

Predictive modelling of aquatic community attributes: biomass, biodiversity, biointegrity and biomonitoring.

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ABSTRACT: Predictive modelling of aquatic community attributes: biomass, biodiversity, biointegrity and biomonitoring. The paper reviews current approaches in the development and application of mathematical models to simulate the functioning of aquatic communities, in terms of key response variables which indicate the status of such communities (such as biomass and biodiversity). The applicability and value of model-based methods for monitoring the biointegrity ("health") of aquatic ecosystems for practical management purposes is assessed, and research needs are outlined. A comparison is provided of schemes for monitoring biointegrity based on predictive modelling of the response of key biota (such as RIVPACS: modelling software which uses benthic macroinvertebrates as the basis of a biomonitoring method for assessing the quality of British rivers), as opposed to multimetric schemes which incorporate a number of indicators of biointegrity utilising a range of biota (for example the Rapid Bioassessment Protocols, developed for lake and river assessment in the USA). The increasing worldwide importance of legislation-driven implementation of biomonitoring schemes utilising modelling approaches for assessment of freshwater systems is emphasised. An example is given of the Water Framework Directive in the European Union, which requires EU member states to implement common approaches, based on modelling procedures, for assessment of aquatic biointegrity, over the period 2003 – 2008.

Key-words: ecological models; freshwater ecology; simulation models; minimal linear models; multimetrics; biomonitoring

RESUMO: Modelagem preditiva de atributos da comunidade aquática: biomassa, biodiversidade, integridade e monitoramento biológicos. O trabalho apresenta uma revisão das abordagens correntes no desenvolvimento e na aplicação de modelos matemáticos para simular o funcionamento de comunidades aquáticas, em termos de variáveis respostas chave que indicam o "status" de tais comunidades (tais como biomassa e biodiversidade). A aplicação e o valor de métodos baseados em modelos para monitorar a integridade biológica ("saúde") de ecossistemas aquáticos para propósitos práticos de manejo são verificados, e perspectivas de investigação são delineadas. Uma comparação é apresentada com esquemas para monitorar a integridade biológica baseada em modelagem preditiva de resposta da biota chave (tais como RIVPACS; software de modelagem que usa os macroinvertebrados bênticos como base de um método de monitoramento biológico para avaliação da qualidade dos rios Britânicos), ao contrário de esquemas multimétricos que incorporam um número de indicadores de integridade biológica utilizando uma gama da biota (por exemplo os Protocolos de Avaliação Biológica Rápida, desenvolvidos para avaliação de lago e rio nos USA). A importância mundial crescente da implementação impulsionada pela legislação de esquemas de monitoramento biológico utilizando abordagens de modelagem para avaliação de sistemas de águas doces é enfatizada. Um exemplo é apresentado através da Diretriz de Estrutura em Água na União Europeia, que requer que os estados membros da Europa implementem abordagens

comuns, baseadas em procedimentos de modelagem, para avaliação da integridade biológica aquática, no período de 2003-2008.

Palavras-chave: modelos ecológicos; ecologia de água doce; modelos de simulação; modelos lineares mínimos; multimétrica; monitoramento biológico.

Introduction

Modelling in aquatic ecology currently emphasises three general approaches (e.g. Tuljapurkar & Caswell 1997). The first utilises more or less complex simulation models, mathematically linking sets of sub-model routines, and aiming to provide outputs for one or more biological or ecological response variables for a defined system. Examples include phytoplankton biomass change with time in response to changing catchment nutrient inputs (Frisk et al 1999); and models of trophic relationships in aquatic ecosystems (e.g. the software packages NETWRK and ECOPATH; Christensen & Pauly 1992; Heymans & Baird 2000; Ulanowicz 1999). Such models may target individual biological components (for example a single species: e.g. Best & Boyd 1996; Chen & Coughenour 1996; Teixeira da Silva & Asmus 2001). Alternatively the models may operate at community scale. Examples are Weisner et al (1997) and Muhammetoglu & Soyupak (2000) for submerged macrophyte vegetation; Asaeda & van Bon (1997) for phytoplankton in shallow eutrophic lakes; Madden & Kemp (1996) for estuarine vegetation; and Ellison & Bedford (1995) for wetland plant communities. The popularity of attempting larger-scale whole-ecosystem modelling has waned somewhat since the general failure of ecosystem-scale modelling attempts during the 1970 - 80s (e.g. Park et al. 1974) though work is ongoing in this field (Fitz et al 1996; Straskraba 2001). As well as biological response variables, models may also involve prediction of water quality or other ecosystem attributes (e.g. Park & Uchirin 1997; Janse 1997; Janse et al 1992, 1998; Li 1988).

A second approach is that of minimal linear models. These are usually multiple-regression based procedures, which are restricted to a given envelope of applicability defined by the input values used in their construction and calibration (Scheffer & Beets 1994). These models may form individual sub-routines within larger simulation models, may be used in stand-alone form to undertake particular tasks (e.g. Ali et al 1999), or may be used as part of spatial modelling procedures, with model outputs being applied via an appropriate platform.

Finally, spatial modelling platforms are usually based on Geographical Information Systems (GIS; e.g. Jensen et al 1992; Lehmann et al 1994, 1997; Janauer 1997), and are particularly well-suited for the depiction of "what-if" scenarios of spatial and temporal change in target response variables, at landscape level. Such approaches commonly form the core of decision support tools currently being developed to aid management of aquatic systems and catchments (e.g. Todini et al 1998).

Whatever the approach, modelling in aquatic ecology often has as its aim the prediction of species, population, or community performance; or attributes of ecosystem processes. Such measurable attributes form the response variable(s) of the models. Two commonly used attributes are biomass (or some other measure of abundance), and biodiversity (measured as number of species present per unit area (species richness); a diversity index (e.g. Simpson's index; Hawksworth 1995); or (more difficult to predict) the assemblage of organisms present. For example in lakes, phytoplankton community chlorophyll_a concentration is commonly used as a surrogate measure of algal biomass and has long been used as a response variable in models ranging from the classic phosphorus - algae equations (Vollenweider 1968; Dillon & Rigler 1974a), to more sophisticated models of phytoplankton temporal change, such as PROTECH (Elliott et al 1999; Reynolds et al 2001).

An additional major, and growing, reason for the use of modelling approaches in aquatic systems is legislative pressure. New environmental laws in Europe (especially the forthcoming European Union Water Framework Directive) and similar

legislation elsewhere (e.g. in Australia and the USA: Barbour et al 1999; Simpson & Norris 2000) have led to a worldwide upsurge of interest in biomonitoring methods to assess the biointegrity ("health") of freshwater ecosystems (Parsons & Norris 1996). Such assessment methodologies are based around the use of predictive models (or, alternatively, multimetric systems) using aquatic organisms (or their attributes) to assess the ecosystem state of a given type of system (e.g. rivers) within a pre-defined area: the so-called ecoregion concept (Hughes & Larsen 1988). As an example, details of assessment protocol systems used for standing waters in the USA as defined by the US Environmental Protection Agency can be inspected (<http://www.epa.gov/owow/monitoring/tech/lakes.html>).

In this paper we present an overview, with examples, of how current modelling approaches may be used to further fundamental understanding of aquatic ecosystem functioning, and to assist the practical management of such systems.

Models in aquatic ecology

The traditional approach in modelling the biological components of aquatic ecosystems (e.g. phytoplankton, invertebrates) uses a combination of physical and chemical predictor variables to generate outputs. Such models either directly predict the biological response of the system (or system components), or may be used to produce indirectly useful outputs for predicting biological response. There are many such models, of varying usefulness, precision and applicability (e.g. Chiarello & Barrat Segretain 1997; Chen & Coughenour 1996; Janse 1998; Olding et al 2000; Vestergaard & Sand-Jensen 2000). The addition of biological variables often improves the precision of such models: for example the incorporation of zooplankton grazing pressure as a predictor variable in lake phytoplankton models, such as PROTECH (Elliott et al 1999) or the Vortsjärv lake model of Frisk et al (1999). Some examples of traditional model usage in aquatic ecology are outlined below.

Catchment models: modelling nutrient-water relationships for catchment management.

During the past 30 years a major effort has been devoted to develop process-based catchment models of nutrient fluxes derived from both point and non-point (diffuse) sources (e.g. Dillon & Rigler 1974b; Bevan & Kirby 1979; Fedra 1983; Arnold et al 1995; Grieve & Gilvear 1994). Such models typically simulate the physical and biogeochemical processes, which govern transport of pollutants (usually nutrients) in a catchment, and have been widely applied. Outputs are useful for spatial modelling of the biological response of the receiving waters to nutrient enrichment, and can provide the basis for examination of "what if" scenarios of pollutant movement. Event-based models, for example AGNPS (Agricultural Nonpoint Source Model; Young et al 1989; Perrone & Madramootoo 1999), simulate transport only during a single event (e.g. a rain storm), while continuous models may simulate seasons, years, or decades.

AGNPS is a widely used example of such models. Developed in the 1980s by the US Agricultural Research Service, it analyzes diffuse pollution movement following individual precipitation events (rainstorms), simulating runoff, sediment and nutrient transport from agricultural catchments (watersheds) into receiving streams. Its main practical use is to prioritise potential water quality problems in rural catchments, using geographic cells of data units at resolutions of 0.4 - 16 ha to represent land and channel conditions. Fig. 1 shows a typical example: a 308 ha catchment divided into 26 cells (each of 16 ha), with drainage fluxes indicated by arrows between the cells. Potential pollutants are routed through cells from catchment edges down to the outflow, by stepwise movement, and flow can be examined at any point between cells. The model has 27 input data parameters: five operating at whole-watershed level, and the rest at cell level. The model structure comprises a series of equations which describe hydrology (runoff volume, peak flow rate), erosion and sediment movement (soil loss to streams and transport of sediment), and chemical transport (N, P, chemical oxygen demand). The model calculates output values for each/ all

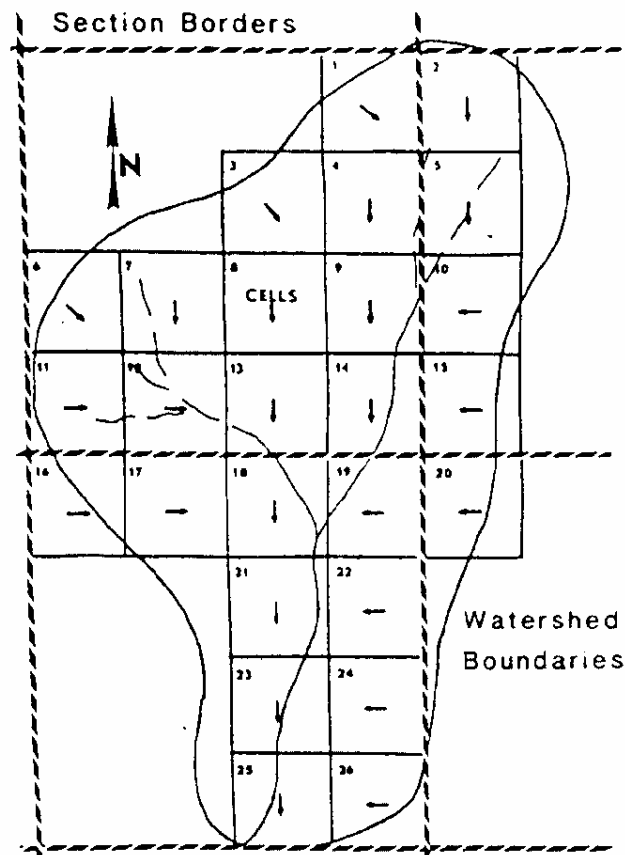


Figure 1: Modelling catchment structure using AGNPS: example of a 308 ha catchment divided into 26 cells (each of 16 ha), with drainage fluxes indicated by arrows between the cells (Young et al 1989).

cell(s) on the basis of values calculated by the model equations (using values supplied for each of the 27 input parameters), for hydrology, sediment and chemical outputs. Cell selection for output depends on the problem being assessed. For example, if a stream section needs protection (e.g. as a trout habitat for fishery purposes), cells with outlets to the stream may be examined. If a problem exists affecting the stream (e.g. nutrient inputs) then appropriate "upstream" land cells could be examined to identify the source of problems, and to help prioritize management solutions. AGNPS is used in several US states to prioritise catchments for potential severity of water quality problems in terms of sediment and nutrient loadings.

Lake phytoplankton models incorporating biological variables.

There are numerous studies, of which two examples will be discussed here. PROTECH is a simulation model which predicts chlorophyll_a concentration (i.e. phytoplankton abundance) in northern temperate lakes (Elliott et al 1999, 2001). It is driven by five ecosystem predictor variables: water temperature, light availability, rate of flushing (water movement through lake), nutrient availability, and abundance of grazer zooplankton. Its ability to predict temporal change in phytoplankton abundance is good - for example it simulates the classic spring and autumn algal blooms, typical of summer temperature-stratified northern lakes (Fig 2). Current research is underway at the Centre for Ecology and Hydrology in the UK to develop PROTECH further as a commercially-available management tool.

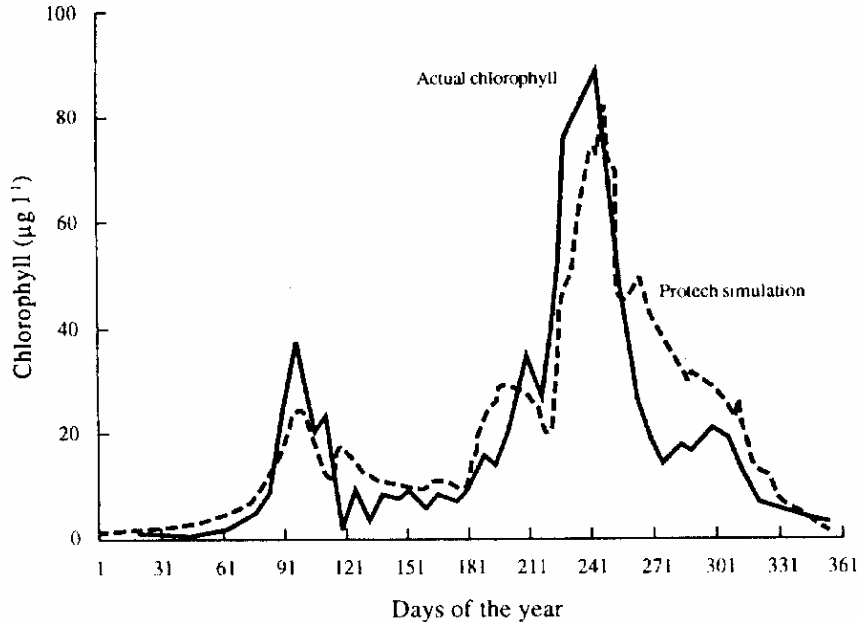


Figure 2: Spring and autumn algal blooms in a temperature-stratified northern lake simulated using PROTECH (Reynolds 1996)

Continuously Stirred Reactor Tank (CSRT) models of phytoplankton abundance in lakes have been used for many years (e.g. Kettunen 1981) to model the dynamics of phytoplankton growth in non-stratifying (continuously mixed) lake systems. An example of a system-specific minimal model using the CSRT approach is the Vortsjärvi model of Frisk et al (1999). Although developed and applied for one specific lake system in Estonia, this approach has considerable potential for modification and use with other mixed lakes.

Lake Vortsjärvi has many of the classic problems of nutrient enrichment seen in lakes throughout the world. It is shallow (mean depth 2.8 m), with an area of 270 km², within a relatively small agricultural catchment (2274 km²). The lake typically shows water level fluctuations (summer drawdown) which accentuate problems of algal blooms (primarily diatoms and cyanobacteria) and nuisance macrophyte growth. During the Communist era in Estonia, attempts to increase agricultural productivity led to big problems of fertiliser run-off which increased the eutrophication problems sharply. Since that time a restoration programme has been implemented, and the model aims to permit predictions of the effects of different possible restoration measures. Its prime outputs are annual nutrient concentrations and total abundance of phytoplankton. Secondary outputs are the dynamics of change in these parameters. Model state variables are concentrations of soluble reactive phosphate (SRP) and Inorganic nitrogen (N), diatom biomass, cyanobacteria biomass and dissolved oxygen (DO) concentration. A mass balance equation is provided for each state variable, including input, output, and the effects of internal reactions. In calculating output, discharge data are used as an input, so as to take account of the effect of changing volume of the lake on mass balance calculations. In total, 20 equations are utilised in building the model, using AQUASIM software (Reichert 1998). The model outputs gave good prediction of actual (measured peak) values of phytoplankton abundance in L. Vortsjärvi, with adequate prediction of the seasonal dynamics of cyanobacteria (Fig. 3), though diatoms were less well simulated.

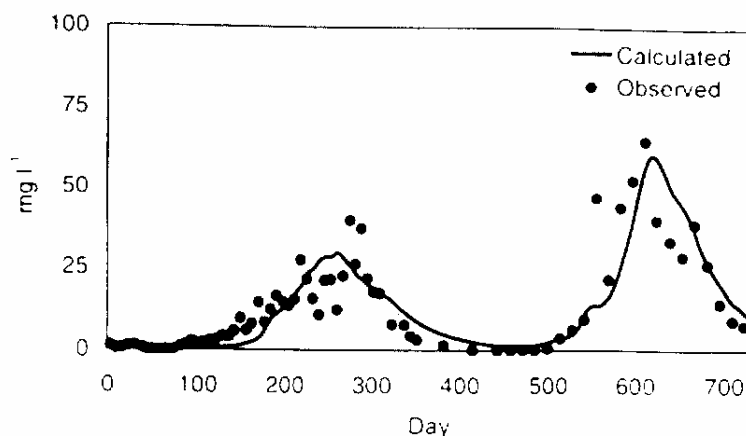


Figure 3: Simulated and actual values of cyanobacteria abundance in Lake Vortsjärvi, Estonia (Frisk et al 1999)

CSRT models are only suitable for certain types of lake. Individual models have a limited applicability outside the system for which they were designed. The Vortsjärvi model probably underestimates the importance of zooplankton grazing (a likely reason for its limited success in simulating diatom dynamics).

Modelling the performance of individual populations or species

Examples are given for aquatic macrophytes. Much is known about the survival and growth of this group of plants, in relation to environmental conditions influencing growth; and also their interactions with other aquatic organisms in a wide range of aquatic habitats (e.g. Ali et al 1995; Søndergaard et al 1996; Sabbatini & Murphy 1996; Fernández et al 1998; Weisner et al 1997; Spink & Murphy 1997; Sidorkewicz et al 1998; Sabbatini et al 1998; Bini et al 1999; Ferreira & Moreira 1999; Dawson et al 1999; O'Hare & Murphy 1999; Basu et al 2000; Vestergaard & Sand-Jensen 2000; Murphy in press). In the past decade specific models published for macrophytes include six models for freshwater and estuarine species, one for seagrasses, and five more generic models. Examples include:

1. A specific simulation model for *Hydrilla verticillata* (HYDRIL: Best & Boyd 1996), a major invasive aquatic weed in sub-tropical to tropical habitats (especially the USA and Asia). Driving variables include light, CO₂, temperature and plant characteristics, while nutrients are considered to be effectively non-limiting (which is typically the case in invasive *Hydrilla* habitats). Mowing is included as a management option, while the model has been calibrated and confirmed for data from Florida and India.

2. A specific model, which simulates the growth and development of *Potamogeton pectinatus*, a submerged aquatic plant of temperate waters (SAGA1: Hootsmans 1994, 1999). Drivers include the effects of light and age, and the model provides outputs on photosynthesis, growth, tuber bank development, vertical biomass distribution developing from different tuber size classes. This model has been used to provide management advice for restoring the species in The Netherlands and for limiting its biomass development in irrigation systems in Argentina (Fig 4).

3. A generic simulation model predicting the community structure of freshwater macrophyte vegetation (Duarte & Roff 1991), which predicts the relative contributions of all species to total community biomass. Model drivers include vegetation architecture and life history variables. This model predicts the performance of the dominant species within the community quite well, but performs less well for associated species.

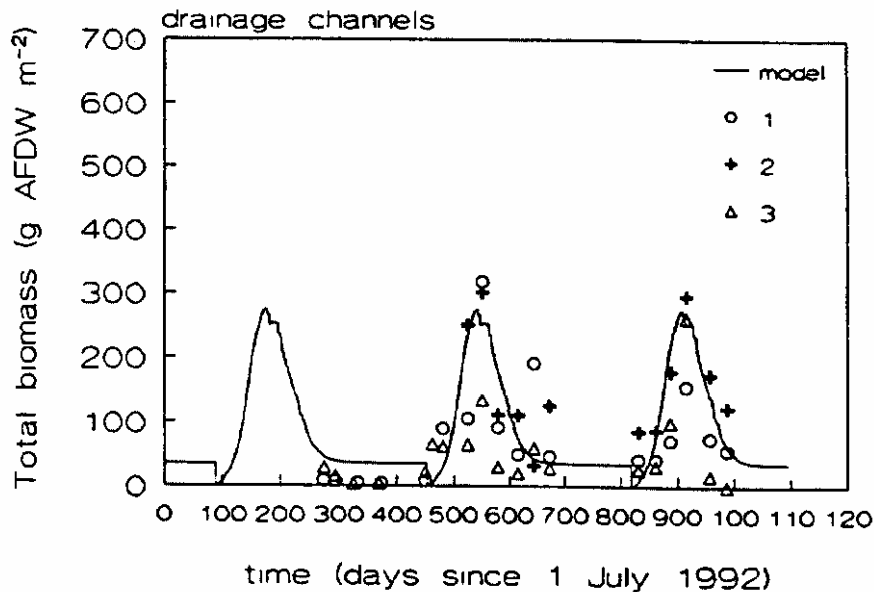


Figure 4: Simulated and observed biomass cycles (ash-free dry weight: AFDW) of *Potamogeton pectinatus* in three Argentine drainage channels (actual values for the three channels shown as o, +, Δ): Hootsmans (1999)

4. A generic model of aquatic plant biomass development (MEGAPLANT: Scheffer et al. 1993). Model drivers here include light, temperature, wave action and bird grazing. A particular plant type can be programmed by setting parameters such as timing of start and end of growth in the season, photosynthetic characteristics, growth form (including propagules and vertical architecture), and dispersal (input of propagules into an area).

Biodiversity modelling

Attempts to model biodiversity have focused on predicting either change in the richness of a target biota, or some measure of diversity incorporating equitability (e.g. diversity indices such as the Simpson index), or have attempted to predict change in assemblage. For example, recent work in Brazilian freshwater lagoon systems has successfully modelled patterns of β -diversity (species "turnover" between individual sites; e.g. for aquatic macrophytes: Souza et al. (in press); Bini et al 2001).

Willby et al (1998) developed a minimal linear model incorporating functional measures of the plant community, to predict plant α -diversity (S: species "richness" as number of species per unit area) in Scottish riverine floodplain wetlands. This model has a high predictive power ($R^2 > 0.9$) within a strictly limited envelope of applicability. Typical of such models, it incorporates a large number of predictor variables, thereby trading off generality of applicability to increase predictive power within a given system. More general models usually limit the number of predictor variables in order to increase the envelope of applicability.

The Scottish floodplain model for plant species richness (S) is:

$$S = -5.016 + 5.5 (\log_{10} \text{STEM}) + 0.43 (\text{Eh7}) + 3.7 (\text{CUT}) + 2.21 (\log_{10} \text{REPR}) - 1.04 (\text{DEEP}) - 1.63 (\log_{10} \text{Mn}) - 13.4 (\text{arcsin BARE})$$

It is driven by two functional attributes of the wetland plant community: stem density (STEM) and density of reproductive structures within the vegetation (REPR):

one management variable (intensity of cutting for hay-making purposes: CUT); and four environmental variables: percentage of bare ground (BARE), soil redox (Eh7), soil manganese content (Mn), and water table depth (DEEP).

More general multiple linear regression models were developed by Weiher & Boylen (1994) to predict patterns of α -diversity for submerged and floating-leaved aquatic plants in lakes of the Adirondack region of New York State (USA). Independent variables in these models were lake surface area, littoral zone area, pH, and measures of isolation and connectivity of the systems. The models that best explained species richness ($R^2 > 0.74$) incorporated pH, a connectivity predictor variable, and either lake surface area or littoral zone area. In a larger-scale study of macrophyte diversity in Scandinavian lakes, Rørslett (1991) similarly found lake area to be a major driver of models predicting macrophyte richness: the larger the lake, the richer its plant community.

Modelling spatial distribution using GIS

Geographical Information Systems (GIS), which provide a tool to generate maps describing changes predicted by models over time and space, are increasingly used as the platform for depicting model outputs in aquatic ecological studies (e.g. Remillard & Welch 1993; Belyaeva 1993; Lehmann & Lachavanne 1997; Todini et al 1998). Overlay maps can show correlations, e.g. for aquatic vegetation (Lehmann et al 1994; Schmeider 1995), between macrophyte distribution and abundance and various environmental parameters. Driving factors can be determined on the basis of the strength of their correlation, and the outputs used to predict plant abundance in a spatial manner, in relation to environmental change.

There is excellent scope for further development of GIS modelling in aquatic ecology to incorporate a range of modelling techniques (e.g. Lehmann 1998: on lake macrophyte distribution; Dennis et al 1999: modelling biodiversity at catchment scale). As an example, in current spatial models of aquatic vegetation, developments in one gridcell most often do not influence processes in neighbouring cells. In addition, the effects of aquatic vegetation on environmental factors are often not incorporated (e.g. resuspension and sedimentation). Faunistic relations and effects may also be of importance to improve prediction of spatial vegetation development (e.g. herbivory by fish and waterfowl, snail grazing of periphyton attached to plants). Spatially-explicit dynamic models can be developed to include such improvements, but there are relatively few examples to date. One such study is by Wortmann et al. (1997). This produced a relatively simple model for *Zostera* seagrass populations, simulating the horizontal growth of a bed. Growth was related to standing biomass, in response to environmental factors such as salinity, flow, and intraspecific competition between neighbouring stands. The inclusion of horizontal development in a spatial grid (resembling cellular automata models: Engelen et al 1995; Silvertown et al 1992) was an interesting feature of this approach.

Biomonitoring: predictive models to monitor change in ecological attributes of aquatic systems

Legislative drivers, such as the European Union Water Framework Directive, require the implementation of biologically-based water quality monitoring systems to assess the "health" (biointegrity) of aquatic ecosystems. These systems are based either on predictive modelling or multimetric approaches. For example, the US Environmental Protection Agency has implemented multimetric freshwater assessment systems (e.g. the Rapid Bioassessment Protocols for use in Streams and Rivers: Barbour et al 1999). Multimetric schemes quantify the concept of biological integrity by allocating values ("metrics") to a number of different biological attributes, then

compare each of these to values expected to occur in the absence of human impact (i.e. the changed state approach). Values of individual indicators are aggregated to give the overall measure of quality. The approach utilises reference sites, on an ecoregion basis, to provide the required baseline data for comparison of states in individual waters.

To meet the requirements of the Water Framework Directive, monitoring approaches used in the European Union (EU) must, from 2003, follow the so-called DPSIR approach, and are largely based on predictive models of changed state. DPSIR stands for Driving forces - Pressures - States - Impacts - Responses. The approach is designed to link policy objectives to information and analysis in the context of management implementation. For the purposes of the Water Framework Directive, the approach is primarily concerned with catchment modelling outputs. The models to be used for this purpose, in all EU nations, must provide deterministic or stochastic simulation procedures, be well-tested with reliable results, and have databases available to run them. In addition, the models must be independent of spatial and temporal scales in order to ensure appropriateness for application at river basin, sub-basin and local scales, and to allow forecasting of water quality at three timescales: 6, 15 and 28 years into the future. Modelling tools must also provide open Graphic User Interfaces (GUI) to allow exchanges of data and results between potential users (e.g. government administration, water supply authorities, environment protection agencies, research organisations). The ideal modelling toolbox will incorporate a range of models, covering all important aspects of the water environment, including the impacts of point and diffuse sources of pollution, transfer to rivers via transitional zones, and delivery to coastal waters.

There is a difference between political desire and scientific reality. The general application of prescribed approaches may tend to force scientists into developing systems which might, in reality, only be able to provide vague general information to policymakers, with no real relevance for local/regional water management authorities (the agencies which are of course primarily responsible for implementing policy). Equally, the models, and the biomonitoring schemes built around them, may either not exist, not work out with strictly limited envelopes of applicability, be unsuitable for biogeographical or other reasons, or may not have reached an appropriate level of development and testing to meet DPSIR requirements. The aim of the Water Framework Directive is good, in that it will force all EU states to come up with more or less comparable standard approaches to water quality assessment. However, it may be questioned whether one EU-wide system can really cater for widely-varying practical situations and requirements in catchment water management needs, at all spatial and temporal scales on a continent-wide basis. Similar questions could be applied to any large-scale modelling-based monitoring system, whether in Europe, Brazil or the USA. It is very important to ensure that local-scale variability in response of aquatic systems is not lost in the application of large-scale standardised schemes.

Bearing this in mind, schemes based on the use of biological indicators of aquatic ecosystem biointegrity should in general aim to meet six criteria (Norris & Hawkins 2000). Effective methods will:

1. quantify and simplify complex ecological phenomena
2. provide easily interpretable outputs
3. respond predictably to damage caused by humans, while being insensitive to natural spatial/ temporal variation
4. relate to an appropriate scale
5. relate to management goals
6. be scientifically defensible

Predictive models which meet these criteria for using biological indicators to quantify the biointegrity of aquatic systems (e.g. Hill et al 2000: using periphyton; Battarbee et al 1988: diatoms; Raddum et al 1988: chironomids; Winter & Duthie 2000: benthic algae), are based on the degree to which a site supports the biota expected

in the absence of human alteration of the site (Hawkins et al 2000; Murphy 2000). Measurements compare the composition of the biota (assemblage) at reference sites (E) and test sites (O) which have similar physical and chemical characteristics. An empirical model is then created using environmental characteristics of the sites unlikely to be (greatly) affected by human activities, and compares these to the probability of a species occurring there. The model is used to make site-specific predictions of expected assemblage, and this is compared (O/E) with the observed assemblage.

Invertebrate-based models

Macroinvertebrate community structure has been the basis for numerous water quality assessment methodologies, worldwide (Metcalf 1989; Coimbra & Graça 1998). Good examples of biomonitoring systems which have been widely adopted are the systems for assessment of river ecosystem health using invertebrate-based predictive models: (RIVPACS: Wright 1995 in the UK, AUSRIVAS: Simpson & Norris 2000 in Australia; BEAST in Canada, Reynoldson et al 1997). These are changed-state predictive modelling systems based on data collected from reference sites (unimpaired or minimally impaired) representing the range of natural conditions across the target regions covered by the models.

RIVPACS (River Invertebrate Prediction and Classification System) is a software package developed in the 1980s using multivariate analysis of data from river surveys in the UK. It allows for natural physical and chemical differences between rivers in comparing scores allocated to the benthic macroinvertebrate community present following a standardised scoring system related to family occurrence in different water quality conditions (as measured by an appropriate biotic index: e.g. BMWP: Armitage et al 1983). The primary function of RIVPACS is to predict the benthic macroinvertebrate taxa to be expected at a particular river site (based on the physical and chemical characteristics of the site) in the absence of environmental stress caused by pollution.

Comparison with the actual biotic index recorded at a given site gives an indication of how severe environmental degradation is, compared to what site score should be in the absence of pollution. An Environmental Quality Index (EQI) is calculated as the ratio of observed to predicted index scores. EQI values close to 1 indicate an unpolluted site. For large-scale (e.g. national) survey purposes, values of EQI are banded to produce water quality classes to which rivers can be assigned. The accuracy of RIVPACS depends heavily on how closely a new site (i.e. the site under survey) fits into the range of reference sites on which RIVPACS is based. RIVPACS Version III utilises a database of 674 UK reference sites forming 42 site-groups. RIVPACS can be applied to select exceptional sites worthy of conservation. Because it provides an objective means of assigning new sites into one of 42 groups based on macroinvertebrates present, communities unusual for a particular geographical area, or in national context, can be identified. Thus, "hotspots" where species richness is higher than expected can be identified and if appropriate, given legal protection.

Case study: modelling aquatic vegetation of the Upper Rio Paraná *várzea*

In this paper we have provided an overview of a number of the ways in which modelling can contribute to understanding how some of the primary attributes of aquatic communities (such as biomass and biodiversity) respond to changes in environmental conditions, and how such models can be used in biomonitoring of ecosystem biointegrity.

To illustrate the application of modelling approaches, some data are presented from a study of the plant communities of a Brazilian sub-tropical riverine floodplain wetland: the *várzea* of the Upper Rio Paraná (Murphy et al, 2003 in review). Previous

work (Souza et al., in Press; Bini et al., 2001) has assessed species richness and β -diversity patterns for aquatic vegetation in some of the aquatic habitats (lagoons) of this system. We sought to find environmental predictors of three primary aquatic vegetation parameters (assemblage, α -diversity, and abundance), and to determine whether functional attributes of the vegetation itself might act either as qualitative markers, or quantitative predictors of these parameters for modelling purposes.

A minimal linear modelling approach was adopted, with an envelope of applicability limited to *várzea* waterbodies of the Upper Rio Paraná. During 1999 the aquatic vegetation was sampled at 45 sites within the Porto Rico stretch of the Rio Paraná (and its tributary the Rio Ivinheima), including main and secondary river channels, backwaters, lagoons and distributaries. The plant community was dominated by four floating and emergent species: *Eichhornia azurea* (54%), *Salvinia herzogii* (14%), *Cyperus diffusus* and *Eichhornia crassipes* (7% each). Another eight species comprised the remaining 18% of dominant species: *Nymphaea amazonum*, *Utricularia foliosa*, *Polygonum ferrugineum*, *Najas conferta*, *Limnobium laevigatum*, *Panicum prionitis*, *Myriophyllum aquaticum*, and *Ludwigia octovalvis*.

Biodiversity and biomass were both modelled:

1. Macrophyte diversity ($R^2 = 63.1\%$; $p < 0.001$)

$$\log_e SPP = 4.75 - 0.237(\log_e Fe_{sed}) - 0.0148 (P_{wat}) + 0.0045 (\log_e TOTW) - 0.000026 (Ca_{sed})$$

2. Macrophyte biomass ($R^2 = 27.2\%$; $p = 0.004$)

$$BIOM = 753.0 + 381.0 (\log_e k) + 260.0 (\log_e TOTW) - 138 (\log_e Fe_{sed}) Ca_{sed}$$

Both models are significant, but biomass was much more poorly predicted than alpha-diversity.

Sediment chemistry variables (especially Fe concentration) were good predictors of both diversity and biomass, and the weight of dominant species was also important in both models. Water trophic status (P_{wat}) was important for the diversity model, but underwater light availability was more important in predicting community plant biomass. These models are currently (2001 - 2002) in process of being tested at independent sites and with temporally-distinct datasets. Assemblage was not modelled quantitatively in this study but qualitative indicator variables were found for each of the three primary plant community types identified as present by TWINSpan classification of the sites x species dataset. There were significant differences in the mean values of a number of environmental and plant community attributes characterising the sites making up each TWINSpan group (Fig.5).

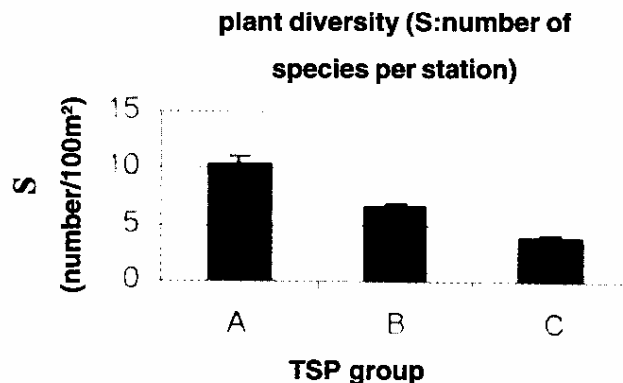


Figure 5: Mean values (\pm standard error) of plant species diversity (S: number of species per 100 m²) showing significant differences ($p < 0.05$; one-way ANOVA), between TWINSpan (TSP) sample site groups A - C in a Brazilian wetland system (Murphy et al., 2002).

Of the plant attributes measured, leaf area was the best marker separating the three assemblage types. However water and sediment variables also showed predictable and highly significant variation associated with assemblage. While no single variable was adequate as a clear indicator of plant community within the varzea waterbodies studied, a combination of 3 – 4 environmental factors plus leaf area proved sufficient to provide a qualitative prediction of likely assemblage occurring at a given site. Thus for example a site supporting species of low leaf area per plant, with low P concentration in water, and low sediment Ca concentration is likely to support a high diversity plant assemblage, with many species of free-floating plants (e.g. *Eichhornia crassipes*, *Limnobiium laevigatum* and *Pistia stratiotes*).

The minimal modelling approach adopted in this case study showed that the aquatic vegetation of waterbodies within the Upper Rio Paraná varzea exhibits predictable variation in its community attributes (size and shape of dominant species; diversity of plant assemblage present; biomass of plant community), along gradients of water and hydrosol physico-chemistry occurring across the floodplain. The composition of the plant community was not modelled, but plant assemblage (i.e. vegetation type) was found to be significantly associated with variations in environmental conditions and certain plant attributes, some of which could act as markers of probable vegetation type present.

Conclusions

In this paper we have attempted to show how modelling approaches in aquatic ecology have moved on from the old ideas of developing and using models in isolation to tackle individual issues, or alternatively attempting whole-ecosystem modelling, which has rarely proved workable in real ecosystems (although some progress is undoubtedly being made: e.g. Fitz et al 1996).

Freshwater ecosystems are increasingly recognised as a resource of absolute value to mankind, but one which is both in limited supply and of diminishing quality (Laws 2000). As a result legislators are, at long last, trying to protect this resource more effectively than hitherto, and new environmental legislation is being introduced and (sometimes) enforced in many parts of the world to this end. Models of community attributes are recognised as vital elements of the integrated predictive modelling techniques, which are needed, under the new laws being introduced in (for example) Europe, Australia and the USA, to assess the biointegrity of freshwater ecosystems, and to determine their probable response to human impacts. These models form an essential part of the "model baskets" and "model toolboxes", which aim to bring together the sets of biological, physical and chemical models needed to meet, for example, DPSIR requirements for aquatic ecosystem monitoring in Europe. The model toolboxes in turn form the basis for the expert systems (e.g. Janssen 2001; Fedra et al 1991; Fedra & Jamieson 1996) needed to support the management decisions and actions required to implement such legislation (e.g. Hilton et al 1992). However, there remain huge holes in the areas of aquatic ecology covered by existing models. Current models are patchy in both availability and coverage of the issues involved, and often under-utilized in terms of spatial application and user-friendliness. They are often also very specific in terms of geographical and/or biological constraints on their applicability. Many existing aquatic ecology models developed are noisy, and rarely produce results which are as precise as the physical and chemical models developed for freshwater systems. While this situation may, in part, be a reflection of the interests of ecological modellers, it also undoubtedly reflects the inherent variability of biological systems, and also in many cases the lack of sufficiently large and detailed datasets for model construction.

There is a need for more generalized models, covering a greater range of issues and systems. More use could be made of Geographical Information Systems, as an

excellent platform for presenting model outcomes (see Dennis et al 1999 for an example of application to a terrestrial ecosystem), and applying them to real systems, in a way which is readily understood by practical users. If we spend time and resources in developing nice models, which accurately depict the responses of aquatic communities to environmental change, but nobody uses them, we have wasted our time. So it is vital to ensure that model outputs (not necessarily the models themselves) are easily available and interpretable by the people who can make good use of them, such as environmental managers, decision-makers and legislators. The development of good Graphic User Interfaces (GUIs) to show the outcome of modelled scenarios in user-friendly formats is almost as important as developing the models themselves. The Internet provides an ideal medium for dissemination, and making models available, especially when the models require (as is often the case) large relational databases for their operation, which can be easily accessed via the Net.

Finally, most current models in freshwater ecology are still wedded to the use of linear modelling algorithms (Crawley 1993). While these have proved useful both in advancing our understanding of the functioning of aquatic communities in freshwater ecosystems, and in terms of practical applications, they are limited in their potential for future development by the fact that biological systems are essentially non-linear, inherently noisy things, which are not easily represented by mathematical functions that take no account of this fact. Non-linear modelling (in part based on chaos theory: e.g. Hilborn 1994; Doebeli & Ruxton 1997) may provide a more promising approach for the future to meet the demands of generality of model application, and improved precision of forecasting outcomes. There is very little current work with such models in freshwater ecology, but the potential is there to make major progress: non-linear modelling may well be seen as standard by the next generation of researchers in aquatic ecology.

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