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Development of an Ecosystem Model of a Turbid Estuary¹

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This paper describes the development of those aspects of the whole ecosystem model, GEMBASE, which are most influenced by water turbidity. Mean values of surface turbidity, determined for a coarse grid of the Bristol Channel, were found to be highly correlated with tidal range and \log_{10} 14-d mean river flow. Parameters derived from multiple regressions of these variables were used to obtain realistic simulations of surface turbidity for an 8-yr period from 1972 to 1980; simulated extinction depths derived from turbidity simulations were also realistic. Results of GEMBASE are discussed for phytoplankton and suspension feeding benthos, the two components of the ecosystem most affected by suspended solids concentrations. Simulations of phytoplankton biomass were obtained which compared well with field data. However, results for suspension feeding benthos were less good and showed slight increases in biomass from year to year which have not been found in the Bristol Channel; possible reasons for this are discussed.

Key words: Bristol Channel, ecosystem modeling, turbidity, extinction depth, phytoplankton, suspension feeding macrofauna

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Les aspects du modèle d'un écosystème entier, GEMBASE, les plus influencés par la turbidité de l'eau sont décrits dans le présent article. On a constaté que les valeurs moyennes de la turbidité de surface, déterminées dans un quadrillage grossier du chenal de Bristol, sont en étroite corrélation avec l'amplitude de la marée et le \log_{10} du débit moyen, par période de 14 jours, de la rivière. Nous avons utilisé des paramètres dérivés des régressions multiples de ces variables afin d'obtenir des simulations réalistes de la turbidité de surface pendant une période de 8 ans, de 1972 à 1980; les profondeurs d'extinction simulées découlant des simulations de turbidité sont également réalistes. Nous examinons les résultats de GEMBASE en relation avec le phytoplancton et le benthos se nourrissant de matière en suspension, les deux composantes de l'écosystème les plus influencées par les concentrations de solides en suspension. Nous obtenons des simulations de biomasse phytoplanctonique qui s'accordent bien avec les données recueillies sur le terrain. Cependant, les résultats relatifs au benthos se nourrissant de matière en suspension sont moins bons et montrent de faibles augmentations de biomasse d'une année à l'autre, qui n'avaient pas été observées dans le chenal de Bristol; nous analysons les raisons possibles de ce phénomène.

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ECOSYSTEM models of estuaries are driven by a variety of environmental forcing functions; some physical processes which determine biological activity are predictable but others have a high degree of randomness. In attempting to model the previous behavior of an ecosystem, environmental data can be included either in digital form, derived from field data, or as

a submodel which simulates the environmental variable concerned. Some forcing functions, such as river runoff or solar radiation are so variable that their impact on an ecosystem can only be modeled by including historic data. However, other forcing functions are more predictable: Radford and Joint (1980) described how the seasonal cycle of water temperature in the Bristol Channel could be adequately described by a sinusoidal curve, fitted to field data obtained over 4 years; this was used as a forcing function in the estuarine ecosystem model, GEMBASE (General Ecosystem Model of the Bristol Channel and Severn Estuary).

Variables dominated by random fluctuations such as solar radiation and river flow are included in GEMBASE as tables

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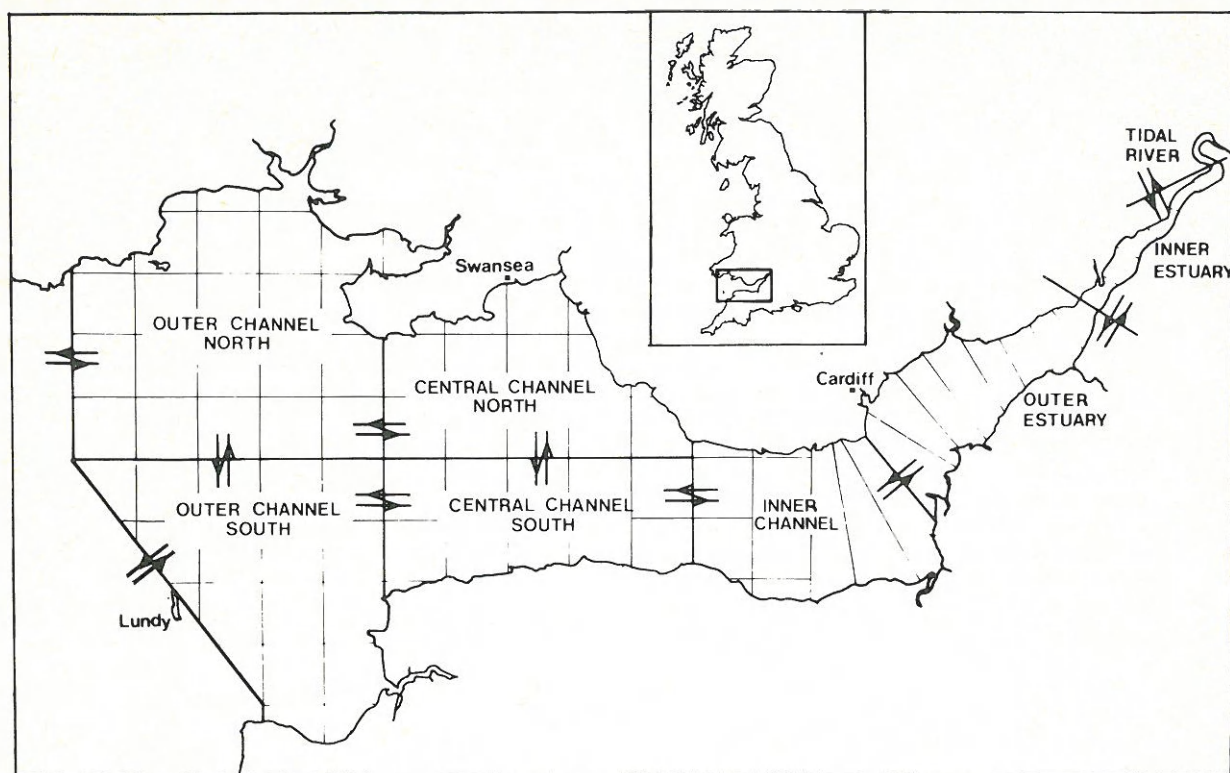


FIG. 1. Bristol Channel showing the seven regions modeled in GEMBASE. The small 5 nautical mile squares are used in calculating mean values of each variable for the large regions.

of digital data derived from field observations (Radford 1979). However, large tables of data tend to make working with a computer simulation model cumbersome and sub-models, if they are not so complicated that they use a lot of computer core and computing time, are easier to use. Sub-models, once verified, also have the advantage that it is no longer necessary to collect field data for that environmental variable at the same intensity of sampling.

Turbidity is one environmental variable which has been successfully included in GEMBASE as a submodel. The Bristol Channel has considerable quantities of particulate matter in suspension in certain regions of the estuary. Turbidity is a crucial forcing function because it affects light penetration into the water column, and hence photosynthesis, as well as affecting the feeding responses of filter feeding animals. The purpose of this paper is to describe the methods which have been used to model turbidity changes in the estuary, within the context of a whole ecosystem model, and to report the results of the model for phytoplankton and suspension feeding benthos.

Methods and Data Treatment

The Bristol Channel (Fig. 1) is one of the major estuaries of the United Kingdom with seven large river systems draining into the upper 100 km. It is a highly dynamic estuary with a tidal range of up to 14 m in the Outer Estuary and a tidal

excursion of up to 25 km. Mean depth ranges from 41 m at the seaward end to 9.5 m in the Outer Estuary.

As part of a multidisciplinary study of the Bristol Channel, the Institute for Marine Environmental Research has been sampling in the estuary since 1971, collecting data on zoobenthos (Warwick and Davies 1977; Warwick et al. 1978), zooplankton (Collins and Williams 1981), phytoplankton and bacterial biomass and production (Joint and Pomroy 1981, 1982) and on physical variables and hydrodynamics (Uncles 1979; Uncles and Jordan 1980; Uncles and Radford 1980). These data form the base initially used to formulate GEMBASE and subsequently to validate and verify the model.

Turbidity was measured on each cruise with a Partech Suspended Solids Monitor which was calibrated by comparison with gravimetric determinations of suspended solids concentrations. From 1972 until 1975 samples were taken on a grid of stations 5 nautical miles apart; after 1977, turbidity measurements were made continuously on water sampled with a submersible pump as the ship steamed round the sampling grid. Before 1975, estimates of extinction depth were also made with a Secchi disc.

Contour charts were prepared for every variable measured on each cruise; the position of each sampling station was corrected to the computed locations at high and low water and the data were contoured using the Surface Approximations and Contour Mapping System (SACM) developed by Appli-

cations Consultants Inc., Texas to give separate charts for the positions the stations would occupy at high water and low water. For the purposes of ecosystem modeling, the Bristol Channel was divided into the coarse grid of seven regions (Radford 1979) shown in Fig. 1 and the mean for each variable was computed for each region. Values for each square of 5 nautical miles (Fig. 1) were read from the contour charts for high and low water, and averaged. A mean for each of the seven large regions was determined from these small square means by weighting the data according to the volume of water in the 5 nautical mile squares. These average values for the large regions were used in GEMBASE development and validation (Radford and Joint 1980).

Results and Discussion

MODELING TURBIDITY

The concentrations of suspended solids vary considerably in the Bristol Channel from the highly turbid Inner Estuary to the Outer Channel which has low particulate loads typical of British coastal waters. In addition to the vertical distribution of suspended particles which is controlled by tidal resuspension, there is a distinct seasonal variation in surface turbidity in the Bristol Channel; Fig. 2 shows typical contour charts for turbidity of surface water in March and August. The very turbid regions show little variation with season but the turbidity of the Inner and Central Channel regions is significantly reduced in summer. It is this seasonal change in turbidity which was modelled in GEMBASE and no attempt was made to model turbidity changes due to the semidiurnal tide.

During model development, various attempts were made to find a simple expression which would successfully simulate seasonal changes in turbidity. An initial correlation of turbidity and daily values of river flow gave a reasonable approximation to observed turbidities. However, the simulated turbidity was highly variable with unreasonable daily fluctuations resulting from the changing river flow. These rapid oscillations were damped by relating turbidity to the logarithm of river runoff, averaged over the previous 14 d. The simulations were based on a regression of mean surface particulate concentration for each region, derived from 14 cruises in 1973 and 1974, and \log_{10} 14-d mean river flow ($r = 0.71$, $P \leq 0.01$). Although this expression gave reasonable seasonal simulations of turbidity, there were still unrealistic daily fluctuations and the simulation was particularly susceptible to short-term increases in river flow. It was also difficult to envisage how river flow could affect turbidity of the whole Bristol Channel, although it might be a crude indication of weather conditions in the region. Attempts were, therefore, made to relate turbidity to those other environmental variables which were intuitively thought more likely to control resuspension in the estuary, such as wind speed and tidal range (as indicators of wind and tidal stress).

Regressions were done between the mean values of turbidity for each of the seven regions and the following variables: (a) mean tidal range on mid-date of cruise, (b) mean tidal range over whole cruise period, (c) range of last Spring tide before cruise, (d) river flow, (e) \log_{10} 14-d mean river flow, (f) mean wind speed over cruise, (g) mean wind speed

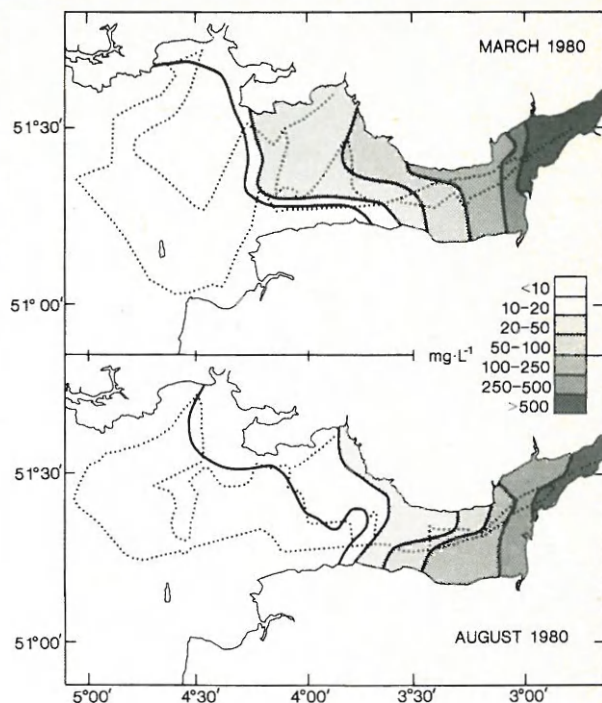


FIG. 2. Contour charts of surface turbidity in the Bristol Channel in March and August 1980: station positions were corrected to the position they would occupy at low water before contouring. The dotted line shows the tidally correct position of the sampling track.

for 7 and 14 d before cruise, (h) westerly component of wind speed for 7 and 14 d before cruise. Significant correlations were obtained between turbidity and \log_{10} 14-d mean river flow and tidal range of the Spring tide prior to data collection. Multiple regression of these two variables together against turbidity resulted in a significantly better correlation coefficient than was obtained against the individual variables; the correlation could not be significantly improved by including any measurement of wind as a third variable. The results of the multiple regressions for the seven regions of the Bristol Channel are given in Table 1; the F ratio is significant at $P \leq 0.05$ for the Inner Channel and South Outer Channel, at $P \leq 0.001$ for the South Central Channel and at $P \leq 0.01$ for the other four regions.

These regression equations form the basis of turbidity simulation in GEMBASE. The results of the simulation for 8 years are shown in Fig. 3 for two contrasting regions, the turbid Inner Channel and the least turbid region, the South Outer Channel. Data points prior to 1975 were used in the formulation of the model and were based on gravimetric determinations of particle load; the data after 1976 were Partech readings and, since these were not used in model formulation, they provide verification of the goodness-of-fit of the simulated and observed turbidities.

The problem of how to validate the output from a model is a very difficult one. Plait and Radach (1981) state that, for complex models that generate time series of many state variables, there is no objective criterion for goodness-of-fit and

TABLE 1. Multiple regression of tidal range of the Spring tide prior to data collection (1st variable) and \log_{10} 14-d mean river flow (2nd variable) against turbidity for seven regions of the Bristol Channel. The equation is

$$\text{Turbidity} = a + (b \times \text{tidal range}) + (c \times \log_{10} \text{river flow})$$

r is the correlation coefficient, F is the ratio of regression mean squared over residual mean squared, and P is the level of significance of the F -ratio.

Region	n	a (SE)	b (SE)	c (SE)	r	F	P
Inner Estuary	24	-565.61 ± 243.46	70.27 ± 19.42	1.16 ± 1.17	0.63	6.67	≤ 0.01
Outer Estuary	24	-763.54 ± 273.16	75.98 ± 19.10	55.51 ± 32.79	0.66	8.15	≤ 0.01
Inner Channel	14	-98.39 ± 56.50	9.90 ± 5.76	6.17 ± 8.73	0.68	4.74	≤ 0.05
North Central Channel	14	-44.81 ± 18.70	3.37 ± 1.91	5.98 ± 2.89	0.82	11.51	≤ 0.01
South Central Channel	14	-38.14 ± 10.54	3.44 ± 1.08	2.71 ± 1.63	0.88	18.76	≤ 0.001
North Outer Channel	13	-27.57 ± 14.63	1.79 ± 1.51	4.02 ± 2.10	0.79	8.14	≤ 0.01
South Outer Channel	12	-13.08 ± 10.07	0.97 ± 1.05	2.01 ± 1.44	0.72	4.75	≤ 0.05

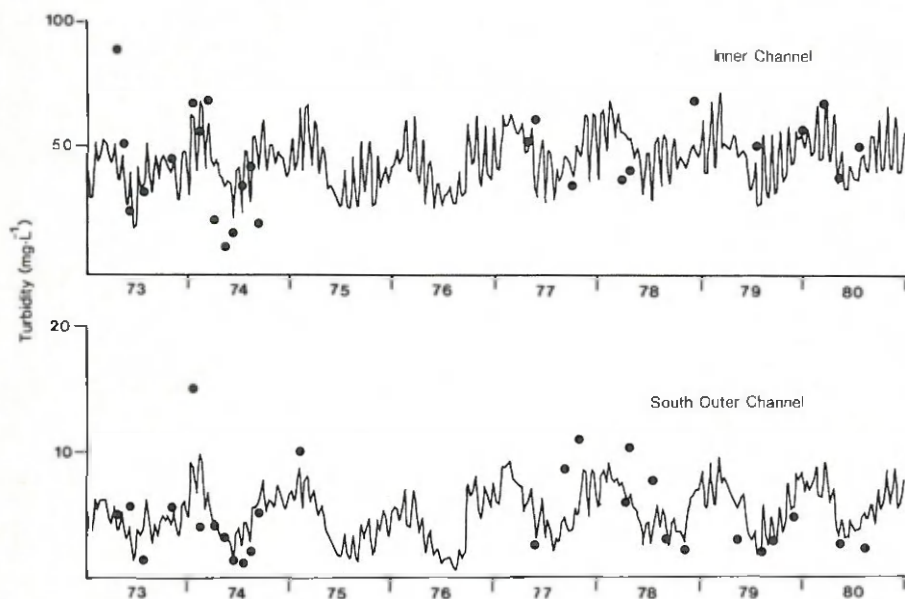


FIG. 3. Simulated values for surface turbidity from 1973 until 1980 for the Inner Channel and South Outer Channel. The data points are mean values of turbidity calculated for each region from field observations.

that most model fits are judged subjectively. Statistical validation of the output from GEMBASE has not been attempted and the results shown on this paper are based on subjective assessments of goodness-of-fit.

Weekly variations in simulated turbidity, which were often considerable, are the result of the spring-neap tidal cycle. The field data also indicate large changes in turbidity over short time periods but our sampling program was too infrequent to determine whether or not the fine detail of the simulation is realistic. It would be naïve to think that such a simple model could be used to simulate short-term changes in turbidity in a finer grid in the Bristol Channel; but, for the purposes of GEMBASE, with the assumed homogeneity over large regions, the results are acceptable. The complexity of many of the biological processes in an estuarine ecosystem are so great that a simulation model is much more likely to break down as a result of poor modeling of the biology than of a poor approximation of water turbidity.

MODELING EXTINCTION DEPTH

Estimates of extinction depth are needed to model the response of phytoplankton to light. A correlation was found between turbidity and Secchi disc depth for the 14 cruises in the Bristol Channel in 1973 and 1974 and formed the basis of simulation of extinction depth in GEMBASE. A regression of reciprocal Secchi disc depth against surface particulate load of the form $1/SD = 0.034 \text{ turbidity} + 0.134$ gave a correlation coefficient of 0.892 ($P \leq 0.001$); extinction depth was, therefore, modeled in GEMBASE by correlating with simulated daily values of turbidity. Figure 4 shows the agreement between simulated and observed Secchi disc depths for the Inner and South Outer Channels from 1973, plotted as \log_{10} Secchi disc depth. Unfortunately, too few Secchi disc measurements were made after 1974 for a meaningful test of the long-term simulation of extinction depth. However, in view of the close fit of simulated and observed turbidities for 1973 until 1980,

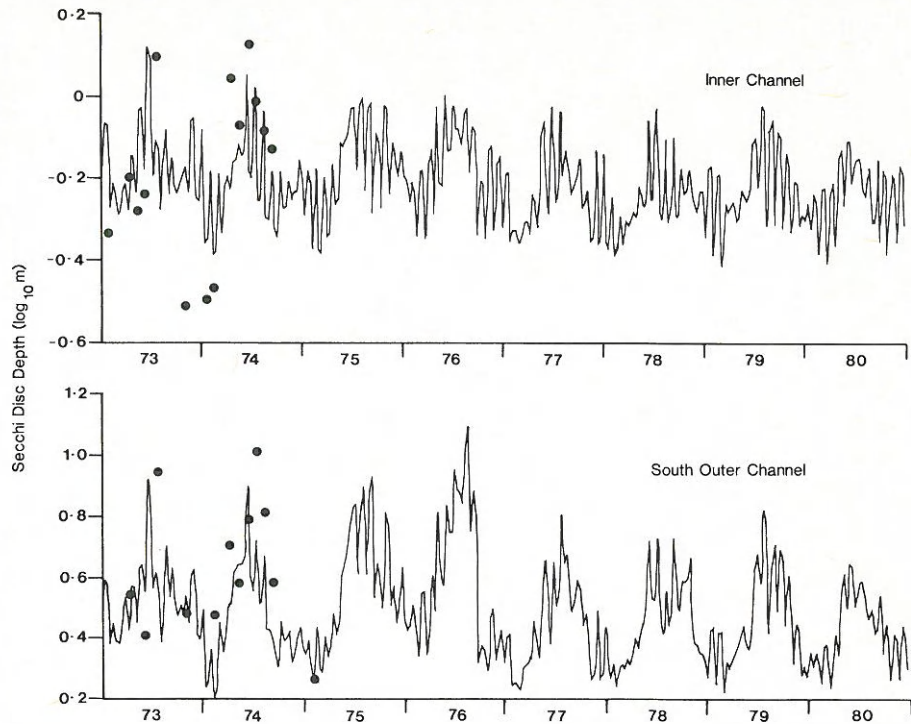


Fig. 4. \log_{10} Secchi disc depth simulated for 1973 until 1980 for the Inner Channel and South Outer Channel; the data points are mean values of Secchi disc calculated for each region from field data.

it seems reasonable to assume that Fig. 4 is a reasonable representation of mean extinction depth in each of the seven regions of the Bristol Channel. Daily values of extinction depth computed in GEMBASE are modified for self-shading by a term which responds to changing phytoplankton density (Kremer and Nixon 1975, 1978) and represents the sum of light attenuation by inorganic particles and phytoplankton cells.

MODELING PHYTOPLANKTON BIOMASS

To model the Bristol Channel in just seven regions, a large degree of spatial homogeneity in the distribution of plankton was assumed. Moreover, it was decided that too fine a temporal scale would also not be appropriate for GEMBASE and that it would not be feasible to model processes with a relaxation time of less than 1 d. With one exception, all ecological processes simulated in GEMBASE are assumed to occur at a constant rate for a time period of 1 d: this is justifiable in modeling processes such as filter feeding because the average food concentration (phytoplankton) is not likely to change dramatically over 24 h and a mean daily feeding rate is a close approximation to reality. However, a similar coarse approach to modeling photosynthesis could not be justified because photosynthesis is influenced more by the instantaneous light intensity than by the daily integrated value. Photosynthesis increases with increasing light intensity until a saturating light level, then the rate decreases due to photoinhibition. It was felt that it would be inappropriate to drive GEMBASE with an

idealized daily value for solar radiation (such as Kremer and Nixon (1978) used in their model of Narragansett Bay) because it would not be possible to adequately model the response of phytoplankton to natural fluctuations in light intensity. The GEMBASE primary production subroutine uses hourly values of solar radiation to model primary production and the hourly rates are summed to give a precise integral for daily primary production; Radford (1979) has described the procedure in detail.

Photosynthesis, integrated down the water column, was modeled using the equation of Steele (1962), assuming a constant value for extinction coefficient over each 24-h period. The estimates of primary production obtained by this model compare well with measurements made in the Bristol Channel (Radford and Joint 1980). All other processes involving primary producers, i.e. respiration, excretion of dissolved organic matter, mortality, grazing by zooplankton and zoobenthos and physical transfer from one region to another, were calculated on a daily basis.

Simulated phytoplankton biomass in five regions is shown in Fig. 5 and compared with mean values of observed biomass for each region; the data and simulations are plotted on a \log_{10} scale to allow better visual comparison of the agreement at both high and low biomass values. There is a tendency for simulated values in the Outer and Central Channels to be too low in winter and too high in summer, and the simulation for the Inner Channel does not agree well with observed data.

Although chlorophyll *a* concentrations in the Inner Channel are similar to those in the Central and Outer Channels, annual

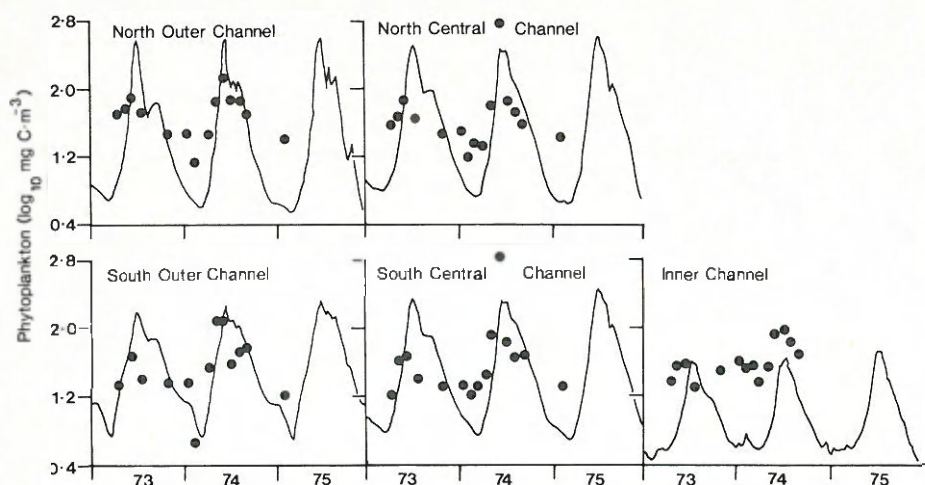


FIG. 5. Simulated and observed standing stock of phytoplankton in five regions of the Bristol Channel from 1973 until 1975 plotted as $\log_{10} \text{mg C} \cdot \text{m}^{-3}$.

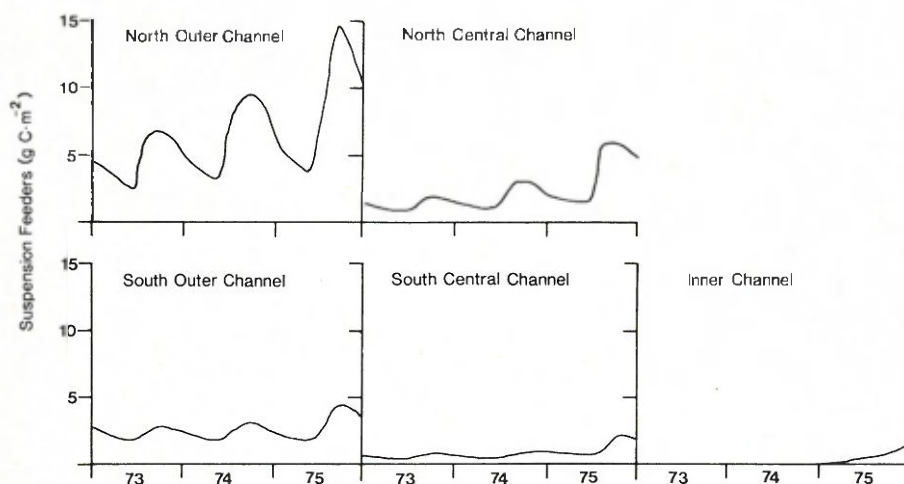


FIG. 6. Simulated biomass of suspension feeding benthos in five regions of the Bristol Channel from 1973 until 1975.

primary production in the Inner Channel is only 4% of that in the Outer Channel (Joint and Pomroy 1981). Radford (1981) has shown that the rate of primary production simulated in GEMBASE compares well with the estimates made by Joint and Pomroy (1981) using the ^{14}C technique. The low simulated biomass must result because a process other than photosynthesis is inadequately modeled by GEMBASE. In the Inner Channel, the impact of grazing is very small because of the low biomass of herbivores in the region (Collins and Williams 1981); therefore, the equations either for mortality, respiration or inter-region transfers are inadequate for the Inner Channel, although they result in realistic simulations for the less turbid regions. Transfers of material from one region to another are unlikely to be at fault because of the good simulation of salinity in GEMBASE (Uncles 1983). If either mortality or respiration of phytoplankton in winter in the Inner Channel is less than assumed then the simulated results would be closer to the observed high constant standing stock of

phytoplankton. However, very little research has been done on phytoplankton physiology in turbid environments. Smayda and Mitchell-Innes (1974) and Antia (1976) have reported that laboratory cultures of algae can retain viability in the dark for many months without forming resting stages. Under conditions of continuous darkness, similar to those experienced by phytoplankton in turbid waters, these authors reported a considerable reduction in respiration rate. However, no field data are available to confirm this observation with natural phytoplankton populations. The behavior of phytoplankton in the darkness of a turbid water column is one example of several where GEMBASE output has highlighted important lacunae in our understanding of estuarine ecology.

MODELING THE BIOMASS OF SUSPENSION FEEDING BENTHOS

Other components of the pelagic ecosystem have been modeled with similar success to phytoplankton; Radford and

Joint (1980) reported realistic results for the simulation of omnivorous and carnivorous zooplankton which compared well with field data. However, the benthic ecosystem, and in particular suspension feeding macrobenthos have proved more difficult to model.

Macrofauna are patchily distributed in the Bristol Channel; this was modeled in GEMBASE by assuming a homogeneous distribution of animals over a notional proportion of each region, the proportion being derived from the field observations of Warwick and Davies (1977). Biomass, expressed as g C, was simulated for each m^2 where suspension feeders occurred. Changes in simulated biomass are the integral of the feeding processes and respiration, excretion, feces production, and grazing.

The model simulates the effect of changing particle concentration on feeding rate; using data obtained with *Mytilus edulis*, Bayne et al. (1976a) derived an expression which resulted in decreasing filtering rate and increasing pseudofeces production with increasing particle concentration; this expression has been used in GEMBASE. Daily feeding rates were computed using results of the simulation for turbidity, phytoplankton, and particulate organic carbon; phytoplankton carbon was ingested by macrofauna with a greater efficiency than detrital carbon and the latter was assumed to be 90% refractory. Equations for routine and standard respiration were based on the data of Bayne et al. (1976b). Predation on benthic macrofauna in GEMBASE was by birds in intertidal regions and by demersal fish and carnivorous invertebrates in those sublittoral regions where macrofauna occurred.

Simulation results, expressed as g C for each m^2 where suspension feeders exist, are shown in Fig. 6 for five regions from 1973 until 1975. Seasonal data for all zoobenthos in the Bristol Channel were not obtained during our sampling program so it is not possible to compare the simulation results with field data. No year-to-year variations in biomass have been found in the zoobenthos of the North Outer Channel (R. M. Warwick, personal communication) so the criterion adopted for judging the success of the simulation is that the output should show a reasonable seasonal cycle with similar biomass in successive years. It is clear from Fig. 6 that this criterion is not satisfied because there is an increase in biomass in successive years, particularly in the North Outer and North Central Channels.

The increases occur in a short period of 30–60 d in late spring when GEMBASE simulates low turbidity (Fig. 3) and rapid increases in standing stock of phytoplankton. Food intake by suspension feeders in GEMBASE is related to food concentration and to water turbidity which modulates filtering efficiency, so the conditions which occur in the model each spring favour ingestion of food at high efficiency by suspension feeding benthos.

There are several explanations for the poor simulation of suspension feeding macrofauna. The relationships used to define feeding rate, ingestion, and pseudofeces production were derived for *Mytilus edulis* and may not be appropriate for other suspension feeding fauna, such as *Sabellaria*, which are abundant in the turbid regions of the Inner Channel. Alternatively, the increase in gross simulated biomass may be reasonable: GEMBASE does not attempt to model processes such as gamete production and a significant proportion of production

which would normally be lost to the particulate organic matter pool may be retained within the simulated suspension feeder biomass resulting in unrealistic net production. If this is the explanation for the poor simulation results, the present level of complexity of GEMBASE may be too simple to allow realistic simulations of suspension feeding benthos and the model must be modified.

Conclusions

A multiple regression of tidal range, river flow and turbidity was the basis of a realistic simulation of turbidity in the ecosystem model GEMBASE. Although this expression is clearly too simple for simulating short-term changes in turbidity, it was adequate to simulate changes in mean turbidity over the large regions of the Bristol Channel modeled in GEMBASE and was used successfully as a forcing function of the model. Another expression derived from a regression of extinction depth with turbidity also resulted in realistic simulation of extinction depth and contributed towards a successful simulation of the pelagic ecosystem. These simple expressions are adequate within the coarse geographic grid adopted in GEMBASE but the success or failure of large ecosystem models depends much more on our understanding and ability to simplify into mathematical expressions the complex interactions occurring within and between the biological components of the ecosystem.

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