# A Bayesian network of eutrophication models for synthesis, prediction, and uncertainty analysis 

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#### Abstract

A Bayesian network consists of a graphical structure and a probabilistic description of the relationships among variables in a system. The graphical structure explicitly represents cause-and-effect assumptions that allow a complex causal chain linking actions to outcomes to be factored into an articulated series of conditional relationships. Each of these relationships can then be independently quantified using a submodel suitable for the type and scale of information available. This approach is particularly useful for ecological modelling because predictable patterns may emerge at a variety of scales, necessitating a multiplicity of model forms. As an example, we describe a Bayesian network integrating models of the various processes involved in eutrophication in the Neuse River estuary, North Carolina. These models were developed using a range of methods, including: process-based models statistically fit to long-term monitoring data, Bayesian hierarchical modelling of cross-system data gathered from the literature, multivariate regression modelling of mesocosm experiments, and judgements elicited from scientific experts. The ability of the network to accommodate such a diversity of methods allowed for the prediction of policy-relevant ecosystem attributes not normally included in models of eutrophication. All of the submodels in the network include estimates of predictive uncertainty in the form of probability distributions which are propagated to model endpoints. Predictions expressed as probabilities give stakeholders and decision-makers a realistic appraisal of the chances of achieving desired outcomes under alternative nutrient management strategies. In general, the further down the causal chain a variable was, the greater the predictive uncertainty. This suggests that a compromise is necessary between policy relevance and predictive precision, and that, to select defensible environmental management strategies, public officials must adopt decision-making methods that deal explicitly with scientific uncertainty.


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## 1. Introduction

Scientists are often asked to contribute to the difficult process of environmental management and decision-making by providing a predictive link between management actions and ecosystem response (Jorgensen, 1995; Clark et al., 2001). However, this link may be a complex causal chain, the entirety of which rarely falls within a single, coordinated research project (Carpenter, 1996). While there have
been recent efforts to expand the scope of projects to encompass all processes relevant to a particular environmental problem (Carpenter et al., 1995; Kinzig, 2001), usually groups of independent researchers study different system features as dictated by their own scientific interests (Norton, 1998). This situation makes it difficult to directly apply the results of scientific studies to the task of forecasting ecological change.

Ecological models represent attempts to combine the understanding gained from multiple projects into a single predictive framework (Jorgensen, 1993; Pielke, 2001; Turner, 2001). Most models do this by endeavouring to simulate all of the physical, chemical, and biological processes occurring in the system at a pre-determined model scale (Fitz et al., 1996). However, depending on the nature of these processes and the design of previous scientific studies, the most predictable relationships among different sets of variables may emerge at a variety of spatial, temporal, or functional scales (Levin, 1992). Therefore, current scientific knowledge might be better represented if each relationship were described at the level of detail at which regular patterns of behaviour have been identified, rather than at a scale that is identical for all processes (Jorgensen, 1995).
Given the diversity of scales at which ecosystem patterns may emerge, a serious challenge for ecological modellers is to integrate quantitative descriptions of these patterns into coherent predictive models (Levin, 1992; MacNally and Quinn, 1998; Pace, 2001). Methodologies are required that allow representation at multiple scales and in a variety of forms, depending on available information. There is also a need to assess how uncertainties in each component of the model translate to uncertainty in the final predictions (Reckhow, 1994b; Reichert and Omlin, 1999). Finally, such models must be able to be easily updated to reflect evolving scientific knowledge and policy needs (Walters, 1986).

We have found Bayesian networks (Pearl, 1988; Jensen, 1996) to be a promising method for performing integrated ecological modelling (Varis et al., 1994). The graphical structure explicitly represents cause-and-effect assumptions between system variables that may be obscured under other approaches. These assumptions allow the complex causal chain linking management actions to ecological conse-
quences to be factored into an articulated sequence of conditional relationships. Each of these relationships can then be quantified independently using an approach suitable for the type and scale of information available. Probabilistic functions describing the relationships allow key known or expected mechanisms to be represented without the full complexity, or information needs, of highly reductionist models. To demonstrate the application of the approach, we develop a Bayesian network representing eutrophication in the Neuse River estuary, North Carolina from a collection of previously published submodels. We then use this synthesis model to generate probabilistic predictions of ecosystem response to alternative nutrient management strategies.

## 2. Bayesian networks

A Bayesian network begins with a graphical depiction of the relationships among the most important variables in the system of interest. In this depiction, the variables are represented by round nodes, and a dependence between one variable and another is represented by an arrow. The conditional independence implied by the absence of a connecting arrow between any two nodes greatly simplifies the modelling process by allowing separate submodels to be developed for each relationship indicated by the presence of an arrow. These submodels may be derived from any combination of process knowledge, statistical correlations, or expert judgement, depending on the information available about that particular relationship (Varis, 1995). This is a practical and realistic approach to ecological prediction, the merits of which are well described by Peters (1991).

Unlike most integrated environmental modelling, however, Bayesian networks utilise probabilistic, rather than deterministic, expressions to describe the relationships among variables. This is an essential characteristic of an ecosystem model if predictions are to be used to guide decision-making (Clark et al., 2001). In a Bayesian network, each dependence indicated by an arrow represents a conditional probability distribution that describes the relative likelihood of each value of the down-arrow node, conditional on every possible combination of values of the parent nodes. A node that has no incoming arrows is said to have no
parents, and such a variable can be described probabilistically by a marginal (or unconditional) probability distribution. The graphical network, therefore, constitutes a description of the probabilistic relationships among the system's variables that amounts to a factorisation of the joint distribution of all variables into a series of marginal and conditional distributions.

The realisation that a graphical network has implications for the dependence structure among variables makes working with probabilistic description of complex systems much easier and has stimulated developments in such models by researchers in artificial intelligence (who often use the term "belief net") (Pearl, 1988), decision analysis (where the term "influence diagram" is common) (Oliver and Smith, 1990), and statistics (where "graphical model" is often used) (Spiegelhalter et al., 1993). These efforts have led to significant advances in the use of Bayesian networks for uncertainty analysis, system diagnosis, experimental design, and automated learning (Jensen, 2001).

Bayesian networks are only beginning to be applied by ecological modellers (Varis and Kuikka, 1999), and applications to date include fisheries assessment (Lee and Rieman, 1997; Kuikka et al., 1999), forest regeneration (Haas et al., 1994), and habitat restoration (Rieman et al., 2001). Most of these studies have either encoded conditional distributions directly, usually using discrete (or discretised continuous) variables, or have used off-line stochastic simulations to generate distributions of uncertain results, which were then discretised for subsequent representation in the network model (e.g. Lee and Rieman, 1997; Kuikka et al., 1999; Dorner et al., 2001; Sahely and Bagley, 2001). We take a different approach, however, by using a Bayesian network as the organising structure for a set of separately developed, continuous, functional models, each of which is capable of real-time solution in the network (see also Varis and Kuikka, 1997). This approach can be expected to lead to greater exploitation of the representational and computational advantages of Bayesian networks, as well as more effective use of available scientific knowledge.

## 3. Problem description

The Neuse River estuary, North Carolina (Fig. 1), has been experiencing severe consequences of eu-


Fig. 1. The Neuse River estuary, North Carolina, indicating the region of concern in the present study.
trophication in recent years including excessive algal blooms, low levels of dissolved oxygen, declining shellfish populations, large fish kills, and outbreaks of toxic micro-organisms. These problems have led to the Neuse River being declared one of the 20 most threatened rivers in the United States (ARF, 1997). The Neuse River estuary has also been listed on the federal list of impaired waters under section 303(d) of the Clean Water Act. Problems in the estuary have been attributed to the high nutrient loading that generally results from the kinds of changes that have occurred in the watershed over the past several decades (Paerl et al., 1995). The upper portion of the Neuse River drainage basin includes much of North Carolina's Research Triangle (defined by the cities of Raleigh, Durham, and Chapel Hill), an area that has experienced economic prosperity and rapid population growth since the 1970s. Population expansion and development are also occurring in lower portions of the basin with an increasing coastal population and a growing commercial animal-farming industry. Treated municipal wastewater, urban runoff, confined animal feeding operations, agricultural fertilisers, and atmospheric deposition are considered to be important sources of nutrients to surface waters draining to the Neuse River.

As in many other marine systems, nitrogen has been identified as the pollutant of concern in the estuary because it is the nutrient believed to be stimulating the excessive growth of algae that is at the root of other ecological problems. Therefore, the United States Environmental Protection Agency (USEPA) has re-
quired that the State of North Carolina implement watershed-based pollutant controls to limit nitrogen inputs to the estuary. The degree of reduction required is to be determined according to the establishment of a Total Maximum Daily Load (TMDL) for nitrogen. A TMDL is an estimate of the maximum pollutant loading to a water body that will still allow it to meet water quality standards and attain its designated uses (Office of Water, 1999). Over the next 10 years, thousands of TMDLs for pollutants must be developed for waterbodies across the nation (National Research Council, 2001).

Typically, the determination of a TMDL is based on the results of a deterministic simulation model that predicts water quality characteristics, such as chlorophyll a level or dissolved oxygen concentration, at a fine spatial and temporal scale (Office of Water, 1997). While these variables may be useful indicators of water quality problems, they have relatively little meaning to the general public and decision-makers. Instead, these groups are more interested in the occurrence of harmful algal blooms, fish kills, and shellfish mortality. At the scale employed by most simulation models, the ecological processes associated with these attributes are too complex or stochastic to be characterised mathematically. However, the aggregate causal relationships are well known, and smaller scale dynamics might be captured probabilistically. Therefore, there is promise that a flexible modelling tool, that can link processes occurring at multiple scales, might lead to better TMDL decisions by more directly addressing stakeholder objectives.

## 4. Development of causal structure

The first step in constructing a Bayesian network is the development of the graphical structure indicating the relevant variables and dependencies. This graphical representation is important because it provides the basis for determining the degree of decomposition to be used in subsequent construction of mathematical models (Varis and Kuikka, 1997). Development of the graphical structure for the Neuse eutrophication network consisted of two distinct tasks. The first was to determine the attributes of the estuarine system for which decision-makers would like to see predictions. Because decisions by public officials should represent
the views of the public, we elicited these attributes from a set of stakeholders who care about the health of the Neuse estuary. The second task consisted of linking these variables to nitrogen inputs using a causal network diagram drawn in conjunction with estuarine research scientists.

### 4.1. Stakeholder elicitation

Identification of measurable ecosystem variables that are meaningful to stakeholders and to their public officials was the first task of our modelling study. The intent was to establish those attributes that would be used by the public and decision-makers to evaluate the success of the nutrient management program and should therefore be predicted by the model. While this may seem like an obvious starting point for the modelling process, it is often overlooked in the rush to gather and analyse data or write computer simulation programs (Reckhow, 1994a). Inadequate attention to this step may lead to an incomplete analysis or an analysis of the wrong problem with respect to important policy interests (Reckhow, 1994a).

Details of the stakeholder elicitation effort are described by Borsuk et al. (2001a). Summarised results (Table 1) show that the public cares about attributes of water quality and ecosystem health beyond those generally predicted by traditional simulation models. These include water quality measures such as water

Table 1
Ecosystem attributes of concern to Neuse River stakeholders
Water quality
Oxygen levels
Chlorophyll a levels
Taste
Odour
Water clarity
Sandy bottom
Algal toxins
Biological quality
Algal blooms
Fish and shellfish abundance and health
Species diversity
Human-induced fishkills
Submerged aquatic vegetation
Human health
Fecal coliform
Toxic micro-organisms
clarity, taste, lack of odour, levels of chlorophyll a and dissolved oxygen, and presence or absence of algal toxins. Important biological quality indicators include algae levels and presence of excessive, submerged aquatic vegetation, as well as abundance, diversity, and health of fish and shellfish. Concerns regarding human health include the presence of faecal coliform and toxic micro-organisms including Pfiesteria piscicida. Rather than forcing decision-makers to extrapolate traditional water quality variables to these ecological attributes, it is the goal of this project to predict them directly using alternative model types integrated into the Bayesian network.

### 4.2. Network development

Development of the causal diagram linking nitrogen inputs to meaningful attributes began with a comprehensive survey of the relevant scientific literature. With the primary attributes of interest defined by the stakeholder process, it was natural to begin by identifying the nodes immediately preceding them in the causal chain, then nodes preceding them, and so on, back to the model inputs, including nitrogen loading. This process was successful in producing a network linking causes and effects that represented the current published opinion of scientists studying the Neuse, but the exact quantitative nature of the relationships was not clear. Therefore, the scientists themselves were consulted for additional information.

Using our literature-based graphical model as a starting point for discussion, we held a series of meetings with researchers to explain the Bayesian network approach and to get their input on the causal diagram (Borsuk, 2001). Almost invariably, they were intrigued by this alternative way of modelling the system and provided extensive information on available data sources and additional contacts. However, all the scientists also had their own "pet processes" that they wanted to see included in the model, usually related to the focus of their own research. These ranged from the role of algal grazers in controlling algal density to the effect of a "mid-estuary gyre". For the purposes of completeness, these were all tentatively included, resulting in a graphical model with 35 nodes and 55 arrows. Clearly some simplification was necessary to make the problem tractable and to keep it consistent with available data.

The inclusion of many important environmental variables and processes may, in principle, produce more precise predictions. If the values of those variables and the rates of the processes are well known, then predictions can be conditioned on them, thereby reducing uncertainty (Reichert and Omlin, 1997). However, if the variables are stochastic or uncontrollable and must be described by marginal probability distributions themselves, then their inclusion is not very useful for informing management decisions (Levin, 1985). Therefore, to design the most parsimonious yet realistic model, each node in the network was reviewed to determine if the variable it represented was either: (1) controllable, (2) predictable, or (3) observable at the scale of the management problem. If not, then the node was removed from the network.

The simplification strategies described above were effective in reducing the network down to 14 nodes and 17 arrows (Fig. 2, centre). Ecosystem attributes consistent with those identified in the stakeholder study include algal density, as measured by chlorophyll a concentration, abundance of the toxic micro-organism Pfiesteria, fish population health, frequency of fish kills, and shellfish abundance. Other variables that the stakeholders would have liked to have seen included in the network, such as taste, odour, aquatic vegetation, and faecal coliform concentrations, were determined to not be affected by nitrogen control, the only management action currently under consideration. Because variables and relationships are only included in the model if they contribute to our ability to predict ecosystem attributes of policy relevance, the model structure can be best explained by starting with these variables and proceeding in the "up-arrow" direction.

### 4.3. Network description

According to the stakeholder study (Table 1), fish kills are an attribute of significant public interest. The current scientific belief is that fish kills are caused by a combination of low oxygen bottom water (hypoxia) and wind conditions that force that bottom water to the surface, trapping fish along the shores where they suffocate. Fish are generally more susceptible if they are already in poor health. Therefore, the occurrence of fish kills depends on the health of the fish population, the temporal extent to which the estuary experiences hypoxic conditions, and the frequency of


Fig. 2. Centre figure: graphical representation of the full Bayesian network for Neuse estuary eutrophication. Variables are indicated with rounded nodes, and causal relationships are indicated with arrows. Surrounding insets: networks representing submodels of the main network. Shaded nodes indicate model parameters. Double-headed, dashed arrows indicate a correlation between marginal variables that may be the result of exogenous factors, rather than causal influence.
cross-channel wind conditions. The temporal extent of hypoxia is determined by the pattern of bottom water oxygen concentrations. Oxygen concentration is controlled by both the rate of sediment oxygen demand by bacterial respiration and the duration that the bottom waters are separated from the surface due to
salinity stratification (Stanley and Nixon, 1992; Paerl et al., 1998). Stratification begins to set up whenever cross-channel winds are calm enough to avoid mixing for more than one day. Therefore, the frequency of strong cross-channel winds is an appropriate immediate cause of stratification.

Sediment oxygen demand is dependent on the amount of organic matter available in the sediments (Rizzo and Christian, 1996). In a eutrophic estuary such as the Neuse, most of the sediment organic matter is internally derived via algal carbon production (Alperin et al., 2000). Because regular measurements are not made of the sediment organic carbon content, this intermediate variable is not included in the model, and a direct link is shown between carbon production and sediment oxygen demand (Fig. 2, centre). This is an instance where the aggregate effect may be better known than the sum of a number of individual, uncertain processes.

Algal carbon production is related to algal density, although water temperature also plays an important role (Mallin et al., 1991). Additionally, light intensity and photic depth have been shown to be significant factors (Cole and Cloern, 1987; Boyer et al., 1993). However, while these are both observable variables (in that they can be measured), they are neither manageable by nitrogen controls nor predictable from other known factors (as water temperature is from the seasonal cycle). Therefore, they are not explicitly included, and the variability they cause becomes part of the predictive uncertainty.

Algal density in the Neuse estuary is controlled by nitrogen inputs, water temperature and river flow (Mallin et al., 1993; Pinckney et al., 1997) which, for the purposes of the present analysis can be considered marginal input nodes. To predict the effects of future nitrogen reductions, river nitrogen concentration will be adjusted accordingly. Other sources of nitrogen to the estuary, including atmospheric sources and groundwater, are not considered in this analysis because the TMDL process only regulates nitrogen inputs from the river.

Another attribute of importance to stakeholders is fish population health. While a number of factors may affect the health of the fish population, only the effects of hypoxia can be controlled through nitrogen reductions. Extensive hypoxia can diminish the health and productivity of the fish population and make it more vulnerable to both disease and episodic fish kill events. The situation is similar for shellfish. However, because shellfish are sessile, it is not only their health, but also their abundance, that is threatened by long-term exposure to low oxygen conditions. Therefore, both the duration and severity of hypoxia are
important considerations, prompting the arrows from nodes representing both duration of stratification and dissolved oxygen concentration.

The toxic dinoflagellate, P. piscicida, is a concern to the public at least in part because of the large amount of media attention it has received in recent years. It has been blamed for having a role in the occurrence of fish kills both by directly attacking the fish and by making them more susceptible to harsh conditions (Burkholder, 1999). Pfiesteria has also been found to adversely impact the health of laboratory researchers studying the organism by causing respiratory and neurological distress (Glasgow et al., 1995). However, the potential threat to people exposed to Pfiesteria under natural conditions is highly controversial (Griffith, 1999), and the distinct role the organism plays in fish kills is uncertain (Stow and Borsuk, 2003). Many of the scientists we spoke with felt that Pfiesteria was just one of many stressors that affect fish, and if Pfiesteria were not present in the estuary, other opportunistic organisms would be. Therefore, to satisfy the interests of the stakeholders, Pfiesteria abundance was included as a variable in the model. However, it was not explicitly linked to fish population health or fish kills, nor was a human health effect included. Perhaps as more laboratory research, fieldwork, and health studies are conducted in the future, the role of Pfiesteria in the network can be modified accordingly.

Pfiesteria is a heterotrophic dinoflagellate that does not synthesise photopigments. However, it can capture chloroplasts from algal prey to produce a photosynthate for use in meeting its nutritional requirements, a process called cleptochloroplasty (Burkholder and Glasgow, 1997). Therefore, when in its non-toxic zoospore stage, Pfiesteria's primary food source is phytoplankton (Burkholder et al., 1995), suggesting a linkage between the zoospore and its prey in natural settings. It is possible that other factors, such as nutrients, mixing, and light, may also control the density of Pfiesteria either directly or indirectly by affecting phytoplankton biomass and species composition. These causal factors will be explored in more detail below.

## 5. Quantification of conditional relationships

With the primary causal relations leading from nitrogen inputs to publicly meaningful ecosystem at-
tributes established, the next step was to quantify all of these relations with conditional probabilities. To do this, we adopted the approach of Pearl (2000) in which the conditional distribution of a variable $X$ is derived using a functional relationship of the form:
$X=f(\boldsymbol{p}, \theta, \varepsilon)$
where $\boldsymbol{p}$ is the set of immediate causes (or parents) of $X, \theta$ is a vector of parameters of the function relating $\boldsymbol{p}$ and $X$, and $\varepsilon$ is an error (or disturbance) term.

The interpretation of Eq. (1) is that causal relationships representing physical mechanisms can described by mathematical functions. Probabilities are then introduced by regarding the arguments of the function as random variables, to which probability distributions are assigned. The distribution of the parameter set $\theta$ represents knowledge uncertainty about the parameter values from a Bayesian perspective and might be derived through a combination of prior judgement and statistical inference (Bernardo and Smith, 1994). The distribution of the disturbance term $\varepsilon$ represents the effects of exogenous factors that, for reasons of either choice or ignorance, have not been explicitly included in the model (Pearl, 2000). A common assumption is that $\varepsilon$ is an independent and identically distributed Gaussian random variable with zero mean and specified variance, although this is not a requirement.

A functional characterisation of causal relationships in a Bayesian network leads to the same advantages of recursive decomposition as the strictly distributional forms. However, specifying functional equations among variables, rather than conditional distributions, is a task more naturally consistent with both the theory and routine practice of process-oriented environmental science. Still, in practice it may be difficult to identify the causal parents of an environmental variable, let alone to specify the functional form of the causal relationship and the joint distribution of its parameters. The disturbance term, $\varepsilon$, must also be characterised. Assuming Gaussian distributions may simplify matters, but unless the function $f$ is linear, the consequent distribution of $X$ will not be Gaussian. Sets of distributional forms, called conjugate families, exist that yield analytical solutions, but in most cases, model calculations will need to be done using a simulation procedure, such as Monte Carlo or Latin Hypercube.

Multiple methods for specifying the terms in Eq. (1) were used for the various eutrophication submodels,
depending on available knowledge and data. The development of these individual submodels has been described in previous papers, so each is summarised only briefly in the sections that follow. Our focus here is on the integration of these submodels into one cohesive network. For simplicity, each of the following sections is titled by the function relating each variable to its parents, disregarding the parameter and disturbance terms. However, these terms are discussed and shown explicitly as additional nodes in the more detailed graphical representations of the submodels (Fig. 2, insets).

### 5.1. Algal density $=f$ (water temperature, river flow, nitrogen concentration)

The relationship between algal density, as measured by chlorophyll a concentration, estuarine location, water temperature, and incoming Neuse River flow and total nitrogen concentration was developed using a regression model fit to approximately 5 years (mid-1994 through 1999) of biweekly monitoring data (Borsuk et al., 2003). Model results indicated a positive relationship between chlorophyll and nitrogen input concentration for all locations in the estuary, with the strongest relationship in the lower section, where nitrogen is most likely a limiting factor for algal growth (Qian et al., 2000). Increased river flow was found to generally exert a negative effect on chlorophyll concentration at upstream locations, possibly due to shortened residence times, lowered salinity, and increased turbidity. However, at mid and lower estuary locations, higher flow was associated with higher chlorophyll for flow values below an empirically estimated breakpoint but with lowered chlorophyll at flows above this value. This may be the result of increased nitrogen delivery from upstream sections at intermediate flow values and a flushing effect at higher flows. A positive relationship between chlorophyll concentration and water temperature was found for all estuarine sections. As measured by the $R^{2}$ value, the model was found to resolve $55 \%$ of the variation in log-transformed chlorophyll concentration-a level of accuracy comparable with more complex simulation models (Stow et al., 2003).

The regression model of algal density has a natural consistency with the general form of Eq. (1). Model parameters $\theta$ consist of the regression coefficients and can be described by a joint distribution
with mean vector and covariance matrix estimated by the regression procedure. Further, the root mean squared error (RMSE) of the regression model characterises the probabilistic error term, assumed to be Gaussian with mean zero and a standard deviation equal to the RMSE. Because the model is linear and Gaussian, the parameter distribution derived from the classical regression procedure is equivalent to the posterior parameter distribution that would result from a Bayesian analysis with non-informative priors (Lee, 1997).

Although algal density, itself, may be an important policy variable, of particular concern is the frequency with which chlorophyll a levels exceed the state water quality standard of $40 \mu \mathrm{~g} / \mathrm{l}$. Therefore, a variable representing this exceedance frequency is shown explicitly in the subnetwork (Fig. 2a) and its distribution can be derived from the distribution of chlorophyll values as described by Borsuk et al. (2002b).

### 5.2. Pfiesteria abundance $=f$ (algal density)

The factors potentially controlling the presence of Pfiesteria cells in the water column were investigated by Pinckney et al. (2000) using a set of mesocosm experiments. These experiments were designed to test the response of Pfiesteria zoospores to a range of environmental conditions and potential prey species. Results showed that the density of Pfiesteria-like cells was positively correlated with phytoplankton productivity and total phytoplankton biomass (as measured by chlorophyll a). These values were higher for mesocosms with nitrate additions, supporting the belief that the phytoplankton community is nitrogen limited. Apart from the correlation with algal biomass and productivity, Pfiesteria-like cells showed no additional significant response to nutrient, sediment, or mixing treatments in any of the experiments. Nor were Pfiesteria-like cells significantly correlated with diatom biomass. These results suggest that Pfiesteria-like zoospores are not separately stimulated by high nutrient concentrations, water turbulence, or the presence of benthic cysts, but, rather, track the abundance of their prey resources. Fensin (1998) also found a positive correlation between Pfiesteria-like zoospores and phytoplankton biomass (as chlorophyll a) in field samples collected from the Neuse estuary during 1994 and 1995.

We used the data of Pinckney et al. to develop a submodel relating algal density and Pfiesteria-like zoospores (Borsuk, 2001). Data collected by Fensin were not available for our analysis. Our results showed that Pfiesteria-like cell counts only reach levels of concern during the summer season. Therefore, the probabilistic relationship between algal density and Pfiesteria was quantified using data collected in the summer only. This relationship was found to be approximately linear after a log-transformation of both variables, so parameters were estimated using ordinary least-squares regression. The $R^{2}$ value of the model indicated that algal density resolves approximately $83 \%$ of the variability in transformed summertime Pfiesteria-like cell counts.

In expressing concern over Pfiesteria abundance, stakeholders were probably particularly concerned about densities that are potentially harmful. A level of 250 cells $/ \mathrm{ml}$ of toxic zoospores has been cited as a concentration sufficiently high to be lethal to fish (Burkholder et al., 1995). Therefore, the frequency of daily cell densities above 250 cells $/ \mathrm{ml}$ in the summer season was included as a separate variable in the network. Because the cell counts recorded by Pinckney et al. include all Pfiesteria-like zoospores, both toxic and non-toxic, the results of our model can be considered an upper estimate of toxic forms.

The Pfiesteria submodel can be represented as a small Bayesian network with parameters shown explicitly as marginal nodes (Fig. 2b). Again, we take the parameter uncertainty to be described by the Bayesian posterior distribution under non-informative priors, which, because of the linear model construction in this case, is multivariate normal with mean vector and covariance matrix estimated by the regression results. The disturbance term is assumed to be additive Gaussian after the log-transformations, with mean zero and standard deviation equal to the RMSE of the regression.

### 5.3. Carbon production $=f($ algal density $)$

To predict primary productivity from algal density, we used a generalised version of the model proposed by Cole and Cloern (1987) and subsequently modified for the Neuse by Mallin et al. (1991) and, later, by Boyer et al. (1993). The model, which expresses daily algal carbon productivity as a function of biomass,
photic depth, surface irradiance, and water temperature was fit to approximately 5 years (mid-1994 through 1999) of biweekly monitoring data at 11 mid-channel sampling locations within the Neuse River estuary (Borsuk et al., 2003). Photic depth and surface irradiance were found to not be significant terms in the model, perhaps because of the variable irradiance method employed in the determination of productivity (Mallin and Paerl, 1992). Consistent with the results of Boyer et al. (1993), the model relationship was found to be significantly different for the oligohaline zone than for the mesohaline zone. Overall the model resolved $73 \%$ of the variability in log-transformed productivity, based on the $R^{2}$ value.

The Bayesian network for productivity is similar to that for Pfiesteria with an added dependence on water temperature (Fig. 2c). Again, because of the linear model construction, the parameter uncertainty can be described by a multivariate normal distribution with mean vector and covariance matrix estimated by the regression results.

### 5.4. Sediment oxygen demand $=$ f(algal carbon production)

While abundant water quality monitoring data exist for the Neuse, the historical values of algal carbon production do not span the range that may be expected under a significant anthropogenic change in nutrient inputs. Therefore, we relied on cross-system data from 34 estuaries and coastal zones to parameterise a simple, mechanistic model relating carbon production and sediment oxygen demand, including the effects of water column decay and sediment burial (Borsuk et al., 2001b). To do this, we employed a hierarchical approach which assumes partial, but not complete, commonality in parameter values across different estuarine systems. Both global and system-specific parameters were estimated using Bayes Theorem with non-informative priors.

Using the parameters estimated for the Neuse estuary, annual average sediment oxygen demand can be expressed as a probabilistic function of annual average carbon production and water depth (Fig. 2d). Average water depth in the middle portion of the Neuse estuary is 2.53 m (Boyer et al., 1993) and annual average algal production can be calculated from the daily predictions of the productivity model described above,
after the appropriate unit conversions and assuming constant, homogeneous photosynthetic rates throughout the water column (consistent with the intent of the variable light measurement method employed) for 9 h per day (Paerl et al., 1998). This annual aggregation eliminates much of the uncertainty associated with the daily predictions and is more consistent with the uses suggested for the model by Boyer et al. (1993). Uncertainty in parameter values and the disturbance term are described by the Bayesian posterior distributions estimated by the hierarchical model (Borsuk et al., 2001b).

### 5.5. Bottom water oxygen concentration $=f$ (sediment oxygen demand)

A process-based model of oxygen depletion was specified that is consistent with established theory yet is simple enough to be empirically parameterised from available monitoring data (Borsuk et al., 2001c). The model represents the processes of microbial oxygen consumption and physical reoxygenation, including the effects of temperature and vertical stratification. Non-linear regression allowed for the direct estimation of rate constants from field data. The resulting model describes $79 \%$ of the variation in daily dissolved oxygen concentration and can be used to probabilistically predict the frequency of bottom water hypoxia, conditional on the annual average rate of benthic oxygen demand predicted by the model described in the previous section (Fig. 2e). Parameter uncertainty is similarly described by a multivariate distribution estimated from the regression procedure, and the disturbance term is assumed to be additive Gaussian with mean zero and standard deviation equal to the RMSE of the regression.

### 5.6. Shellfish survival $=f$ (bottom water oxygen concentration)

To relate oxygen status to shellfish abundance in the Neuse River estuary, we developed a survival model for the clam species Macoma balthica (Borsuk et al., 2002a). Survival modelling characterises the probability of death as it relates to the value of a stressor and exposure time. The survival rate of M. balthica was chosen as an indicator for shellfish abundance because M. balthica plays a critical role in the Neuse ecosystem. This later-succession bivalve is the major com-
ponent of benthic biomass in the estuary as well as a valuable food resource for demersal fish species, such as spot, croaker, and flounder. Blue crabs also prey upon this species because of its thin shell (Skilleter and Peterson, 1994).

Field studies have shown that the late-summer pattern of abundance of M. balthica in the Neuse closely matches the pattern of extended exposure to summertime hypoxia (Powers et al., submitted for publication). However, experimental studies have not yet been performed to directly address the sensitivity of this species to low oxygen conditions. Therefore, this submodel relied upon the expert judgement of two marine biologists (S.P. Powers and C.H. Peterson, Institute of Marine Sciences, Morehead City, NC) to provide the data used in model building. Well-developed methods exist for eliciting expert judgements (Morgan and Henrion, 1990; Meyer and Booker, 1991), and the marine science literature and the experts' own experience form a solid foundation for accurate assessment. The elicitation method that we used was based on a series of questions to establish points on the cumulative distribution function of times-to-death for multiple dissolved oxygen concentrations. Model parameters were then estimated from the assessed data using Bayes' Theorem. The resulting model probabilistically relates survival of M. balthica to time of exposure (duration of stratification) and dissolved oxygen concentration, as required for the network model (Fig. 2f).

### 5.7. Fish population health $=f$ (bottom water oxygen concentration)

One approach to predicting the population consequences of sublethal oxygen effects has been to develop individual-based models (Huston et al., 1988) linking fish to all the processes and subprocesses associated with the effects (Breitburg et al., 1999). However, information of sufficient detail to parameterise such a model does not exist for the Neuse estuary. Therefore, we relied upon the elicited judgement of two experienced estuarine fisheries researchers (L.A. Eby and L.B. Crowder, Duke University Marine Laboratory, Beaufort, NC) to characterise the relationship between fish population health and the annual extent of bottom water hypoxia (Borsuk, 2003). Many different definitions of population health are possible. Therefore, we asked the researchers to develop a def-
inition that was consistent with their knowledge and experience. They chose to use a categorical variable, with levels defined as,

Excellent High average growth rates ( $>0.6 \mathrm{~mm}$ per day); low incidence of visible disease ( $<1 \%$ ) on all fish but menhaden;
Good Medium average growth rates ( $\leq 0.6$ and $\geq 0.2 \mathrm{~mm}$ per day); low incidence of visible disease ( $<1 \%$ ) on all fish but menhaden;
Poor Poor average growth rates ( $<0.2 \mathrm{~mm}$ per day); medium/high incidence of visible disease ( $\geq 1 \%$ ) on all fish but menhaden;
where growth rate is measured in the field as described by Eby (2001). Atlantic menhaden were specifically excluded from measures of the incidence of visible disease because of their high susceptibility to infections and parasites and the seasonal nature of their disease patterns irrespective of oxygen conditions (Goldman, 2000).

With the health categories defined, questions were next asked regarding the probability of population health being in each of the categories, given a particular temporal extent of low oxygen. Since earlier studies have revealed that low oxygen is only a concern at high water temperatures (Borsuk et al., 2001c), we focused attention on the summer season. A typical question was

Given a summer in which bottom water oxygen concentration (at depth greater than 1.5 m ) in the mid-channel of the Neuse estuary averages less than $2.0 \mathrm{mg} / \mathrm{l}$ for 10 out of 92 days in July, August, and September, what is the probability that fish population health at the end of the summer can be characterised as "Excellent"? "Good"? "Poor"? (Another way to think about this would be: if you were to observe 100 such years, in how many would fish health be characterised as Excellent, Good, and Poor?)

This question was repeated for multiple oxygen concentration values and multiple numbers of days. The scientists' assessments were based on the results of their monthly fish trawling and water quality sampling program in the Neuse estuary, as well as a set of in situ caging experiments (Eby, 2001). Such experience-based, probabilistic judgements represent
the estimated net result of a number of interacting processes and sources of uncertainty.

Results of the assessments (Borsuk, 2003) indicated that a bottom water oxygen concentration of $2.0 \mathrm{mg} / \mathrm{l}$ serves as an effective tolerance breakpoint for fish, with the probabilities of the various levels of fish health depending primarily on the number of days with concentrations less than $2.0 \mathrm{mg} / \mathrm{l}$. For convenience, we refer to this oxygen condition as "hypoxia". According to the scientists' assessments, the health of the fish population declines non-linearly with increasing temporal extent of hypoxia. However, a number of factors in addition to oxygen were also believed to affect fish health. Because these other factors were not explicitly included in the network, they are manifest as disturbance terms, resulting in the attribution of some likelihood to more than one fish health category for each assessment.

To generalise the fish health category estimates to numbers of hypoxic days intermediate to the values used in the assessments, a cumulative logit regression model was constructed (Borsuk, 2003). This model is an extension of the familiar logistic regression model for binary responses, to allow for responses with multiple ordered categories. This model was fit to the assessment data, using an equivalent sample size estimation to express assessment uncertainty. Under this conceptualisation, all uncertainty is included in the parameter distributions and a separate disturbance term is not included (Fig. 2g).

### 5.8. Fish kills $=f(f i s h ~ p o p u l a t i o n ~ h e a l t h, ~ b o t t o m ~$ water oxygen concentration)

Large fish kills in the Neuse estuary are believed to be caused by a combination of low oxygen bottom water and a unique set of wind conditions (Paerl et al., 1999). In this scenario, wind blowing across the estuary pushes surface water toward the downwind shore. A compensating flow of bottom water occurs in the opposite direction, causing upwelling along the upwind shore. If the upwelled bottom water is depleted in oxygen, there is the potential for fish to be trapped without an escape route. Of course, a fish kill requires the presence of fish in the area of the upwelling, concurrent with the strong cross-channel winds and the presence of oxygen depleted bottom water. Even with this combination, fish may be able to react and swim away from
the upwelling, making predictions of the exact timing of fish kills impossible. The interacting effects of unpredictable natural events and anthropogenic changes in water quality is a common source of difficulty in developing predictive models for fisheries management (Rose, 2000) and suggests a probabilistic approach.

The probabilities of fish kills of varying magnitudes, conditioned on a given state of fish population health, the occurrence of a strong cross channel wind, and varying bottom water oxygen concentrations, were elicited from the same estuarine fisheries scientists questioned for the fish health model (Borsuk, 2003). Asking for a probability conditioned on a number of circumstances allowed the scientists to focus on the likelihood of a fish kill only under certain given circumstances (upon the coincidence of a number of causative factors), rather than having to simultaneously consider the background frequency of cross-channel winds, low oxygen, or a particular state of fish health (all of which are being predicted separately in the network). A typical question was

Given a fish population in "poor" health, a day in which bottom water oxygen concentrations average $0.5 \mathrm{mg} / \mathrm{l}$ at mid-channel locations, and the strength and direction of winds are such that the bottom water is being brought to the surface along the windward shore, what is the probability of more than 100,000 fish being trapped and dying? (Another way to think about this would be: if this event were to happen 100 times, in how many instances would at least 100,000 fish be killed?)

This question was repeated for multiple oxygen concentration values and multiple numbers of fish. The scientists' assessments of these probabilities were based on their knowledge of fish movement in response to low oxygen from their monthly fish trawling program and their knowledge of sensitivity to low oxygen from their caging experiments.

Assessment results (Borsuk, 2003) showed that fish kills are expected to be relatively rare, even with all the conditions being right, with conditional probabilities exceeding $50 \%$ only for kills involving more than 1000 fish and a population in poor health. These probabilities drop substantially for kills involving more fish in better health, with an assessed probability of only about $1 \%$ for a kill involving 100,000 fish in good or excellent health, even at the lowest oxy-
gen concentrations. The scientists did not believe that there would be a difference in susceptibility to fish kill conditions between populations with good or excellent health status, but did believe that fish of poor health were somewhat more susceptible. Again, a bottom water oxygen concentration of $2.0 \mathrm{mg} / \mathrm{l}$ served as an effective breakpoint, with an equal assessed chance of a kill occurring at all concentrations below $2.0 \mathrm{mg} / \mathrm{l}$ and a negligible chance of a low oxygen-induced kill occurring at higher concentrations.

The assessed conditional probabilities of fish kills of varying magnitudes can be used directly in the network model. The finding that only days with an oxygen concentration less than $2 \mathrm{mg} / \mathrm{l}$ have the potential for a fish kill suggests the use of a "collector node" to represent the scenarios of concern (Abramson et al., 1996). A node labelled "Days with Trapping Conditions" was added to represent the days with the joint occurrence of strong cross-channel winds and hypoxic bottom water. The probability of such conditions is a joint probability, calculated as the product of the distributions describing these two nodes. The assessed fish kill probabilities are then conditioned on the occurrence of "trapping conditions" and fish population health status (Fig. 2h).

## 6. Integrated network

The full Bayesian network composed of the set of conditional probabilistic relationships described in the previous section was implemented in Analytica, a commercially available software program for evaluating graphical probability models (Lumina, 1997). Other, non-commercial software packages are also available. We chose Analytica because it allows for the use of continuous or discrete variables related by any functional expression. Uncertainty can be represented by a wide variety of probability distributions and is propagated through the network using Monte Carlo or Latin Hypercube sampling. Analytica also allows models to be graphically depicted as nested modules so that complex networks can be represented at different levels of detail (Fig. 2).

Although many of the functional relationships among variables were developed to be applicable to multiple regions of the estuary, we chose the "middle" region (Fig. 1) as the focus of the integrated model.

This is historically the region with the greatest extent of hypoxia and the most frequent occurrence of fish kills. It is also the section from which data used to fit both the oxygen dynamics and Pfiesteria submodels were collected. Because the Neuse River TMDL is to be expressed in terms of a percent nitrogen reduction relative to a 1991-1995 baseline (NC DWQ, 2001b), daily data from those years served as the basis for the marginal variables: river flow, total nitrogen concentration, and water temperature at Fort Barnwell, the most downstream river monitoring station. These variables were represented in the network as a multivariate empirical distribution to maintain any underlying dependencies. Missing values for the marginal variables were estimated from flow models as described by Borsuk et al. (2003). The Latin Hypercube sampling method was used to draw 1000 samples of all model parameter and error distributions. The dependence structure implicit in the joint distribution of the parameters was factored into a series of conditional distributions (represented by arrows between parameter nodes in the subnetworks in Fig. 2) using the Cholesky decomposition of the parameter variance-covariance matrix (Golub and Van Loan, 1983).

To predict the effect of a substantial reduction in nitrogen inputs to the Neuse estuary, the marginal distribution of riverine nitrogen concentrations was multiplied by one half. All other functions and marginal nodes in the model were left unchanged, and new distributions were computed for the ecological variables of interest.

All results are presented as full probability distributions, rather than statistical summaries, to provide a more complete representation of predictive uncertainty. Consideration of full distributions often has important consequences for both theoretical understanding and practical decision-making (Ludwig, 1996).

## 7. Results

The marginal distributions of policy-relevant ecosystem attributes (Fig. 3, solid curves) show the relative likelihood of alternative values under the baseline scenario (no nitrogen reduction). The annual average chlorophyll a concentration in the middle region of the estuary is expected to be slightly above $20 \mu \mathrm{~g} / \mathrm{l}$


Fig. 3. Predictive probability distributions of policy-relevant ecosystem attributes. The baseline (no nitrogen reduction) scenario is shown as a solid curve, and the management scenario, corresponding to a $50 \%$ reduction in total nitrogen inputs, is shown as a dashed curve or diagonally striped bar.
( $90 \%$ credible interval (CI): $18.3-26.5 \mu \mathrm{~g} / \mathrm{l}$ ), and the state chlorophyll standard of $40 \mu \mathrm{~g} / \mathrm{l}$ will most likely be exceeded on more than $10 \%$ of the days ( $90 \% \mathrm{CI}$ : $9.8-18.8 \%$ ). Pfiesteria-like cell densities at levels of concern are only expected to occur between 6 and 15
days ( $90 \% \mathrm{CI}$ ) during the summer season. The summer survival rate of Macoma clams is predicted to be low, with a mean value of $12 \%$ and a $90 \%$ CI of $1-38 \%$. For comparison, during the summer of 1997 , the first year of extensive benthic surveying, the Macoma clam


Fig. 4. Predictive probability distributions of intermediate diagnostic variables in the network. The baseline scenario is shown as a solid curve, and the management scenario is shown as a dashed curve.
community was estimated to be reduced to less than $20 \%$ of its spring population (Peterson et al., 2000).

Under the baseline scenario, the most likely state of fish population health is "good" with a probability of 0.55 , while "excellent" has a probability of 0.32 and "poor" of 0.13 . Fish kills of any size are predicted to be relatively infrequent events. Therefore, probabilities are expressed as the expected number of fish kills in a 10-year period. The model predicts between 6 and 21 kills ( $90 \% \mathrm{CI}$ ) in 10 years involving more than 1000 fish, between 1 and 4 involving more than 10,000 fish, and an average of between 0.2 and 0.8 involving 100,000 fish. For reference, there were 8,5 , and 2 documented fish kills of sizes $>1000,>10,000$, and $>100,000$ fish, respectively, during the 10 years 1989 through 1999 in the middle portion of the estuary. Additionally there were six kills in which the number of fish involved was not reported (NC DWQ, 2001a).

While not ecosystem attributes of direct concern to the public, the intermediate nodes representing algal carbon production and days of summertime hypoxia are useful diagnostic variables. Values for these variables are commonly estimated for the Neuse and other estuaries. The Bayesian network predicts that, under the baseline scenario, annual carbon production will be between approximately 356 and $476 \mathrm{gC} / \mathrm{m}^{2}$ per year ( $90 \%$ CI, Fig. 3). Measurements made during the years 1985-1988 resulted in estimates of $395,455,491$, and $493 \mathrm{gC} / \mathrm{m}^{2}$ per year, respectively (Boyer et al., 1993). Predictions of summertime hypoxia range from 10 to 34 days out of 90 (11-38\% frequency). For reference, 21 out of the 66 ( $31 \%$ ) weekly/biweekly oxygen measurements taken during the summer in the middle estuary from 1994 to 1999 had values less than $2 \mathrm{mg} / \mathrm{l}$. Additionally, a spatially distributed sampling
scheme conducting during the summers of 1997 and 1998 found an average of $25 \%$ of the middle portion of the estuary to have an oxygen concentration below $2 \mathrm{mg} / \mathrm{l}$ (Eby and Crowder, 2000).

Under the scenario of a $50 \%$ reduction in nitrogen inputs (Fig. 3, dashed curves), annual average chlorophyll a concentration is predicted to decrease approximately $20 \%$. However, this estimate is accompanied by an increase in predictive uncertainty, as indicated by a slightly wider distribution ( $90 \% \mathrm{CI}: 14.1-23.3 \mu \mathrm{~g} / \mathrm{l}$ ). The frequency of chlorophyll standard exceedances can be expected to decrease accordingly, with an average value slightly less than $10 \%$. The mean number of days with levels of concern for Pfiesteria decreases somewhat, to between 3 and 13 days. The distribution of Macoma survival rates shows a non-zero mode near $10 \%$ and has a mean value of $17 \%$ ( $90 \%$ CI: $3-46 \%$ ). Fish health is only expected to increase very slightly with probabilities of $0.12,0.53$, and 0.35 for Poor, Good, and Excellent, respectively. Fish kill probabilities of all sizes decrease, but not substantially.

The reason for the relatively minor response of most ecological attributes can be discovered by looking at the trends in carbon production and days of summertime hypoxia (Fig. 4). While carbon production is expected to decrease by approximately $15 \%$ in response to reduced algal stimulation, this effect is dampened further down the causal chain, so that the reduction in the number of days of resulting hypoxia is only $11 \%$.

## 8. Discussion

Our purpose in developing the Bayesian network was not to create a model that more realistically rep-
resents the actual Neuse River ecosystem, but rather to develop a model that more realistically represents our knowledge about that system. In particular, we wanted to represent current scientific knowledge about the linkage between nitrogen inputs and the ecosystem attributes that are of interest to the public and decision-makers. In this sense, the Bayesian network should not be seen as a suggested replacement for other models in current use, but rather as an integrator of all forms of knowledge, whether expressed as a process-based description, a data-based relationship, or a quantification of expert judgement. To the extent that an existing simulation model appropriately represents our level of understanding about the functioning of the system, that model can be used as the basis for a set of relationships in a Bayesian network. However, because knowledge in all forms is inherently uncertain, and Bayesian networks represent that uncertainty using conditional probability distributions, the predictive accuracy of the process description must be fully quantified. While progress has been made recently in characterising the uncertainty of complex models (Poole and Raftery, 2000; Kennedy and O'Hagan, 2001; Reichert et al., 2002), most commonly used aquatic ecosystem models have not undergone a rigorous uncertainty analysis (Reckhow, 1994c). Therefore, when we used process models as an expression of knowledge in the Bayesian network, they were applied at a considerably more aggregate scale.
In developing aggregate functional relationships among variables, it did not seem sensible to use tabulated coefficient values, which are generally measured at a fine spatial and temporal scale. Therefore, expressions describing pattern-generating mechanisms, whether of smaller or greater scale, were quantified using historical data or other observational evidence. In this way, the estimated model parameter values are directly applicable to the scale of the data used in their derivation (Young, 1998). For example, estuarine oxygen dynamics were described by a mathematical expression characterising current knowledge about the primary controlling mechanisms. This equation related bottom water oxygen concentration to the rate of sediment oxygen demand (itself a function of temperature) and duration of stratification. Such a model successfully reproduced the patterns observed in the data, while still being identifiable from existing monitoring data. Undoubtedly, finer scale processes
exist that influence oxygen concentration at any given time and place, but these processes are not relevant for reproducing the observed patterns and for linking these patterns to management actions. Moreover, the effects of these processes were not neglected but were included in the probabilistic disturbance term.

Because there is no single scale at which scientists have studied the Neuse system, there is no single scale at which all model relationships could be developed. Therefore, a characteristic of the Bayesian network that we exploited is its ability to integrate submodels of disparate scales. For example, while sufficient data existed to characterise a model relating the distribution of daily bottom water oxygen concentrations to sediment oxygen demand, temperature, and duration of stratification, there was not enough site-specific information from the Neuse to predict future changes in sediment oxygen demand in response to reductions in carbon loading. Therefore, a model was developed using cross-system data from a number of estuaries to predict annual average oxygen demand from annual average carbon loading. This annual average demand was then assumed to represent a steady state mean, the short-term fluctuations around which could be predicted from water temperature changes using the oxygen dynamics model. Expected changes in this mean rate of oxygen demand in response to carbon load reductions were then predicted from the cross-system model. This technique of expressing rate equations involving fast variables as functions of slower variables is referred to as "variable speed splitting" (Walters and Korman, 1999) and may be a useful general method for cross-scale modelling (Auger et al., 2000).

Choosing the various scales of representation in a ecological model should be a dynamic and iterative process (Jorgensen, 1995). This is because while the intent is to choose scales that yield predictable patterns of the natural system, it is more often the case that scales are imposed by observational constraints (Levin, 1992) which may evolve over time. Further, the scale of prediction should correspond to the needs of decision-makers, which may also change with time as they gain understanding of the problem. Such updating of the model is facilitated by the conditional independencies identified in the causal network representation. These independencies, implied by the lack of a connecting arrow between two nodes, allow for the modularization of the full model into independent
causal structures. When the nature of one of these sub-structures is revised, because of either a change in knowledge or a change in environmental conditions, the other structures remain unaltered (Pearl, 2000).

For some variables in our network, suitable "hard data" did not exist for quantifying functional relationships. In these cases, we relied on the formally elicited judgement of a discipline-specific scientist. While the use of assessed quantities for model building may appear to be a subjective process, it must be kept in mind that professional judgement is already implicit in all scientific modelling (Korfmacher, 1998). Whether it is involved in deciding what processes to consider, what mathematical form appropriately characterises those processes, what experimental results are relevant, or how to extrapolate experimental results to the natural system, judgement is used in every step of the modelling process. Therefore, when directly relevant data are limited, and yet policy needs require model construction, the use of carefully elicited judgement is preferable to a situation in which decision-makers are left in the difficult position of having to extend conventional model results on their own.

The Bayesian network approach to ecological modelling is not without its shortcomings. Perhaps the most profound is the inability to explicitly represent system feedbacks. Bayesian networks are defined as being directed acyclic graphs, so relationships must represent either one-way causal influences at a particular instant in time or net influences on eventual steady-state conditions. An alternative is to construct a dynamic Bayesian network (Haas et al., 1994) in which a down-arrow variable in one time step can influence an up-arrow variable in the next. Such a model requires significantly more information to quantify the time dynamics. However, insufficiently representing dynamic aspects of system behaviour can lead to unexpected consequences that are not adequately captured by the probabilistic predictions (Jorgensen, 1999; Jorgensen et al., 2002).

Indeed, Bayesian networks do not improve our ability to represent structural uncertainty in ecological models. As with other modelling approaches, network models are subject to uncertainty in the causal structure itself, in addition to the parameter uncertainty and natural variation that are captured by probabil-
ity distributions (Draper, 1995). This unaccounted for source implies that the real uncertainty in model predictions will be greater than that suggested by the model (Reichert and Omlin, 1997). Options that have been suggested for addressing uncertainty in model structure include Bayesian model averaging, learning from additional data (Chatfield, 1995), and, of course, rigorous model testing.

When possible, we have compared the predictions of our model with data, with favourable results. This comparison does not provide a true validation, as much of the model was based upon the same research that generated the data. However, in most cases, the data represent the net result of multiple processes represented by various submodels, so a close match between predictions and observations is not guaranteed. Of course, before placing much faith in the model, it should be tested against new data, preferably representing a change in conditions of the same magnitude as the management actions being considered.

Most goodness-of-fit statistics currently used for model testing pertain to deterministic, or singlevalued, predictions. When predictions are expressed probabilistically, as they are in the Bayesian network, different methods for evaluation are required. Fortunately, methods have been developed for assessing probabilistic weather predictions, and these are equally applicable to the ecological modelling domain. Most serve to characterise different attributes of the joint distribution of predictions and observations (Murphy and Winkler, 1987). Various factorisations of this joint distribution provide different measures of prediction quality. For example, one measure addresses the question, "How often did different observations occur when a particular probabilistic prediction was given?" thus indicating the probabilistic accuracy of predictions. Another calculates how often different values of the probabilistic prediction were used, in order to assess the usefulness of the predictions relative to a naïve forecast, such as one that simply uses the historical base rate of occurrence (Winkler and Poses, 1993). As data are collected under the presumably changed conditions of the Neuse estuary in the future, these methods can be used to evaluate the success of the predictions generated by the Bayesian network model. Such an ongoing evaluation process can serve as the basis for model revisions.

## 9. Conclusions

The Bayesian network approach does not solve all problems associated with predictive ecological modelling. Nevertheless, it encourages the modeller to take what we believe to be a useful perspective. That is, the realisation that ecosystem data are often abundant, but not at the spatial and temporal scale required by highly detailed simulation models. Scientific understanding of mechanism is advanced, but only to the point of being able to identify the existence of aggregate causal relationships, not to quantify all of the small-scale dynamics. Physical, chemical, and biological processes are complex and stochastic, making representation by probability distributions appropriate. Bayesian networks provide a methodology for combining expert knowledge of causal structure and aggregate ecosystem response with condensed models that are identifiable from available data. The probabilistic predictions give stakeholders and decision-makers a realistic appraisal of the chances of achieving desired outcomes-information critical to the decision process.

There are currently multiple estuarine response models being used to inform the near-term selection of a TMDL for the Neuse River estuary (Stow et al., 2003). However, the Bayesian network is the first to quantitatively predict changes in policy-relevant ecosystem attributes. Our results show that ecological improvement is likely to result from nitrogen reductions, but the predictive uncertainty arising from natural variation and lack of knowledge is high. The magnitude of the combined sources of uncertainty depends on the nature of the variable being predicted. We found that, in general, the less observable, less frequent, and further down the causal chain a variable was, the greater the predictive uncertainty. However, this type of variable is precisely the one of most interest to stakeholders (e.g. fish kills, shellfish survival). This observation suggests that a compromise is necessary between achieving policy relevance and predictive precision. Selecting the appropriate degree of compromise is a task that can best be performed by decision-makers.

Another task arguably better addressed by public officials than by scientists is the choice of target values for the predicted ecosystem attributes. The selection of specific targets determines the degree of pollution
reduction required, and thus the extent of management costs incurred. Scientific predictions only provide estimates of ecosystem response, which then require societal value judgements concerning costs and benefits in order to reach a rational decision. This fact was recognised only recently in the Neuse TMDL process by public officials and stakeholders who had the initial expectation that somehow scientists would resolve all policy decisions by building accurate models. However, a combination of scientific models and social values is required, and the literature on environmental standard setting (Barnett and O'Hagan, 1997), multi-attribute decision theory (Keeney and Raiffa, 1976) and adaptive ecosystem management (Walters, 1986) can provide helpful guidance for this process.

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