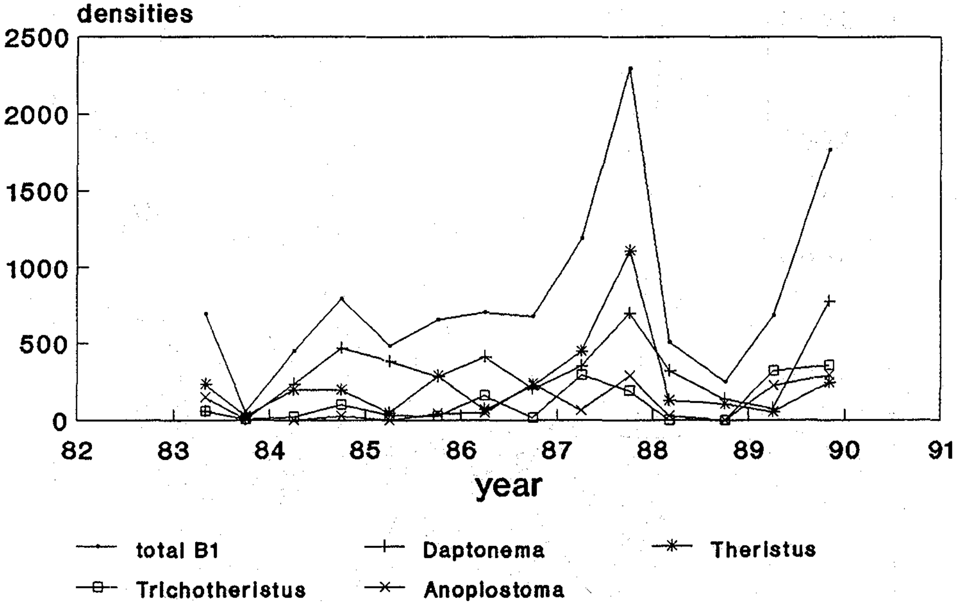


Fig. 7. The temporal distribution of predators densities from station 1 (densities=-ind./10cm²).

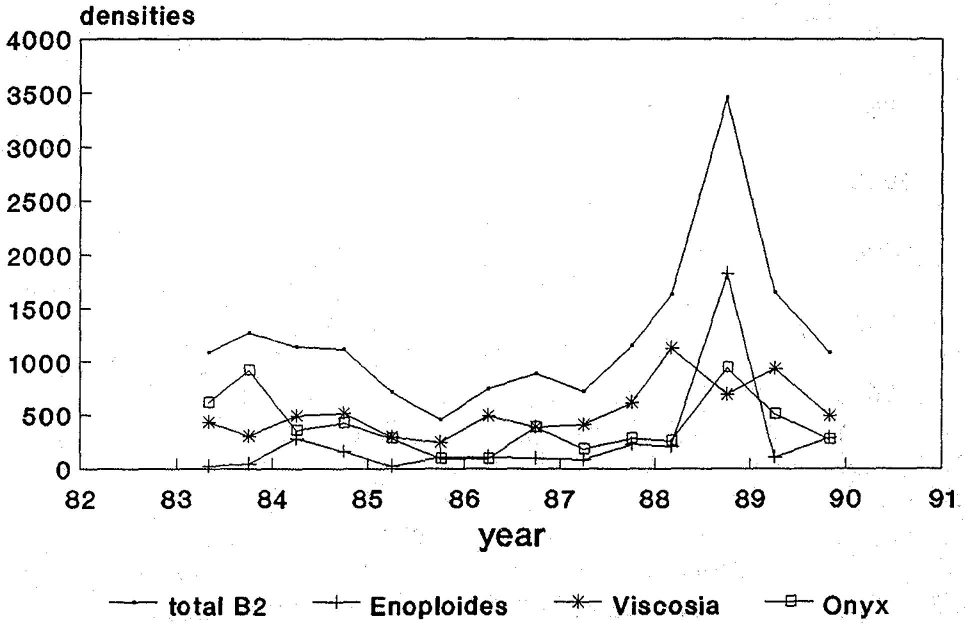


Fig. 8. The temporal distribution of non-selective deposit-feeders densities from station 1 (densities=ind./10cm²).

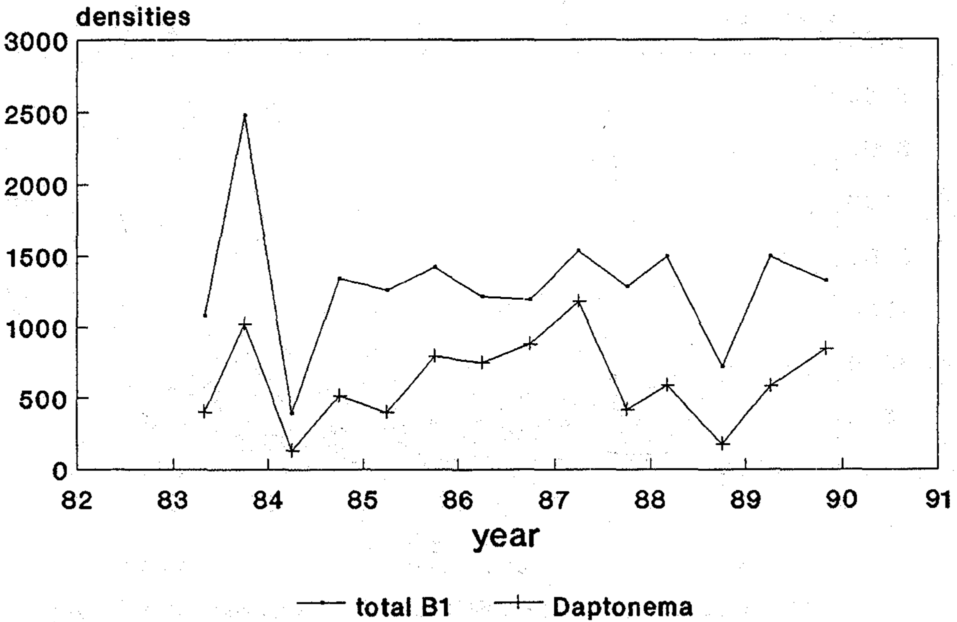


Fig. 9. The temporal distribution of epigrowth-feeders densities from station 1 (densities=ind./10cm²).

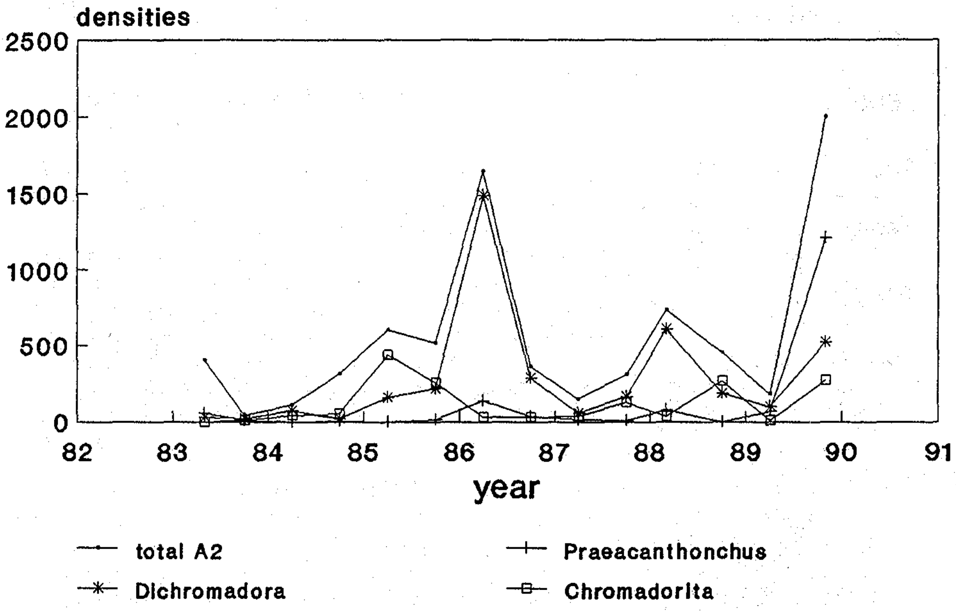
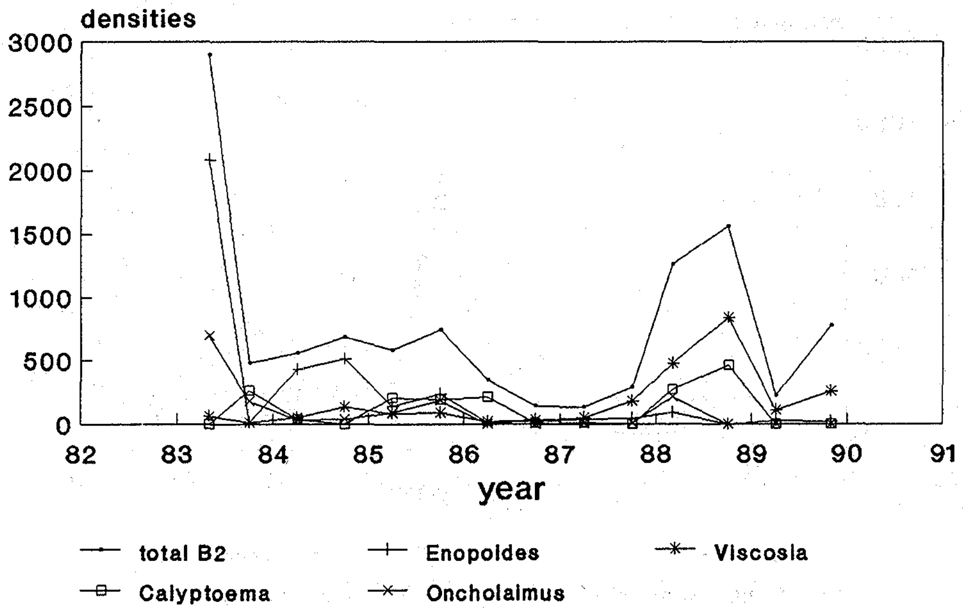


Fig.10. The temporal distribution of predators densities from station 2 (densities=ind./10cm²).



SUMMARY REPORT OF THE DISCUSSIONS

P.M.J. Herman and C. Heip

Delta Institute for Hydrobiological Research, Vierstraat 28,
4401 EA Yerseke, The Netherlands

INTRODUCTION.

During the workshop several approaches to 'modelling' the benthos have been confronted with each other.

Multivariate statistical methods aim at detecting patterns. These patterns can be found in space, in which case one usually has a completely static approach. However, time dynamics may be incorporated under certain assumptions. Statistical time series analysis and system identification techniques (such as ARIMA models) may relate several univariate time series to one another, and rigorously test hypotheses about ecological relationships. In general, in the statistical approach one makes simplifying assumptions about the ecological relationships (e.g. linearity etc.), and fits a parsimonious model to the data, taking care that the model 'explains' more variation in the data than expected by chance only. Statistical models of the fauna can take into account results of other (e.g. hydrodynamical) models.

Dynamic deterministic models on the other hand are (by definition) not static in time and are (by computational limitations) restricted in their spatial resolution. The models are usually more complex and non-linear: simplification lies not in the model formulation. Rather, the representation of field or laboratory observations is usually tested more loosely. The models are heuristic: they attempt to represent the consequences of processes throughout a system. Some models, such as matrix population models and yearly averaged energy flow models which were also presented during the workshop, are intermediate between the statistical and the dynamic approach. These models are less of a black box than the statistical models, but they also lack the detailed formulation and the time dynamics of dynamic deterministic models.

Between these different approaches sits the benthic researcher with his/her observations, knowledge on the biology of the species, questions about the patterns that seem to appear in the data, and doubts about the relevance of the field work in view of the sophistication of the modelers' toolbox. What should benthic researchers do in order to 'feed' the models, and to test their hypotheses?

'MODELLING IS TOO IMPORTANT TO BE LEFT TO MODELERS'.

One important conclusion from the discussions in the workshop is that modelling is far too important for scientific work to be left to 'the modelers'. 'Modelers' is here used as a term for mathematically trained people constructing ecosystem models, but often lacking a solid biological knowledge. It was stressed by several participants that benthic ecologists should start modelling themselves, i.e. translate their ideas, hypotheses etc. into formal representations. Modelers, it was said, know more than enough already about primary production. Processes in the benthos, however, are far from well known. It are the benthic ecologists primarily who possess this knowledge, or at least can formulate hypotheses. By starting to play with small models themselves, they can greatly enhance the description of benthic processes. It was also stressed that modelling is more important and more interesting than the models resulting from the process: while modelling scientists are forced to focus their ideas, formulate and clarify hypotheses and assumptions, and develop a communication language with other ecologists. By focussing several aspects of ecological research around a model, the quality of the research can be enhanced.

The technology for creating a 'broad front of modelling' is now available: powerful computers have become cheap, and modelling packages such as BSIM and SENECA, presented during the workshop, greatly facilitate the programming burden of modelling. Thus, modelling can become part of an ecologists' toolkit, just like multivariate statistical methods. The organization of courses and practical workshops may be very worthwhile in this respect (see below)

WHAT SHOULD BE MODELLED ? - THE NEED FOR CONCEPTUALIZATION.

Ecosystem modelers have many questions to ask to benthic ecologists. Some examples of these were given. They relate to the relation between structure of benthic communities, functional role of these communities in the overall system, and effects of stress in the system.

E.g. 1. Is a difference in structure, as indicated by a different species composition, indicative of a different function in the ecosystem (i.e. a different influence on energy throughput or important control processes). If so, is it possible to model the important structural characteristics of benthic communities. What processes contribute to this structure?

2. Does the benthos show structural reactions to eutrophication. If so, what are the proper formulations to describe these changes.

3. What are proper benthic state variables in ecosystem models anyway ? Is there an alternative for the concepts of 'suspension feeders' and 'deposit feeders'.

Questions like these stress the need for conceptualization by benthic ecologists.

Conceptualization, it has been argued, could greatly be helped by the use of statistical modelling techniques. Statistical analysis of data can uncover patterns, that yield hypotheses to be tested in dynamic models. If applied with caution (e.g. handling non-linearities may be a difficult problem) and skill statistical analysis may also be used as a filter of observational data. During the workshop methods for partialling out the effect of space as a driving variable were discussed. These approaches may further clarify relationships between biological variables.

Conceptualization is also largely influenced by such practical aspects as the possibilities for experimentation and measurement. If it proves impossible, e.g. to classify most species in appropriate feeding guilds, either the concept should be changed into a more practical one, or instrumentation and/or observation methods should be improved. Conceptually, one could e.g. put forward size as a better way to represent the functional role of a species. Alternatively, one could try to devise methods for in situ observation of species.

A DIVERSITY OF MODELS.

It was remarked by several people that questions relevant for ecosystem modelling, are not necessarily the questions asked by benthic ecologists in their research. It seems not possible, nor necessary, to incorporate population-dynamical models into complex ecosystem models. And whereas population dynamics may probably be modelled independently from other processes, for other models of benthic activity a tighter coupling with ecosystem models may be necessary. For these an approach such as in the ERSEM project may be advocated : the development of a general 'framework' model, within which several submodels can be constructed and evaluated. The same concept could be used with different hierarchical levels.
On the other hand, it may be very useful to develop several independent modelling

approaches for the same type of problems. A comparison with fisheries can be made : whereas V.P.A. is better suited than ecosystem modelling for predictions of standing stocks of single species of fish, it works out worse for general predictions of fish biomass.

It can be concluded in general that the questions to be asked from the model should be clear before the model design. The modelling approach used should be adapted to these questions : the model aim determines its ideal form, practical considerations should limit the modelling effort. Modelling is an iterative process towards better conceptualization and better understanding. The problem is how to get the iterative cycle going.

The use of statistical modelling as a first 'pattern-describing' step has already been discussed. Statistical approaches could also be used as a means of reconciling different modelling efforts. If different limited models are constructed, each with a particular spatial and temporal scale, their output could be transformed and combined in a statistical explanation of observed structure.

It is important to think about statistical methods also as a way of constructing models. We have, in fact, a continuum of models differing in time and space scales, in degree of non-linearity, in 'black-box-ness', in technical implementation and in ways of estimating parameters. All these methods are more or less easily available now to benthic researchers.

Faced with this diversity, it should be recommended not to focus on any method. A data matrix is barren in itself - it does not suggest a method of analysis automatically. One should think in terms of the system, not of the methods. In this way the best solution(s) can be found, possibly in a combination of approaches.

A TEST CASE FOR COMPARISON OF METHODS.

A plan for the investigation of different approaches with a common test case data set raised much enthusiasm. It was decided in principle to look for an appropriate problem, where the different methods used for the study of the benthos could be applied in practice.

It was stressed that the example problem should be sufficiently broad, and the data available of sufficiently diverse type, to make several approaches possible. Statistical inference from spatial patterns e.g., should be possible concomitant with dynamical models representing simultaneous time series of many ecological variables. The data sets should not be too excessively large, in order to make all approaches practically feasible.

The aim of the exercise should be to gain a better insight into the role of the benthos in ecosystem regulations on the one hand, and the response of the benthos to changes in the ecosystem on the other hand.
This workshop should be prepared by a compilation of the data sets for the example problem, and a sufficiently detailed introduction into the problem. Participants should prepare their approaches beforehand, but work them out during the workshop. Technical instruction to the other participants should be of primary importance.

As a possible test problem the eutrophication of Lagoon of Venice or the Adriatic Sea was suggested.