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Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance

Elizabeth A. Fulton [a,*], John S. Parslow [a], Anthony D.M. Smith [a], Craig R. Johnson [b]

[a] *CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tasmania 7001, Australia*
[b] *School of Zoology and Tasmanian Aquaculture and Fisheries Institute [TAFI], University of Tasmania,
GPO Box 252-05, Hobart, Tasmania 7001, Australia*

Abstract

The level of detail required to efficiently capture system dynamics in ecosystem models has not been well defined. To this end an ecosystem model of a generalised temperate bay, Bay Model 2 (BM2), was constructed. It is a trophically diverse biogeochemical model built using the functional groups from another ecosystem model, the Integrated Generic Bay Ecosystem Model (IGBEM) and the general framework from a model of Port Phillip Bay (PPB), Australia. BM2 captures the essential features of real marine systems, it is also capable of reproducing realistic levels of biomass and conforms with known ecological relationships. The model's performance is not as good for some of the poorly known groups (like infauna) or when environmental conditions undergo extreme change. Despite this, the overall performance of BM2 indicated, it is as capable of representing systems as accurately as more physiologically detailed ecosystem models, such as IGBEM. This shows that physiological detail is not always required and that simpler formulations, such as those employed in BM2, are generally adequate for learning and general predictive purposes. This is important because, in comparison with IGBEM, BM2 uses substantially fewer parameters and has lower development, computation and maintenance costs.
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1. Introduction: ecosystem models and physiological detail

The evolution of ecosystem models has often seen a tendency to incorporate increasingly detailed process formulations and model structure. The mixed success and potentially large computational demands of early attempts at highly detailed reductionist ecosystem models (Hedgpeth, 1977; Platt et al., 1981) lead to a return to 'simple' models during the late 1970s through to the mid-1990s. With advances in computing power and the growth of ecosystem and ecological theory large models that are flexible enough to be applied in a range of locations, and that account for a large amount of the system, are becoming attractive again. For instance, over 130 ECOPATH with ECOSIM models have been published (Christensen et al., 2000) and the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al., 1995) has been applied in 18 locations. This rise in popularity is driven by at least three things: (1) an international push for the management of ecosystems rather than individual resources, (2) it is hard to compare results across systems if they are built on differing premises and assump-

* Corresponding author. Tel.: +61-3-6232-5018;
fax: +61-3-6232-5053.
E-mail address: beth.fulton@csiro.au (E.A. Fulton).

tions, and (3) little has been published on the effects of complexity on ecosystem model performance. Given the increasingly widespread use of marine ecosystem models, it is clear that the effect of model complexity on model performance is an important issue begging immediate attention.

Insight gained during the construction of the Integrated Bay Ecosystem Model (IGBEM), suggested that building another process-based ecosystem model that is less parameter intensive may prove useful. This enabled a study of the effects of differing forms and levels of model formulation on model performance. The approach used was the 'deep–shallow' model comparison method that has been used extensively and successfully in fisheries (e.g. Ludwig and Walters, 1981). This method begins with a highly detailed model, which incorporates some of the known complexities of the real world, and then makes systematic comparisons with simpler models. This paper discusses the results of the comparison of two trophic flow ecosystem models that are both reasonably large and complex, but which contain very different levels of formulation detail (Table 1). IGBEM (Fulton et al., this volume) is heavily based on physiological detail and explicitly represents processes such as uptake, excretion, defecation, mortality, basal-, activity- and stress-respiration. In contrast, Bay Model 2 (BM2) uses simpler assimilation and generalised handling equations, which aggregate the physiological processes into three equations—one each for growth, the release of nutrients and the production of detritus. These differences allow for consideration of the impact of the formulation of internal physiological details on marine ecosystem models dealing with multiple trophic levels. This is an important consideration once it is recognised that the simpler formulations used in BM2 means that, in comparison with IGBEM, it uses far fewer parameters (<50% of the number used in IGBEM) and required substantially less time (by an order of magnitude) to develop, maintain and implement.

2. Building BM2

2.1. The structure of BM2

For convenience many acronyms are used throughout this paper, they are defined when first used, but for quick reference a list is given in Table A.1. BM2 is a process model that tracks the nitrogen and silicon pools of 25 living, two dead, four nutrient, six physical components and a gaseous component (Table A.2). The foundation for BM2 was constructed by replacing the detailed process equations used for each invertebrate group (listed in Table A.2) in IGBEM (Fulton et al., this volume) with the general form of the process equations implemented for the biological components in the Port Phillip Bay Intergrated Model (Murray and Parslow, 1997). Some modifications to this basic form were made and these are detailed below.

The other model used in this work, IGBEM, uses the same functional groups, but employs the ERSEM 'standard organism' concept (Baretta et al., 1995; Fulton et al., this volume). Space precludes a detailed description of IGBEM here, but a summary of the major assumptions and differences between the models can be found in Table 1 and full details of IGBEM may be found in Fulton et al. (this volume). While there are substantial differences in the degree of formulation detail used in IGBEM and BM2 for the invertebrate groups, the fish groups in BM2 are much closer to the 'average individual' model used in IGBEM. The fish grazing and excretion processes have been simplified though, to keep them in line with the level of resolution found in the rest of BM2. The general formulations for the phototrophic, invertebrate consumer and fish groups are given in Appendix B.

The groups used in IGBEM and BM2 were closely matched to allow for direct comparisons. BM2 contains a single trophic group and a small number of food web linkages that IGBEM does not (marked in bold in Fig. 1). In BM2 the pelagic bacteria were split into free and attached forms, while there is only a single lumped group in IGBEM. Since the size of the attached bacterial pool in BM2 is strongly dependent upon the water column pool of labile detritus (rather than the converse), differences in trophic structure in the models are unlikely to confound comparisons. The additional food web linkages are related to the introduction of two new processes in BM2—mixotrophy in the dinoflagellate group and a new method of dealing with bacterial groups (particularly those in the sediment). These were two areas where IGBEM was found to be in need of improvement. Since behaviour of the entire model system is one of the most important issues in question, the benefit of adding extra linkages

Table 1
Comparison of the underlying assumptions and formulations of the standard implementations of BM2 and the IGBEM

| Feature	BM2	IGBEM
General features		
Biomass units	$mg\,N\,m^{-3}$	$mg\,m^{-3}$ of C, N, P, Si
Input forcing	Nutrients and physics on interannual, seasonal, tidal frequencies	Nutrients and physics on interannual, seasonal, tidal frequencies
Level of group detail	Functional group	Functional group
Resolution of the formulation used for the invertebrate groups	Follow the dynamics of the entire biomass pool of the functional group in the cell	Follow the dynamics of the entire biomass pool of the functional group in the cell
Resolution of the formulation used for the fish groups	Follow the biomass dynamics (structural and reserve weight) of the 'average individual' for the functional group in the cell and the number of individuals in the cell	Follow the biomass dynamics (structural and reserve weight) of the 'average individual' for the functional group in the cell and the number of individuals in the cell
Process related		
Bioturbation and bioirrigation	Yes	Yes
Consumption formulation	Type II	Mixed (type II, type III)
Equations	Five general sets of rate of change equations used (autrophs, invertebrate consumer, vertebrate consumer, bacteria, inanimate)	Eight general sets of rate of change equations used (microautotrophs, macrophytes, small zooplankton, mesozooplankton, fish, zoobenthos, bacteria, inanimate)
Formulation detail	General: only growth, mortality and excretion explicit	Physiological: the processes of assimilation, basal/activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit
Light limitation	Optimal irradiance fixed	Phytoplankton can acclimate to ambient light levels
Mixotrophy	Dinoflagellates	None
Nutrient limitation	External nutrients determine uptake	Internal nutrient ratio determines nutrient uptake and disposal
Nutrient ratio	Redfield	Internal specific nutrient ratio
Oxygen limitation	Yes	Yes
Sediment burial	If enabled, then very low	Yes
Sediment chemistry	Dynamic, with sediment bacteria	Empirical, sediment bacteria are a tracer only
Shading of primary producers	Yes	Yes
Spatial structure	Flexible with the potential for multiple vertical and horizontal cells	Flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	Yes	Yes
Transport model used for hydrodynamics flows	Yes	Yes
Model closure		
Top predators represented by static loss terms	Yes	Yes
Linear mortality terms	Yes	Yes
Quadratic mortality terms	Yes	No
Fish and fisheries related		
Age structure for the fish groups	Nine age classes	Nine age classes
Fishery discards	Target species only	Target species only
Invertebrate fisheries	Yes	No
Stock-recruit relationship	Constant recruitment	Constant recruitment
Stock structure	External: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock	External: reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock
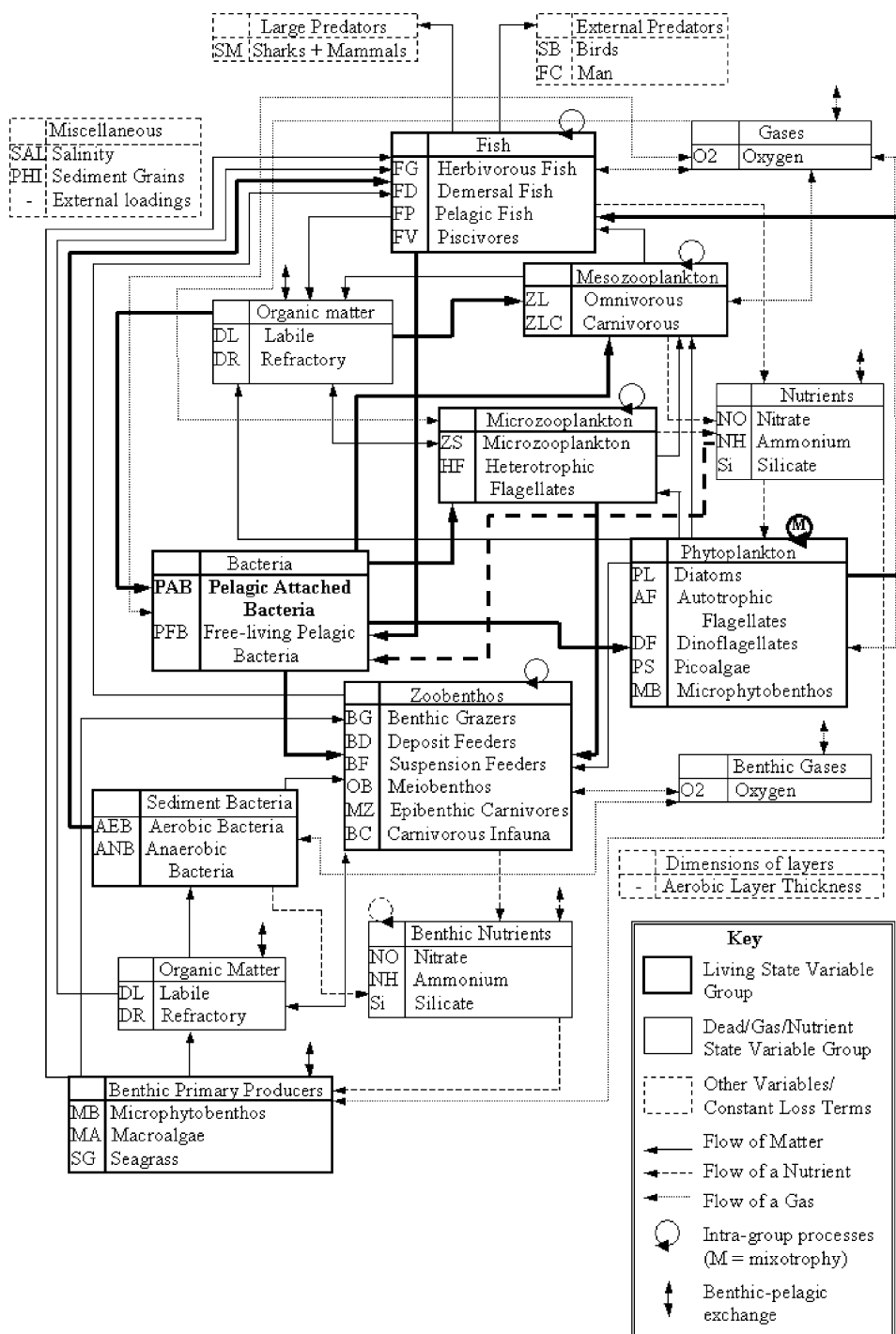
Fig. 1. Biological and physical interactions between the components used in BM2. The pelagic attached bacteria and flows (arrows) in bold are the component and linkages built specifically for BM2 that do not also appear in the IGBEM. The figure is modified from that for the ERSEM (Blackford and Radford, 1995).

necessary to accommodate changes in the handling of these two outweighs the 'cost' of omitting them on the grounds of straightforward comparability with IGBEM.

Dinoflagellates are frequently represented explicitly in ecological models of the water column, but mixotrophy is not. Apart from a handful of models examining the microbial loop in detail (such as Stickney et al., 2000), mixotrophy is usually ignored in ecosystem models. This is because, in the past, little was known about it and because it was considered to have negligible impacts. However, there is now clear evidence that dinoflagellates can have significant impacts (via predation and competition) on phytoplankton and zooplankton, despite their relatively low densities and growth rates (Hall et al., 1993; Jacobson, 1999). In addition, experience gained from working with PPBIM and IGBEM suggested that some mechanism crucial in nature is lacking from standard water quality and ecosystem models. The behaviour and persistence of dinoflagellates observed in natural systems had previously proved difficult to reproduce in simulations and mixotrophy seemed a prime candidate for this missing process as the type of dinoflagellates in question display mixotrophy in the field to offset low nutrient uptake affinities, low maximum photosynthetic rates and high respiration costs (Smayda, 1997; Legrand et al., 1998; Broekhuizen, 1999; Stoecker, 1999; Li et al., 2000). Thus, the type II (primarily phototrophic) mixotrophs from Stickney et al. (2000) were used as a guide during the formulation of the mixotrophic dinoflagellates in BM2 (given in Appendix C).

The other part of the system treated unconventionally in BM2 is bacteria and their associated effects on sediment chemistry and remineralisation. Ecosystem and water quality models have traditionally treated bacteria in much the same way as all other invertebrates, using the same formulations and making only minor modifications to linkages, resource utilisation terms and parameter values. This approach is adopted for the free-floating pelagic bacteria in BM2, following the time-evolution equations for bacteria of Fasham (1993). However, a different approach is used for the three groups of attached bacteria. The growth rates of attached bacterial populations (water column and sediment alike) were equated to the availability of colonisable substrata (the detrital groups) rather than to more grazer-like consumption of prey resources. The for-

mulations used for bacteria and their integration with the nitrification–denitrification submodel are given in Appendix D.

BM2 and IGBEM use a transport model, modified from one developed for PPBIM (Murray and Parslow, 1999a; Walker, 1999). It is vertically resolved into three layers (water column, epibenthic, sediment) and the fluxes driving this transport model are derived from a spatially and temporally finely resolved three-dimensional non-linear, variable density hydrodynamics model (Walker, 1999). As a result these models are driven by seasonal variation in irradiance and temperature, as well as nutrient inputs from point sources, atmospheric deposition of dissolved inorganic nitrogen (DIN) and exchanges with an oceanic boundary condition box. As they share a transport model, BM2 and IGBEM are identical with regard to the physical parts of the system, with the exception that the rate of sediment burial out of the modelled sediment layer in BM2 was greatly reduced based on observations made during the validation of IGBEM (Fulton et al., this volume).

For computational efficiency, a daily time-step is used wherever possible. Within the biological modules however, a daily time-step may make the variables with fast dynamics become unstable. Therefore, while some groups (e.g. fish) work on a daily time-step, other groups (e.g. the phytoplankton groups) use an adaptive time-step, which is repeated until a full 24-h period has been completed. Once this has occurred the transport model steps (which also employ a daily time-step) are performed.

2.2. Parameterising BM2

As the study was concerned with considering the effects of model structure in general rather than modelling a specific bay much of the work done was set in a hypothetical generic system. For convenience, the spatial geometry developed for the Port Phillip Bay Integrated Model (PPBIM, Murray and Parslow, 1999a; Walker, 1999) was used here to define the physical system being modelled. Thus, the spatial geometry is one made up of 59 polygons (boxes) which correspond to the geographical form of Port Phillip Bay (PPB), Melbourne, Australia. The area and shape of the polygons reflect the speed with which physical variables change within particular parts of the bay (Fig. 2).
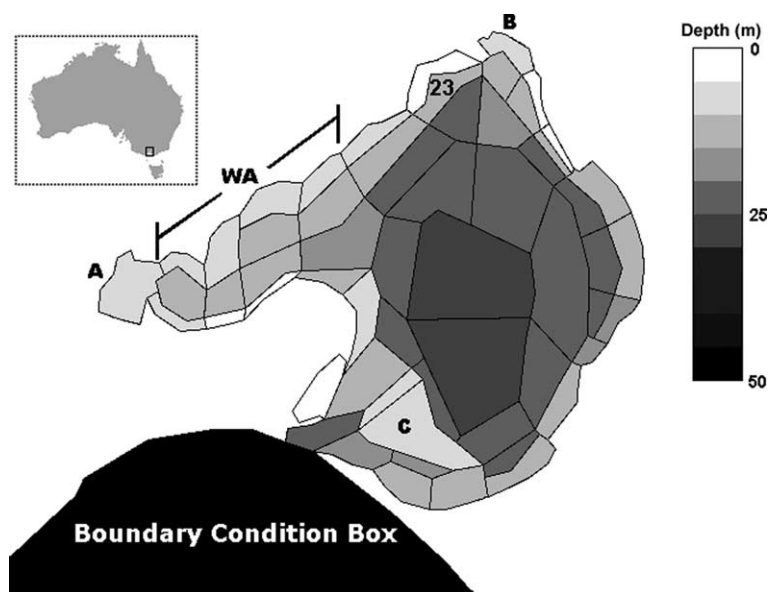
Fig. 2. Map of the geometry used for the standard runs of BM2. It represents PPB, Melbourne, Australia (location marked on map inset). The letters and box number 23 are referred to in the text.

Biologically, the models were parameterised to reflect a generic temperate bay ecosystem, rather than specific species from a specific ecosystem. As with IGBEM, general parameter values were used in BM2, though they did require some calibration to achieve numerical stability. The number of process parameters required by BM2 is much smaller than that of IGBEM, but there are still far too many for a systematic sensitivity analysis. Consequently, the guidelines given in Murray and Parslow (1997) for the parameterisation of PPBIM were used to determine values for the majority of parameters in BM2. The final calibration of BM2 was completed by tuning the temperature-dependent maximum growth and mortality rates for all groups and the maximum clearance rates of the consumer groups, as these parameters had been identified as the most important in a factor screening. Tuning was carried out until all groups persisted and numerical stability was achieved. In the tuning procedure it was ensured that all parameter values were within the range of empirical values found in the general literature. As a consequence of this method of tuning, parameter values did not always reflect a particular observation or reported value, but they did reflect values from the literature.

3. Model runs

The model runs used here span a 20-year time period (beginning after a 10-year 'burn-in' period), with output recorded every 14 days. Simulations lasting 100 years were also undertaken to check for long period cycles and to verify that the models had reached a representative state at the end of the 30-year period. Looping of the forcing files for the physical transport model is necessary, as the files only spanned 4 years, and this is done in the same manner as for IGBEM (Fulton et al., this volume).

The assumptions underlying the formulations for the recruitment and movement of fish are some of the weakest in these models. Other formulations examined included alternative recruitment formulations and a forage- and density-dependent fish movement, which allocates fish to the cells based on available resources, clumping around good resources and dispersing if conditions were poor (rather than a fixed, prescribed, matrix of proportions) (Appendix E). As these alternative schemes make little if any difference to the results presented here they will not be discussed here.

To evaluate the performance of BM2 under varying environmental conditions, and to judge how well

Fig. 3. Map of the world showing the bays used to evaluate the performance of BM2. Symbols mark the locations of all the systems for which marine biomass or production estimates were available for comparison with the output of BM2. The bays marked with a black symbol are the bays used to set the alternative nutrient load scenarios for BM2.

the model replicates the behaviour of natural systems, the nutrient forcing files for BM2 were scaled so that the new values matched the area-corrected inputs (from Monbet, 1992) for a number of other bays from around the world (Fig. 3). The geometry and hydrodynamics remained unchanged, but the levels of inflowing nutrient were altered in an attempt to capture the state of other bays. As the parameters in the standard parameter set were based on species from temperate bays across the globe, there was no retuning with each change in nutrient loading. This approach was also used with IGBEM (Fulton et al., this volume) and proved to be robust. A range of measures, including levels of Chlorophyll a (Chl a), DIN, biomasses and system indices, were used to judge the model performance against available data across the entire set of bays shown in Fig. 3.

PPB has not become eutrophic, despite anthropogenic pressure, and as a result, during the evaluation of BM's ability to reflect changes in a system as it becomes eutrophic, it was necessary to use values from another bay to represent the (expected) eutrophic

values of PPB. Of the bays where there is sufficient available biological information to give an assessment of model performance, Chesapeake Bay is closest to the expected form of a eutrophic PPB. Thus, when judging how well BM2 replicates state changes due to eutrophication, values from the runs using nutrient loadings from PPB (PM run) and Chesapeake Bay (CM run) were compared to empirical values from these two bays.

4. Results

4.1. BM2 versus IGBEM and real bays

Aggregation of model output is necessary for comparison with data from real bays, which is not available at the same resolution. To differentiate between the highly resolved output of the models and the aggregated forms, the latter are referred to as trophic sets. The list of trophic sets consists of: Chl a (as a proxy for total phytoplankton), zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, ben-

Table 2
Absolute values of Student's t statistic calculated using the empirical values and model values BM2 and the IGBEM for each trophic set

Trophic set	BM2 (t)	IGBEM (t)	d.f.
Chl a	1.21	1.35	99
Zooplankton	1.00	0.32	44
Fish	1.68	0.71	82
Macrophytes	0.13	1.08	40
Microphytobenthos	2.50[a]	2.58[a]	44
Benthos	4.23[a]	3.81[a]	80
Meiobenthos	1.79	0.73	51
Detritus	1.96	1.16	21
DIN	0.25	1.45	99

[a] Significant at $\alpha = 0.05$.

thos (all the other benthic consumer groups) and detritus (labile and refractory).

4.1.1. Average biomass

Average values of the biomass for each trophic set and the values produced under specific conditions were informative in assessing model performance. Accounting for the magnitude of the range in the field values, the average values produced by BM2 are similar to those reported by IGBEM and observed empirically in temperate bays (Fig. 4). For both models only the predicted average values for benthos and microphytobenthos are significantly different to the average empirical value (Table 2). Using the relative deviation of the model averages from the true average values as a performance measure (Table 3), both models did equally well for microphytobenthos; the predictions of IGBEM were better than BM2 for

Table 3
The relative deviation of the model predicted average biomass values from the observed average biomasses for BM2 and the IGBEM for each trophic set

Trophic set	BM2	IGBEM
Chl a	0.07	0.06
Zooplankton	0.13	0.02
Fish	0.15	0.06
Macrophytes	0.01	0.09
Microphytobenthos	0.28	0.28
Benthos	0.32	0.26
Meiobenthos	0.12	0.05
Detritus	0.25	0.12
DIN	0.02	0.11

zooplankton, fish, meiobenthos, benthos and detritus; while the performance of BM2 surpassed that of IGBEM for the macrophytes, Chl a and DIN. Importantly, the performance of IGBEM is not consistently superior to that of BM2.

The results for zooplankton (Fig. 4, Table 3) indicate a need for improvement of this component. The results for average biomass of zooplankton given by BM2 are restricted to the upper end of those given by IGBEM. While acceptable in a generic situation as a heuristic tool, it suggests caution in prognostic application of BM2 to natural systems.

4.1.2. Biomass in comparison with Port Phillip Bay and Chesapeake Bay

Comparison of empirical measures for each pooled set in PPB and Chesapeake Bay with the predicted values of BM2 and IGBEM under corresponding nutrient load levels indicated good performance of BM2 (Table 4). In most cases the values predicted by BM2 were within interannual variation of the field values. However, there were some exceptions. The predicted biomass of meiobenthos was high for both the CM and PM runs (Table 4), but meiobenthos is difficult to sample (Schwinghamer, 1981) and slight increases in the empirical estimates would see the predicted values fall within interannual variation. Nevertheless, it is likely that a limitation term for crowding in the meiobenthos is needed in BM2.

The macrophyte biomass in the CM run was also high (Table 4). While this level of biomass is not representative of Chesapeake Bay, it is found in other systems with similar nutrient loading (Lotze et al., 1999). The difference in model predictions for macrophytes under increased nutrients can be traced back to the differing behaviour of phytoplankton in BM2 and IGBEM with increasing nutrients. Both models include an epibenthic fouling term for seagrass, which sees seagrass decline quite sharply under high nutrients, and this in turn frees resources for other benthic primary producers. The bloom dynamics of the phytoplankton in each model then determine whether the remaining primary producers (macroalgae and microphytobenthos) exploit these resources. The phytoplankton in IGBEM produce intense blooms under increased nutrient conditions and these starve the underlying phytobenthos of light, preventing very large increases in biomass supported by the excess
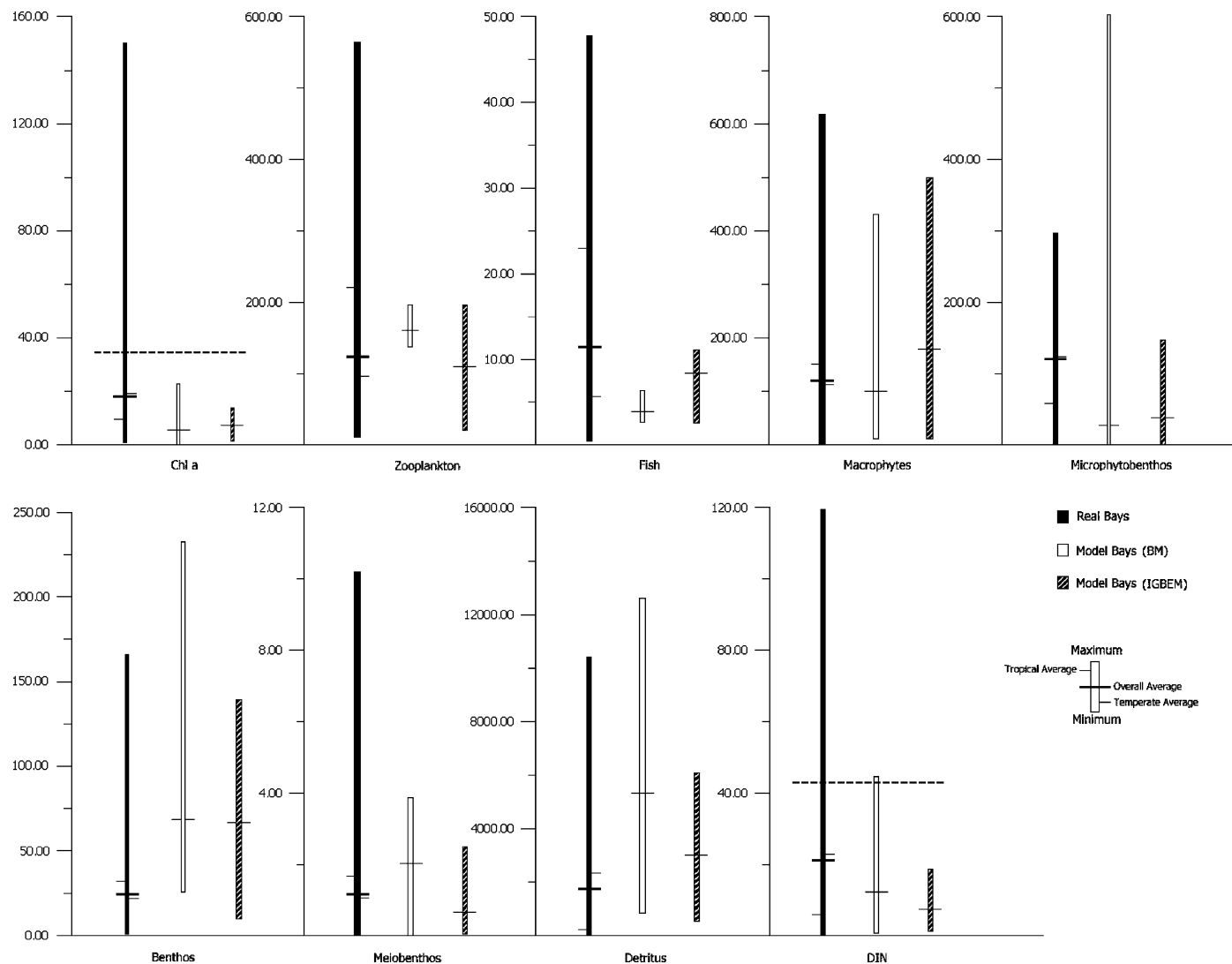
Fig. 4. Range and average value for each of the main trophic sets of BM2 compared with values from empirical observations and from the output of the IGBEM. The y-axis for zooplankton is biomass in mg AFDW m^{-3}; for fish, macrophytes, benthos, meiobenthos and detritus the y-axis is biomass in g AFDW m^{-2}; the y-axis for Chl a is mg Chl a m^{-3}; for DIN it is mmol DIN m^{-3}; and for microphytobenthos it is mg Chl a m^{-2}. The dashed line cutting the black bar in Chl a and DIN marks the maximum value of Chl a and DIN recorded for those bays with the same nutrient loads as used to run BM2 and IGBEM. The values from the empirical observations are taken from the appendix of Fulton et al. (this volume).

Table 4
Average value for each set observed in PPB and CB and predicted by the associated runs (PM and CM, respectively) of BM2 and the IGBEM

Trophic set	Units	PPB	PM–BM2	PM–IGBEM	CB	CM–BM2	CM–IGBEM
Chl a	mg Chl a m^{-3}	1.04	1.00	1.40	15.85	8.95	10.10
Zooplankton	mg AFDW m^{-3}	68.47	149.17[a]	84.34	112.74	165.62	149.62
Fish	g AFDW m^{-2}	3.33	3.89	2.60	6.61	6.27	9.51
Macrophytes	g AFDW m^{-2}	7.75	15.19	12.52	123.60	260.84[a]	99.17
Microphytobenthos	mg Chl a m^{-2}	38.35	3.05[a]	5.13[a]	35.00	46.93	54.93
Benthos	g AFDW m^{-2}	29.95	45.90	32.89	80.82	85.18	82.10
Meiobenthos	g AFDW m^{-2}	0.24	1.00[a]	0.15	1.41	2.31[a]	0.84
Detritus	g AFDW m^{-2}	2953.37	3720.62	1771.96[a]	10417.00	7156.19[a]	6041.44[a]
DIN	mmol DIN m^{-3}	1.00	1.472	1.49	19.49	20.20	13.50

DIN stands for dissolved inorganic nitrogen. The values used to determine the ranges and averages for the sets observed in CB and PPB are taken from the Appendix of Fulton et al. (this volume).

[a] Outside the range of interannual variation reported for the field.

nutrients. In contrast, BM2 predicts only moderate blooms and these do not impede the transmission of light to the same extent as occurs in IGBEM. Consequently, light levels reaching the sediment are high enough to allow an increase in the biomasses of macroalgae and microphytobenthos. The pattern of change and bloom dynamics predicted by IGBEM is the more common pattern in natural systems, but the pattern predicted by BM2 also arises (Conley, 1999; Herbert, 1999; Lotze et al., 1999).

As with IGBEM, microphytobenthos biomasses predicted by BM2 do not match those observed in the field and they do not match the empirically observed patterns of change with increasing nutrients (Table 4). This may be due to the factors causing corresponding problems in IGBEM; the microphytobenthos are restricted to deeper, more inhospitable parts of the bay due to competitive exclusion by the macrophytes, and (overly efficient) infauna feeding on the microphytobenthos keeps it cropped to low levels (Fulton et al., this volume). Similarly, the low levels of detritus predicted for the CM run by BM2 (Table 4) may reflect low input levels of detritus and overly efficient detrital feeders. The latter problem is exacerbated in BM2 as detritus feeding infauna reach higher biomasses than in IGBEM.

Potentially the most important problem with BM2 was that the predicted zooplankton biomass in the PM run was high compared to recorded values from PPB (Table 4). Water column modelling is well developed and usually results in very good fits to reality (Fransz et al., 1991). The failure in this case suggests that BM2 may require some tuning on a site-by-site basis. If it

were strictly a mis-specification it could be expected that the results would be problematic for all runs, not just those under specific nutrient loads. Notably, calibrating BM2 to the dominant species in PPB results in predictions much closer to values measured in PPB and to the output of IGBEM (Fig. 5).

4.1.3. Community composition

The relative composition of communities (in terms of biomass) is another informative comparison, particularly for the fish and benthic groups. This comparison was only possible for the PM run (Table 5) and shows that BM2 well represented patterns of relative abundance.

Estimates of the fish community produced by BM2 are substantially closer to the PPB values than those predicted by IGBEM. While planktivorous fish are relatively overestimated by BM2, this is much less of a problem than in IGBEM. Results for the benthic groups also reflect favourably on BM2. The predicted community composition reflects that observed in PPB and BM2 performs better than IGBEM for benthic groups. Despite minor divergences, our results show that BM2 captures the large-scale community level dynamics of the fish and benthic groups.

4.1.4. Standard relationships

Monbet (1992), Schwinghamer (1981) and Sheldon et al. (1972) identified strong system level relationships (ecological and physical) that hold for systems from around the world. Any ecosystem model, particularly one used as a foundation model for an investigation of model structure and behaviour, should
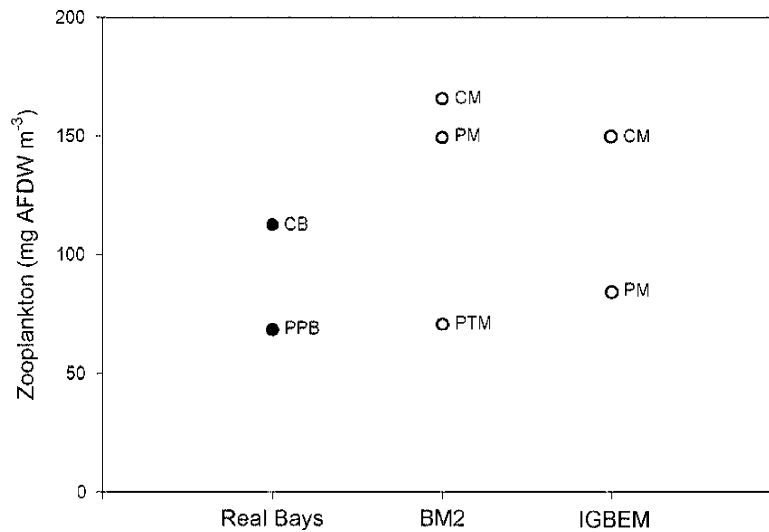
Fig. 5. Average value for the zooplankton in BM2, in comparison with values for those sets in the field and in the output of the IGBEM. The values used to determine the averages for the real world sets are taken from the Appendix of Fulton et al. (this volume). CB stands for Chesapeake Bay, PPB for Port Phillip Bay, PM for the model run with the nutrient loading from PPB, CM for the model run with the nutrient loading from CB, and PTM is the run of BM2 which uses a parameter set tuned to represent the biological groups of PPB rather than a standard parameter set.

produce output that conforms to these relationships. BM2 meets this requirement.

Monbet (1992) found a strong positive linear relationship between the logarithms of the water column concentrations of Chl a ($mg\,m^{-3}$) and DIN ($mmol\,m^{-3}$). Tidal range is also an important part of this relationship as macrotidal and microtidal ($>2\,m$

and $<2\,m$ tidal range, respectively) systems cluster separately, with little overlap (the model system is microtidal). Both BM2 and IGBEM generally comply with Monbet's relationship because their predicted values fall within the range of observed values (Fig. 6). The performance of IGBEM is better than that of BM2 however, as the response of Chl a to DIN

Table 5
Comparison of the community composition for the fish and benthic groups observed in PPB and predicted by BM2 and IGBEM in the runs with conditions matching those in PPB

Functional group	Percentage of total community biomass		
	BM2	IGBEM	PPB
Fish community			
Planktivores	50.0	46.1	31.2
Piscivores	3.1	13.6	8.5
Demersal fish	41.2	36.1	50.3
Demersal herbivorous fish	5.7	4.2	10.0
Benthic community			
Macrozoobenthos (epifaunal carnivores)	1.5	4.3	1.1
Benthic (epifaunal) grazers	11.1	4.5	4.3
Benthic suspension feeders	45.8	45.8	50.0
Infaunal carnivores	2.0	11.4	6.3
Benthic deposit feeders	39.7	34.0	38.3

The values given for PPB for the fish groups only include those species used to parameterise the dynamic groups explicitly included in the two models (BM2 and IGBEM).
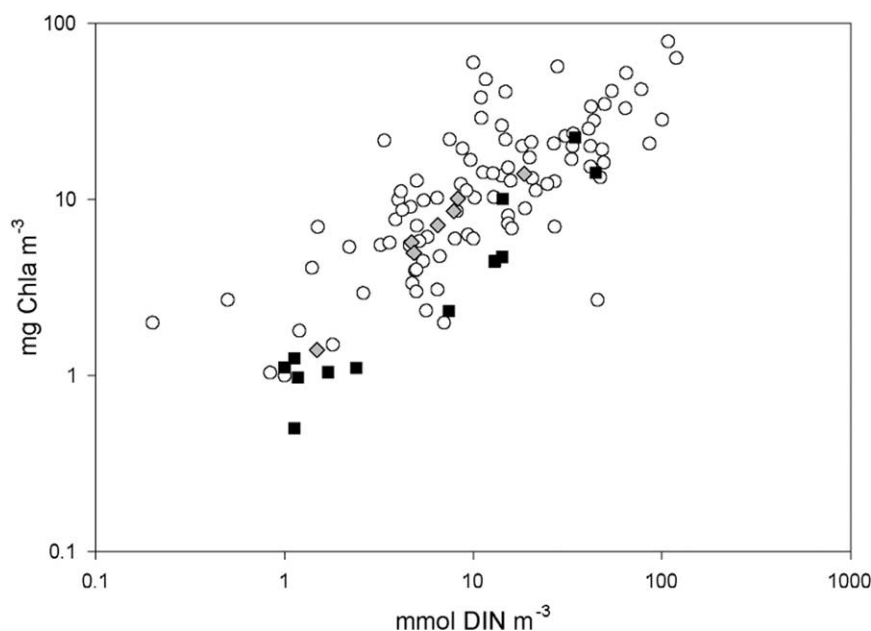
Fig. 6. Comparison of the mean annual DIN against mean annual Chl a for real microtidal marine systems (based on Monbet, 1992 and additional values from the literature (Fulton et al., this volume), BM2 and IGBEM.

is too flat in BM2. This flat response means there is a significant difference between regression lines fitted to BM2 and empirical values ($F_{2,102} = 11.19$, $P < 0.0005$), while there is no significant difference between regression lines fitted to IGBEM and empirical values (Fulton et al., this volume). This difference between regression lines fitted to BM2 and empirical values is due a difference in the elevations ($F_{2,103} = 20.13$, $P < 0.0005$) not the slopes ($F_{2,102} = 2.05$, $P > 0.1$) of the lines.

Two of the most significant biological relationships uncovered in marine systems are the size spectra (or 'Sheldon spectra') identified by Sheldon et al. (1972) for the pelagos, and Schwinghamer (1981) for the benthos. The Sheldon spectrum for pelagic life is essentially flat (Sheldon et al., 1972), while the corresponding spectrum for the benthos is W-shaped (Schwinghamer, 1981). The classes identified by Schwinghamer were pooled to match the size resolution used in the models, which converted the benthic size spectrum from a 'W' into a 'U'. The pooled spectrum calculated for BM2 match well with those of Sheldon et al. (1972) and Schwinghamer (1981), while those for IGBEM do not (Tables 6 and 7). This is especially true for the microscopic classes, par-

ticularly in the benthos (Table 7). The behaviour of these classes are a major weakness of IGBEM, but not of BM2. Values for benthic classes from BM2 are well within the confidence intervals given by Schwinghamer for his general spectrum, while those of IGBEM are not (Table 7).

4.1.5. System indices

Just as ecosystem models should conform to observed empirical relationships (e.g. size spectra) they must also give realistic values for system level indices. Several of these (after Christensen, 1992) were used

Table 6
A summary of the Sheldon spectra for the pelagic classes in the run of BM2 and the IGBEM where the environmental conditions match those in PPB

Class	BM2 ($cm^3 m^{-2}$)	IGBEM ($cm^3 m^{-2}$)
Bacteria	3.48	40.50
Phytoplankton	8.72	10.02
Zooplankton	16.26	10.47
Planktivorous fish	8.84	5.45
Other (larger) fish	8.85	6.37

Following the convention set by Schwinghamer (1981) the unit area biomasses are given in $cm^3 m^{-2}$.

Table 7
A summary of the pooled Sheldon spectra for the benthic classes in the run of BM2 and the IGBEM where the environmental conditions match those in PPB

Class	BM2 ($cm^3\,m^{-2}$)	IGBEM ($cm^3\,m^{-2}$)	Average Schwinghamer ($cm^3\,m^{-2}$)	Minimum Schwinghamer ($cm^3\,m^{-2}$)	Maximum Schwinghamer ($cm^3\,m^{-2}$)
Bacteria	24.9	0.2	80.1	8.1	168.2
Meiobenthos and microphytobenthos	5.63	0.7	6.1	0.9	37.0
Macrofauna	208.7	149.5	473.0	1.6	1817.0

The values given by Schwinghamer (1981) are included for comparison.

to compare BM2 to IGBEM, PPB and the maximum, minimum and average values from a range of other coastal systems from around the world (Table 8). A correlation coefficient calculated between the average values for each index (except total throughput, which overwhelmed the contributions from the other indices if included) for the real bays and the BM2 runs indicates that BM2 conforms well with the real systems ($r = 0.94$). This is a slightly better performance than that of IGBEM ($r = 0.91$, Fulton et al., this volume). Like IGBEM, BM2 predicts a total throughput that is outside the range given by the coastal systems summarised by Christensen (1992), and this probably reflects that the nutrient loads used in the CM runs are beyond those experienced by any of the bays covered by Christensen (1992).

In comparison with IGBEM, the PM run of BM2 also better matches the system level indices estimated for PPB ($r = 0.94$ for BM2, compared with $r = 0.90$ for IGBEM), with the predicted value of 9 of the 11 indices within a factor of 2 of the PPB estimates (compared with only 4 indices for IGBEM). This suggests that while the models and PPB are all quite similar in their gross form, there are internal mechanisms, linkages and other details which culminate in substantial differences in specific details and this is captured in the value of system indices such as the System Omnivory Index.

4.2. Spatial and temporal form of meso- and eutrophic runs

Temporal and spatial behaviour are also important indicators of model performance. The spatio-temporal dynamics of BM2 and IGBEM are similar, and can produce sophisticated behaviours (such as competitive exclusion and long period cycles) and reproduce spatial zonation and events observed in PPB.

4.2.1. Spatial structure

The predicted average biomasses per box over the final 4 years of the CM and PM runs, using both BM2 and IGBEM, were analysed to determine whether there were boxes that had similar biological and physical properties, which would suggest spatial patterns in the model output. Only these two runs of BM2 and IGBEM were analysed in this way because they encapsulate the general form and dynamics of the 'mesotrophic' and 'eutrophic' states of the models under the current geometry and forcing.

The fourth root transform of the average biomasses of all groups in each box were compared on a two-dimensional non-metric Multidimensional Scaling (MDS) plot derived from a Bray Curtis similarity matrix to identify groups of boxes of similar community structure. The average values of the physical variables and the biomass per group were then examined (using the SIMPER routine of the Primer software package, Clarke and Warwick, 1994) to ascertain which groups determined the clustering seen. This analysis identified 'areas' (boxes in the model sharing biological and physical characteristics) in the model output.

The two models contained a similar number of areas that were located in similar positions around the bay (Figs. 7 and 8). Certain functional groups that consistently occur together with high biomasses in the same cells were grouped as 'communities' (Table 9). Areas predicted to share communities in each model were pooled to produce 'zones' and, as with the 'areas', the two models showed a good deal of agreement (Fig. 9). More importantly, the PM run of each model also produces a set of zones broadly similar to those identified empirically in PPB, although zonation patterns of BM2 better represent those observed in PPB than do those from IGBEM.

The zones marked with an E (Fig. 9) contain the same or very similar communities, which are

Table 8
List of indices and their associated values for PPB and the runs of the ecosystem models BM2 and IGBEM where the environmental conditions reflect those found in PPB (the PM run) or Chesapeake Bay (the CM run)

System (or run)/index	Sum of flows (throughput)	Primary production/ biomass	Biomass/ throughput	Biomass supported	System om-nivory index	Dominance of detritus	Average organ-ism size	Path length	Residence time	Schrodinger ratio	Relative ascendency
Maximum	41929	74.9	0.071	0.151	0.35	0.36	0.198	5.14	0.26	52.03	36.0
Minimum	1444	3.9	0.004	0.008	0.03	0.78	0.010	2.98	0.01	2.79	21.7
Average	12204	18.9	0.026	0.057	0.19	0.57	0.083	3.70	0.10	16.76	31.1
Port Phillip Bay, Australia	13956	14.1	0.016	0.033	0.18	0.64	0.053	4.00	0.06	16.00	32.3
PM-B run (BM2 standard nutrients)	18686	11.0	0.025	0.065	0.05	0.59	0.091	3.75	0.09	4.28	33.1
CM-B run (BM2 nutrients ×10)	66216	12.9	0.021	0.048	0.05	0.60	0.077	4.04	0.09	8.03	29.2
PM-I run (IGBEM standard nutrients)	4702	4.6	0.051	0.130	0.14	0.62	0.128	4.21	0.21	3.16	32.3
CM-I run (IGBEM nutrients ×10)	50702	18.7	0.019	0.040	0.15	0.47	0.042	3.36	0.06	4.59	29.8

The maximum, minimum and averages refer to values of these indices calculated for eight coastal areas from around the world (from Christensen, 1992).
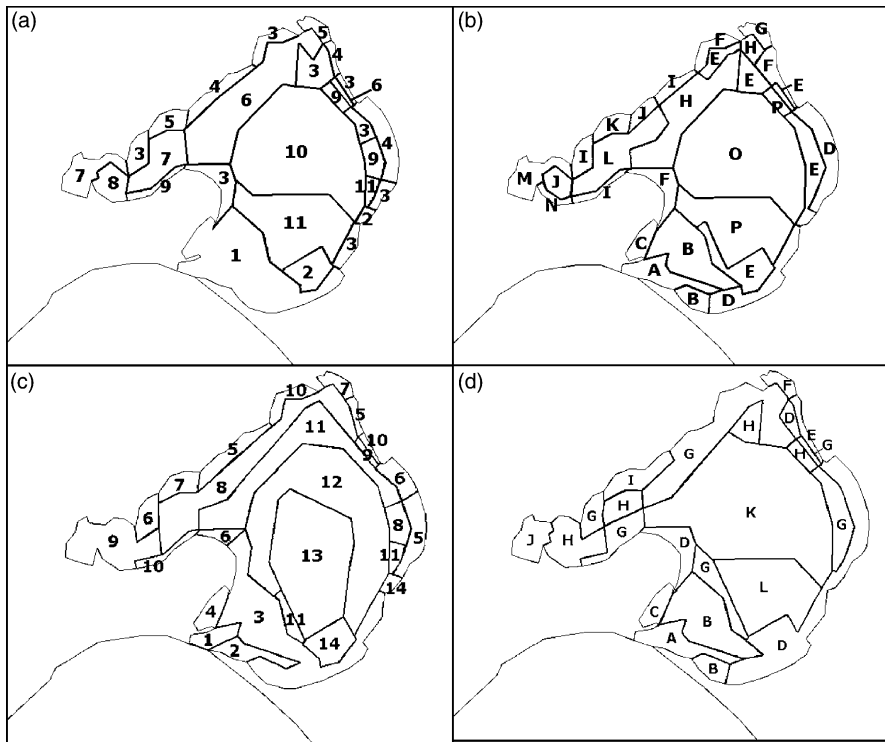
Fig. 7. Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analysis of the runs using the loadings for PPB (the PM run) of BM2 and the IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis (lettering and numbering between maps is independent). (a) Biological areas identified for BM2, (b) physical areas identified for BM2, (c) biological areas identified for IGBEM, and (d) physical areas identified for IGBEM.

consistently found along the edges of the bay and are largely associated with sand and rock substrate. Communities associated with the zone marked with a C in the centre of the bay are in deeper water associated with a mud substratum. The composition of the 'edge' and 'centre' communities (Table 9) shows some overlap (primarily in the water column groups), but there are also clear differences (especially in the epibenthos). The shallow to moderately deep zones along the edge of the bay are usually dominated by one of two alternative plankton assemblages, and a rich assemblage of fish, macrophyte and benthic macrofauna. In contrast, the deeper central parts of the bay are marked by a largely discrete plankton assemblage, and the macrofauna and flora typical of the bay edge have been replaced by microfauna (meiobenthos, microphytobenthos, and bacteria) which are more suited to the more stressful physical conditions found there.

There were two notable points of difference between the model and observed distributions of some groups. First, the dominance of the plankton community in the southern boxes of the models are overstated because of tidal influences, this appears to be a boundary condition artefact. This has little impact on the overall community composition and resulting zones produced by the models. The second point is that field observations (Beardall and Light, 1997) and the output of the Port Phillip Bay Integrated Model (PPBIM) created by Murray and Parslow (1997) show that the highest densities of microphytobenthos are along the north-west shore, from A to the B (Fig. 2), but reasonable levels exist throughout the bay north of C (Fig. 2). BM2 gives some indication of this, predicting the highest levels of microphytobenthos at points on the north-west shore, but this is patchy and the only continuous populations are in the centre of the bay.
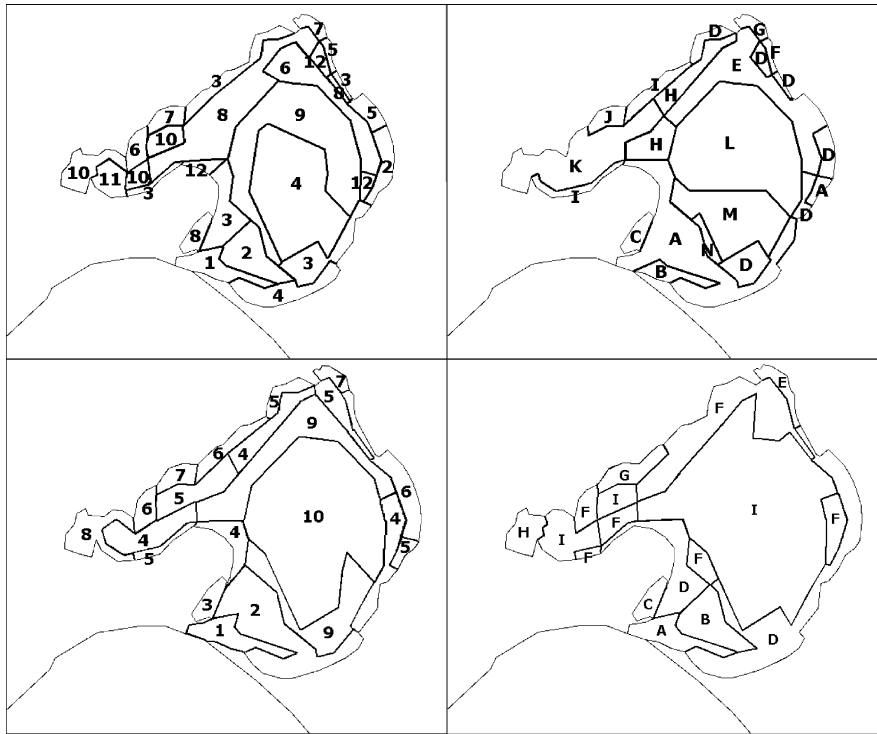
Fig. 8. Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analysis of the runs using the loadings for Chesapeake Bay (the CM run) of BM2 and the IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis (lettering and numbering between maps is independent) and do not correspond to any of the numbers or letters in Fig. 7. (a) Biological areas identified for BM2, (b) physical areas identified for BM2, (c) biological areas identified for IGBEM, and (d) physical areas identified for IGBEM.

IGBEM predicts that microphytobenthos are restricted to the centre of the bay. Again, this does not have an overwhelming effect on the wider agreement between observed and predicted communities.

A number of factors produced the zonation predicted by the models and habitat suitability alone does not explain the sharp distinction between the community assemblages around the edge of the bay and those of the central zones of the bay. In the models, these discontinuities are due to predator–prey dynamics (suppression and supply), resource partitioning and competitive exclusion, particularly in the benthos. These sophisticated behaviours are emergent in the models.

4.2.2. Temporal dynamics

BM2 displayed many of the temporal dynamics observed for IGBEM (Fulton et al., this volume). Both models demonstrate seasonal bloom dynamics, interannual variation and the long-term 'macrophyte-

barren' dynamics. In BM2 however, the interannual variation is often damped in the epibenthos, particularly in the macrozoobenthos, which shows little interannual variation. Similarly the 'macrophyte-barrens' cycle is also different in BM2 compared with IGBEM. This cycle did not occur in all boxes populated by macrophytes in BM2, but arose only in the more marginal macrophyte habitats. Populations in more favourable sites showed only interannual fluctuations related to the hydrodynamic forcing and nutrient inputs. Moreover, where a 'macrophyte-barren' cycle did occur it tended to have a shorter period and smaller amplitude than in IGBEM. A 'macrophyte-barren' cycle has not been observed in PPB, so the dynamics predicted by BM2 appear to be closer to the natural state of PPB.

The much richer dynamics of the microfauna in BM2 translated into a wide range of temporal dynamics. These groups displayed cycles in the short,

Table 9
Dominant biological groups distinguishing the 'edge' and 'central' communities

Community	Biological components						Physical characteristics
	Planktonic	Fish	Epibenthic	Benthic	Macrophyte	Remin	
Edge	Diatoms, autotrophic flagellates or picophytoplankton, microzooplankon	Planktivores, piscivores, demersal fish, herbivorous demersal fish	Filter feeders, benthic grazers, macrozoobenthos	Deposit feeders, benthic infaunal carnivores	Macroalgae or seagrass	Pelagic bacteria, refractory detritus[a], labile detritus[a]	Moderate to high light levels, shallow to moderate depth, with high levels of bottom stress, tidal influences and DIN at some locations
Central	Picophytoplankton, autotrophic flagellates, dinoflagellates, heterotrophic flagellates, large omnivorous zooplankton, large carnivorous zooplankton		Filter feeders, macrozoobenthos[b]	Meiobenthis, microphytobenthos		Sediment bacteria, refractory detritus, labile detritus	Low light, moderate to deep, with lower levels of DIN

These groups are identified consistently in the output of both models (BM2 and IGBEM) and from field observations in PPB. Those groups separated by an "or" indicate groups (or sets of groups) where one or the other is present at high levels, but rarely both. Remin stands for the remineralisation groups (those groups, alive and dead, associated with remineralisation). The physical characteristics of the environment inhabited by each 'community' type are included for reference.

[a] Only in the western arm of the bay (marked as WA in Fig. 2).
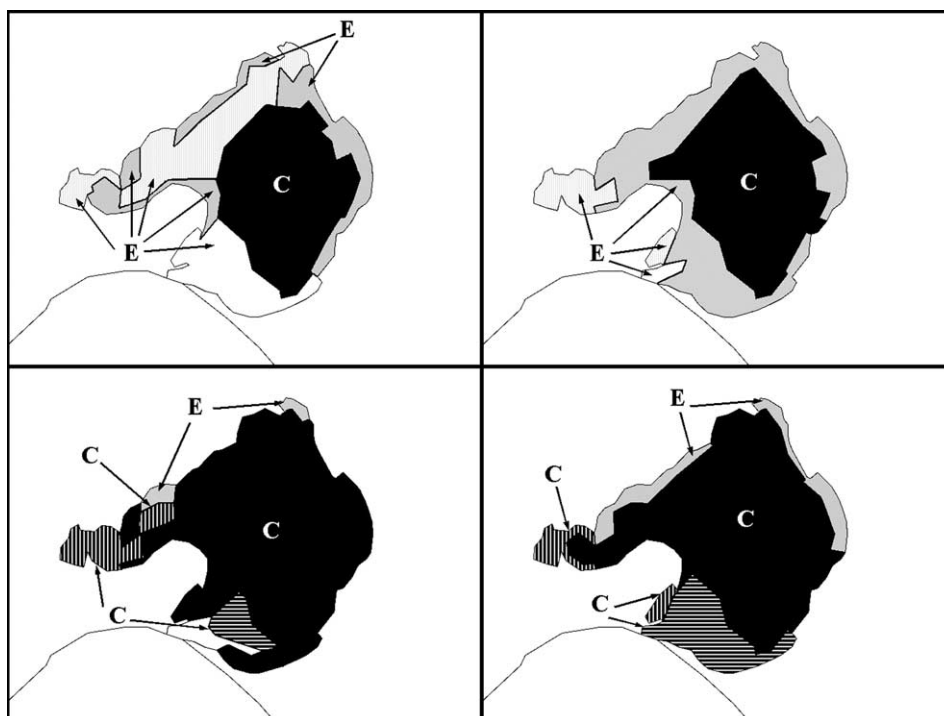
[b] Not predicted by IGBEM.

Fig. 9. Distribution of the main zones identified in the output of BM2 and the IGBEM (a) PM run of BM2, (b) PM run of IGBEM, (c) CM run of BM2, and (d) CM run of IGBEM. The zones in white are part of Bass Strait or heavily influenced by it; the light grey zones are characterised by specific plankton assemblages (dominated by diatoms or microplankton), as well as a rich assemblages of fish, macrophyte and benthic macrofauna; while the dark zones are characterised by another plankton assemblage (dominated by flagellates and mesozooplankton), and well developed populations of meiobenthos, microphytobenthos, and bacteria. Zones marked with an E contain 'edge' communities and those marked with a C contain 'centre' communities (see text for details).

medium and long-term (Fig. 10). The short-term patterns reflected seasonal changes in growth and the availability of food. The medium term cycles gave a clear indication of the impact of the hydrodynamic forcing, which acts in the same way as reported for IGBEM (Fulton et al., this volume) and PPBIM (Murray and Parslow, 1997). The long-term dynamics were not as regular as the short and medium term patterns. Instead they often represented transient events (although these could last for a decade or more), after which the group would return to biomass levels and cycle characteristics very similar to those before the event (one such event is included in Fig. 10). These 'events' were caused by the coincidental occurrence of conducive physical and biological conditions (primarily the densities of predators, prey and competitors). That both models suggest that physical and biological interactions, free from the impacts of esca-

lating human activities, can cause substantial changes in biomass that persist for a decade or more is intriguing. It also suggests that current efforts, focused by concern over climatic change and other human impacts, may not be completely successful in separating natural dynamics and anthropogenically driven change.

4.2.3. Effects of eutrophication

While models can highlight that not all major changes in ecosystem structure and function are necessarily due to human intervention, they can also be instructive in showing where to look for human induced change. To be useful in identifying critical human-induced ecosystem behaviours, ecosystem models must be able to capture the gross changes that occur when a system becomes eutrophied. Both BM2 and IGBEM capture the major system changes
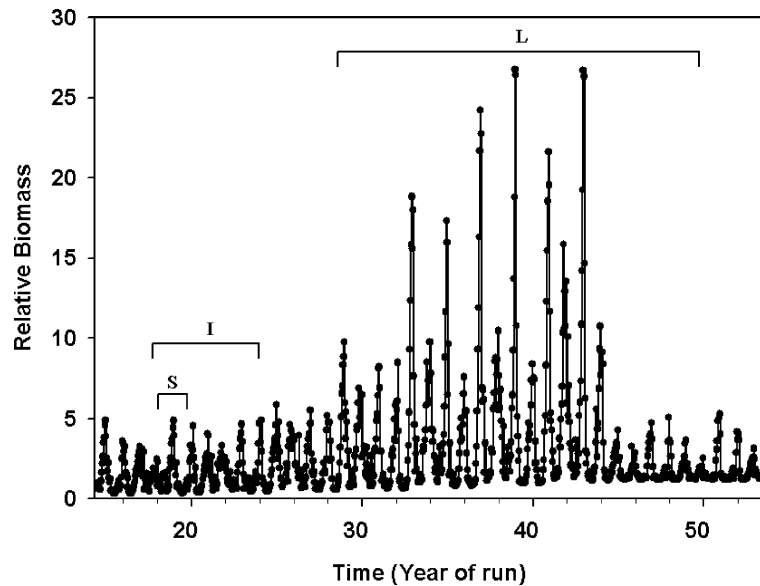
Fig. 10. The biomass (mg AFDW m^{-2}) through time for the aerobic bacteria in box 23 (see Fig. 2) of BM2 (time series taken from a 100-year run), it reveals examples of seasonal, interannual and long-term variation. The small span marked with S is an example of seasonal variation, the larger span marked with I is an example of interannual variation and the largest span marked with an L is an example of long-term variation.

that occur with eutrophication, i.e. simplification in biological structure, changes in relative community composition, a 'left-shift' to smaller animals in the size spectrum and an eventual drop in productivity.

BM2 (like IGBEM, Fulton et al., this volume) predicts that, with an increase in nutrients, the communities usually found in the deep central parts of the bay expand to displace the communities typically found in shallower water along the edge of the bay (compare Fig. 9). This in turn causes the decline of some groups (such as the benthic grazers) and the effective extinction of seagrass. Thus, the dynamics of BM2 reflect the simplification in habitat and biological diversity observed in real systems following eutrophication (Gray, 1992). The only macrofaunal groups to increase are deposit feeders, which are tracked by benthic infaunal carnivores, as the levels of detritus in the sediments increase. This is symptomatic of the general habitat change that accompanies replacement of a primary production-based trophic web with a detritus-based web. Notably, the initial rises in biomass and productivity predicted by BM2 under a modest rise in nutrients are completely reversed when nutrients rise by ×10 or more, at which point productivity drops to between 20 and 50% of the original levels and biomass drops by more than half. This is in agreement with the results of IGBEM (Fulton et al., this volume) and field monitoring studies (Harris et al., 1996).

The concordance of predicted dynamics in BM2 with those in nature is also evident for water column groups. While the gross dynamics captured by IGBEM are sound, it does not capture all of the changes in relative community composition that occur with eutrophication (Fulton et al., this volume). In contrast, BM2 correctly captures the changes in composition of all planktonic groups (Table 10). With an increase in nutrient load in BM2, there is a strong increase in the relative abundance of the larger phytoplankton (diatoms and dinoflagellates) and a substantial (50%) decline in the relative abundance of the large zooplankton. This closely follows observations in the field (Murray and Parslow, 1997; Park and Marshal, 2000).

Neither BM2 nor IGBEM predict extensive anoxia and subsequent die off of benthic and fish fauna (as seen in places such as the Baltic), but BM2 does predict seasonal drops in oxygen levels of up to 30% (due to the breakdown of phytoplankton blooms). That this does not progress to anoxia is because the bay

Table 10
Relative abundance of the large and small size fractions of the phytoplankton and zooplankton communities in the runs of BM2 and IGBEM using the nutrient loadings of PPB (PM run) and CB (CM run)

Size fraction	PM–BM2	PM–IGBEM	PPB	CM–BM2	CM–IGBEM	CB
Large phytoplankton (>20 μm)	0.30	0.27	0.28	0.65	0.22	0.75
Small phytoplankton (0.2–20 μm)	0.70	0.73	0.72	0.35	0.78	0.25
Large zooplankton (2–200 μm)	0.6	0.55	0.64	0.23	0.35	0.19
Small zooplankton (0.2–20 mm)	0.4	0.45	0.36	0.77	0.65	0.81

Empirical values for CB (Madden and Kemp, 1996) and PPB (Harris et al., 1996) are included for comparison.

is well mixed. The formulations used in BM2 and IGBEM should allow for the development of anoxia in suitable physical conditions, but as yet physical geometries more conducive to the formation of anoxic conditions under high loading (e.g. a deeper or more stratified bay) have not been tested. While there is no anoxia-related collapse of the fish, BM2 does predict a decline in the average size of fish. This is most severe for herbivorous fish, which decline in size by 10% or more and this agrees with patterns recorded in the field (Tober et al., 1996). This not only leaves fish vulnerable to predation for longer, but it could significantly affect recruitment. This potential effect is masked by the constant recruitment function employed in the default runs of BM2 and IGBEM.

There are important physical and chemical consequences of increased nutrient load, and these are more evident in BM2 due to its improved handling of the microfauna in the sediments. There is a severe drop in denitrification efficiency, particularly in the centre of the bay, as nutrient levels rise. This is severe enough under even a moderate (fivefold) rise in nutrients that the usual route of nitrogen disposal (via denitrification) is overwhelmed and nutrients build up to sufficiently high levels that they can now only be exported by flushing. This pattern of behaviour was also observed in PPBIM (Murray and Parslow, 1999a,b) and has not been diluted by addition of other trophic groups, or the modifications made to the sediment model (see Appendix D), during the construction of BM2.

4.3. Model formulation and sensitivity

Without site specific tuning the generic form of BM2 captures the magnitude of the system and accurately reflects the trends in community dynamics that would be caused by large-scale changes in nutrient loading. This qualitative level of information is suffi-cient for giving advice on management strategies and the expected effects of change, but more accurate predictions may still be desired and these can only be supplied by site-specific tuning. The groups most sensitive to the parameter setting used in BM2 appear to be the zooplankton, zoobenthos (mainly the epifaunal carnivores, deposit feeders and meiobenthos) and the benthic primary producers (particularly the seagrass and microphytobenthos). Using the default parameter values for these groups will produce spatial distributions, relative biomasses and community compositions that are close to those of the real system being modelled. However, there is a substantial improvement in biomass, production and consumption estimates given by BM2 with the site-specific tuning of these groups.

As it requires more tuning on a case-by-case basis BM2 is more sensitive to parameter settings than IGBEM. This sensitivity was noted in PPBIM (Murray and Parslow, 1997) and may be a general feature of the kind of formulation used in PPBIM and BM2. This suggests that this simpler type of formulation is not as robust as that used in IGBEM and ERSEM against changes in species composition, as it is more sensitive to shifts in parameter values that would probably accompany such changes in composition. In addition, many of the trophic sets in BM2 have a wider range of biomass values than in IGBEM suggesting that the simpler process formulation used in BM2 is not as limiting as the use of internal nutrient ratios in IGBEM. This may explain why the biomass ranges for the benthic groups in BM2 tend to be large. The simple assimilation equations used in BM2 apparently lack the degree of potential population regulation captured in the use of internal nutrient ratios in IGBEM.

Equations of the form used for the invertebrate groups in BM2 are commonly used in water quality modelling. The field of water quality (and plankton) modelling is well developed and so the equations used

have been examined extensively and their limitations and associated remedies (e.g. model closure using quadratic mortality, Steele and Henderson, 1992; Edwards and Brindley, 1999; Murray and Parslow, 1999b; Edwards and Yool, 2000) are well understood. By comparison, ecological modelling of benthic communities is at an early stage. In particular, processes controlling the food web based on detritus are rather unclear. Therefore, the general form of the pelagic invertebrate groups is also used for the benthic invertebrates in BM2, with the addition of space-based limitation of sedentary epifauna and oxygen-related constraints on the infauna. This structure is adopted because there is no available information indicating that many additional processes were necessary. However, our results suggest that benthic groups and processes may be more constrained than previously thought.

Explosive growth and associated trophic cascades were not seen in IGBEM, but they were observed occasionally in BM2, primarily in the benthic groups. In particular, the benthic deposit feeders and microphytobenthos were observed to escape predators and undergo almost exponential growth (in turn depressing competitors and prey) under certain parameterisations and nutrient conditions. While this may be symptomatic of the sensitivity of BM2 to parameter settings, it may also imply that a critical limiting factor (such as the availability of space) has been omitted from the formulation of the benthic groups. As benthic modelling matures it may be pertinent to include spatial limitation, similar to that applied to the benthic suspension (filter) feeders, even for mobile groups and those not confined to the sediment–water interface. Given that these animals, regardless of their mobility, are largely confined to the aerobic layers of the sediment (Barnes, 1987; Webber and Thurman, 1991), which is typically shallow, there is a sound biological basis for this idea. Alternatively, more sophisticated and dynamic grazing functions, ones that incorporate bounds or reflect the effects of predator avoidance on feeding behaviours, may produce better performance (Fulton et al., 2003b).

4.4. Nutrient limitation

Models such as BM2 use the external (water column) nutrient ratio to determine the effective uptake of nutrients by the primary producers, whereas models such as IGBEM use the internal (cellular) nutrient ratios to determine nutrient uptake (Baretta-Bekker et al., 1997) (also see Table 1). Under oligotrophic conditions the use of external nitrogen-based nutrient limitation may not work. In the case of highly oligotrophic systems, such as the Baltic Sea (Thomas et al., 1999), there is evidence that only internally based Droop-like equations (formulated following the ideas of Droop, 1973, 1974) will accurately reflect the dynamics of the primary producers (Baretta-Bekker et al., 1997). The nitrogen and phosphorus of the POM in these areas is preferentially remineralised and the resulting decline in DIC over the growing season is much greater than predicted from a fixed (Redfield) ratio conversion of the decline in nutrients (Thomas et al., 1999; Osterroht and Thomas, 2000). Simulation runs completed for IGBEM and BM2 in which nutrient inputs were 20% of those in standard runs match these observations. The new production predicted by IGBEM is between 1.2 and 2.5 times that given by BM2 and this agrees with the findings of Osterroht and Thomas (2000) that new production based on DIC consumption is, on average, 1.5 times that based on nitrate consumption. These findings indicate that simple nutrient uptake and growth, like that in BM2, is sufficient when nutrients are in excess. However, when nutrients are low the luxury uptake facilitated by Droop-like equations is required if system level behaviour is to be captured faithfully.

4.5. Mixotrophy

In a comparison of runs with and without mixotrophy, the biomass of dinoflagellates is increased 10-fold if mixotrophy is allowed. Further, the rate of growth increased by 1.5–1000 times with mixotrophy and this matches the increases seen in laboratory experiments comparing phototrophic and mixotrophic growth in the dinoflagellates *Fragilidium* (Jeong et al., 1999) and *Gyrodinium galatheanum* (Li et al., 1999). This boost to growth allowed the dinoflagellates to persist when they would have dropped to negligible levels if dependent on phototropic growth alone. Thus, a weakness in many previous models is corrected by the inclusion of a rudimentary representation of a real biological process, rather than by setting growth rates to the upper bounds given in the literature (as

is necessary to even partially correct the problem in IGBEM).

4.6. Attached bacteria and the sediment chemistry

The method of handling attached bacteria in BM2 also works well. It produces bacterial biomasses that match field estimates. For instance, the estimate is within 10% of that for the Kromme Estuary in South Africa (Heymans and Baird, 1995), one of the few for which estimates of bacterial biomass has been made. It also reproduces estimates of annual efflux that are of realistic levels. The prediction by BM2 that the efflux for a PPB-like bay is roughly 6500 t of DIN per year matches the sediment chamber estimate for PPB of about 11,000–16,000 t DIN well. In contrast, the process-based representation of bacteria and denitrification trialled in an early version of IGBEM was incapable of producing realistic sediment chemistry.

4.7. Overall performance

A summary of all of the results (Table 11) indicates that in spite of its sensitivities and potential weaknesses, BM2 does capture the major changes seen in systems that are under pressure. In comparison with IGBEM, the behaviour of BM2 was not as flexible when spanning large changes in ecosystem forcing (e.g. large changes in external inputs of nutrients) and BM2 occasionally produces anomalous behaviours, such as the almost exponential growth of the deposit feeders under certain parameterisations and nutrient conditions. Crucially however, the performance of BM2 compares favourably with that of IGBEM under the same conditions and can even be better than it for some aspects of the system (e.g. the community composition of the benthos). As a result, for the purposes of understanding the general trends in system dynamics under current or changing conditions, BM2 is as capable of representing system behaviour as the more detailed model IGBEM. These results make it clear that simpler formulations are as capable of capturing the emergent properties and characteristics of marine ecosystems as larger models that include detailed physiology. This shows that physiological detail is not always required and that simpler formulations, such as those employed in BM2, are usually adequate for learning and general predictive

purposes. This is important because, in comparison with IGBEM, BM2 uses less than half the number of parameters, required less than one sixth of the development time, and one tenth of the time to validate, verify and calibrate.

4.8. Minimum marine ecosystem model requirements

BM2 and IGBEM share many common features (like the trophic web), but they do cover a slightly different set of processes (for instance, BM2 incorporates mixotrophy while IGBEM does not). Considering their differences and their relative performances, as well as findings from the broader study of model structure on performance (Fulton et al., 2003a) that this research was part of, there appears to be a few minimum requirements for successful system models. If a coastal ecosystem model is going to be used to aid in understanding system dynamics or predict change associated with various nutrient loads then one of the most crucial features it must include is a good representation of denitrification and sediment chemistry. This facet of the model can have a disproportionate effect on model dynamics and if handled poorly the model will not give a good indication of the effects of loading (Murray and Parslow, 1997; Fulton et al., 2003a). More generally, ecosystem models (whether biogeochemical or not) must incorporate enough of the trophic web to capture alternative system states and community shifts associated with anthropogenic pressures, such as fishing or changing nutrient loads. This means that not only groups of interest (like harvested or indicator species) should be included, but their "supporting groups" too. These "supporting groups" often provide the links in the system which tie different habitats together (e.g. the pelagic and demersal in shallow coastal systems) or allow for the state of the system to shift, as they have different tolerances or allow for a redirection of trophic flows when old paths are no longer efficient or available (Baretta et al., 1995; Pahl-Wostl, 1997; Fulton et al., 2003a). The trophic web included in a model has a big impact on predictions regarding productivity, community composition and habitat structure. In one way or another these are the primary concerns of all ecosystem models. The inclusion of a good sediment chemistry model (if concerned with the effects of nutrient loads) and more importantly a food web with appropriate trophic

Table 11
Comparison of the overviews of all results for BM2 and the IGBEM

Measure	Results for BM2	Results for IGBEM
Average biomass	Only benthos and microphytobenthos have average model values that are significantly different from the average empirical value. BM2's predictions are closer to empirical values than IGBEM's for macrophytes, chlorophyll a and dissolved inorganic nitrogen. The models behave equally well for microphytobenthos.	Only benthos and microphytobenthos have average model values that are significantly different from the average empirical value. IGBEM predictions are closer to empirical values than BM2's for zooplankton, fish, meiobenthos, benthos and detritus.
Biomass—PM vs. PPB	BM2's predicted biomass for all trophic sets except meiobenthos, microphytobenthos and zooplankton are within the bounds of empirical interannual variation.	IGBEM's predicted biomass for all trophic sets except microphytobenthos and detritus are within the bounds of empirical interannual variation.
Biomass—CM vs. CB	BM2's predicted biomass for all trophic sets except meiobenthos, macrophytes and detritus are within the bounds of empirical interannual variation.	IGBEM's predicted biomass for all trophic sets except detritus are within the bounds of empirical interannual variation.
Community composition (PM vs. PPB)	BM2's predicted community composition for both fish and benthos reflect those of PPB and are closer than those predicted by IGBEM.	IGBEM over represents pelagic fish groups. Relative community composition of the benthos in the model is close to that of PPB, though there is some suggestion that the model underplays the detritus-based web.
Monbet relationship (Chl a vs. DIN)	Model points are within the range of observed values, but there is a significant difference between regression lines through empirical and model points ($F_{2,102} = 11.19$, $P < 0.0005$), due to a difference in elevations ($F_{2,103} = 20.13$, $P < 0.0005$), but not slopes ($F_{2,102} = 2.05$, $P > 0.1$).	No difference between the regression lines through the empirical and model points ($F_{2,97} = 0.86$, $P > 0.25$).
Size spectra	Size spectra of pelagos holds well with Sheldon et al.'s (1972) observations for real ecosystems. The size spectra of the benthos holds with Schwinghammer's relationship for all groups. The size spectra for BM2 reasonable those of real systems more closely than the size spectra from IGBEM do.	Size spectra of pelagos holds with Sheldon et al.'s (1972) observations for real ecosystems. Benthos does not hold with Schwinghammer's relationship, as the bacteria in the model are <2% of the field average (from Schwinghamer, 1981).
System indices—range	Only total throughput for the CM run is beyond the range of values given by real ecosystems.	Only total throughput for the CM run is beyond the range of values given by real ecosystems.
System indices—average	Model values conform well with empirical values ($r = 0.94$), and are marginally better than IGBEM.	Model values conform well with empirical values ($r = 0.91$).
System indices—PM vs. PPB	There is a strong match between model and empirical estimates ($r = 0.94$) and the predicted value of 9 of the 11 indices are within a factor of two of the empirical estimates.	Overall a strong relationship exists between the model and empirical values ($r = 0.90$), but only 4 of the 11 indices have model values that are within a factor of two of the empirical estimates.
Spatial structure	Eleven biological areas and 16 geophysical areas exist in the PM run, and 12 biological areas and 14 physical areas. Biological interactions and physical factors produce the biological areas. 'Central communities' and 'edge communities' exist. When areas sharing communities are pooled to produce zones, these zones match observed zonation patterns more closely than zones predicted by IGBEM.	Fourteen biological areas and 12 geophysical areas exist in the PM run, and 10 biological areas and 9 physical areas in the CM run. Biological interactions and physical factors produce the biological areas. 'Central communities' and 'edge communities' exist.
Temporal structure	Seasonal, interannual and long-term (5–20 years) cycles are evident, though variation is damped in the epibenthos.	Seasonal, interannual and long-term (5–20 years) cycles are evident.

Table 11 (*Continued*)

Measure	Results for BM2	Results for IGBEM
Effects of eutrophication	With an increase in nutrients, BM2 predicts a loss of biological diversity (seagrass is lost from the system and benthic grazers decline substantially), a simplification in habitat structure, a shift in the relative dominance of primary production and detritus-based food webs, a peak and decline in benthic productivity, a change in the composition of planktonic groups (proportion due to large phytoplankton rises, while the proportion due to large zooplankton falls), and an expansion of communities tolerant to stressful conditions. BM2 does fail to predict fish stock collapses seen in severely eutrophied ecosystems, but its representation of the other pelagic components is consistent with that observed in real systems (unlike the predictions for plankton in IGBEM).	No groups are lost from the model as nutrients increase, but it does predict changes in habitat structure, increase in production and biomass of pelagic groups, a peak and then decline in benthic groups, shifts in community composition to more opportunistic (smaller, faster growing) groups and an expansion of communities tolerant to low light and high levels of nutrients and detritus. This matches general characteristics of the observed changes in real systems with eutrophication (Harris et al., 1996). However, the shift in the phytoplankton community composition is not consistent with that observed in real systems (the model predicts rise in small phytoplankton rather than the diatoms). IGBEM also fails to predict any fish stock collapses, as seen in severely eutrophied ecosystems.
Model sensitivity	The default parameter set is able to qualitatively capture gross system dynamics over a wide range of conditions, but for more accurate results retuning is required for some groups (in particular zooplankton, epifaunal carnivores, deposit feeders, meiobenthos, seagrass, and microphytobenthos). BM2 is more sensitive to parameter settings and changes in species composition than IGBEM.	The default parameter set is able to capture gross system dynamics over a wide range of conditions without the need for case-by-case retuning.
Nutrient limitation	Under oligotrophic conditions new production is on average 1.5 times lower than it should be.	New production is of the correct magnitude regardless of the prevailing nutrient conditions.
Mixotrophy	Dinoflagellates persist at levels observed in real systems in laboratory experiments.	Dinoflagellates usually fall to negligible levels.
Sediment chemistry	Bacterial biomasses are close field estimates, as are estimate levels of annual efflux and water column DIN concentrations across a range of nutrient loadings.	Process-based version unable to capture realistic sediment chemistry dynamics, predicted high levels of DIN in the water column irrespective of the external loads imposed.

coverage and resolution seems to be much more important than the level of detail incorporated in the formulation of these features.

5. Conclusions

A holistic approach to the environment is becoming an integrated part of the way resource use is thought about and dealt with (Gislason et al., 2000). As a result ecosystem models are being developed as predictive and heuristic tools. Although a lot of work remains to be done with regard to understanding the most efficient and effective ways of constructing these models. As one step in this process, BM2 was constructed to allow for an analysis of the effect of formulation detail on model behaviour and performance.

Overall, BM2 does function well, reproducing patterns and values that match far more detailed models and reality. This makes it a good basis for further study of model complexity, for example, to investigate the effects of the form of grazing and mortality terms. It also indicates that it is possible to capture the qualitative dynamics of systems without resorting to highly detailed physiological structures that characterise other ecosystem models (e.g. ERSEM, Baretta et al., 1995; Baretta-Bekker and Baretta, 1997; or IGBEM, Fulton et al., this volume). This is not to say that models such as BM2 are not without drawbacks. There will be occasions when the simple formulations used in BM2 will be incapable of reproducing the real dynamics accurately, e.g. in oligotrophic waters Droop-like equations would be needed to describe phytoplankton growth. The simpler structure used in BM2 also means it is not as flexible as that of the more physiologically detailed model like IGBEM. This means that BM2 requires more tuning on a site-to-site basis and may quantitatively break down under very large changes in nutrient loading. In many instances it would not take much effort to modify BM2 to include formulations (such as Droop-like equations) that correct or temper this problems. Moreover, the BM2's weakness are tied to specific conditions (e.g. oligotrophic conditions), or are highlighted by anomalous behaviour (e.g. excessive benthic population expansions), or alleviated by site-specific tuning and so they are easily detected, acknowledged or avoided. Nevertheless, even without such modification and with

an eye to consideration of common system dynamics and the representation of a generic temperate marine bay system, models like BM2 are instructive while requiring less information than other biogeochemical ecosystem models currently in use, such as ERSEM (Baretta et al., 1995; Baretta-Bekker and Baretta, 1997) or IGBEM (Fulton et al., this volume).

Acknowledgements

Appendix A

Meaning of the acronyms, functional group codes and symbols used (Tables A.1–A.3).

Appendix B. Rate of change and process equations

B.1. Rate of change equations

B.1.1. Autotrophs

Rate of change for standard water column primary producer (PX):

$$\frac{d(PX_w)}{dt} = G_{PX_w} - M_{lys,PX_w} - \sum_{i=\text{predator groups}} P_{PX_w,i} \quad (B.1)$$

Table A.1
List of acronyms used in this paper

Acronym	Meaning
BM2	Bay Model 2
CM	Model runs with nutrient loadings scaled to match the loadings of Chesapeake Bay
IGBEM	Integrated Generic Bay Ecosystem Model
PPB	Port Phillip Bay (near Melbourne, Australia)
PPBIM	Port Phillip Bay Integrated Model
PM	Model runs with nutrient loadings scaled to match the loadings of Port Phillip Bay

Table A.2
List of components in BM2 and the IGBEM, compared to those in the PPBIM

Component	Code name	Model	
		BM2/ IGBEM	PPBIM
Diatoms[a]	PL	Y	Y
Autotrophic flagellates	AF	Y	
Picophytoplankton	PS	Y	Y
Dinoflagellates	DF	Y	Y
Free-living pelagic bacteria	PFB	Y	
Pelagic attached bacteria[b]	PAB	Y	
Heterotrophic flagellates	HF	Y	
Microzooplankton	ZS	Y	Y
Large omnivorous zooplankton	ZL	Y	
Large carnivorous zooplankton	ZLC	Y	Y
Planktivorous fish	FP	Y	
Piscivorous fish	FV	Y	
Demersal fish	FD	Y	
Demersal herbivorous fish	FG	Y	
Macroalgae	MA	Y	Y
Seagrass	SG	Y	Y
Microphytobenthos[a]	MB	Y	Y
Macrozoobenthos (epifaunal carnivores)	MZ	Y	
Benthic (epifaunal) grazers	BG	Y	
Benthic suspension feeders	BF	Y	Y
Infaunal carnivores	BC	Y	
Benthic deposit feeders	BD	Y	
Meiobenthos	OB	Y	
Aerobic bacteria	AEB	Y	
Anaerobic bacteria	ANB	Y	
Labile detritus	DL	Y	Y
Refractory detritus[a]	DR	Y	Y
DON	DON	Y	Y
Ammonia	NH	Y	Y
Nitrate	NO	Y	Y
Dissolved silicate	Si	Y	Y
Dissolved oxygen	O_2	Y	Y[c]
Light	IRR	Y	Y
Salinity	SAL	Y	Y
Sediment grain types	PHI	Y	Y
Bottom stress	STRESS	Y	Y
Porosity	POR	Y	Y
Volume	VOL	Y	Y

All living and dead components have nitrogen pools in all three models, in IGBEM they also have carbon and phosphorous pools.
[a] Also have an internal silicon pool.
[b] This component is only present as a separate entity in BM2, in IGBEM there is a single pelagic bacteria component.
[c] Handled as nitrogen fluxes scaled by the Redfield ratio N:O = 1:16.

Table A.3
List of main terms used in the equations in Appendices B–E

Term	Meaning
E	Excretion (ammonia produced by a consumer)
F	Fishing (catch)
G	Growth
M	Mortality
P	Uptake
R	Remineralisation
S	Sediment chemistry (nitrification or denitrification, the subscript will denote which on a case-by-case basis)
W	Waste (detritus produced by a consumer)
XX	All doubles (and triples) refer to components of the model (see Table A.2 for definitions). They do not represent multiplications at any time and any multiplications will be explicitly denoted by a '($\cdot$)'.

All terms, variables, constants and expressions are defined in the relevant appendices, but this may be a useful quick reference for the main terms and conventions.

$$\frac{d(PX_{sed})}{dt} = -M_{nat,PX_{sed}} \tag{B.2}$$

where G_{PX} stands for the growth of PX, $M_{lys,PX}$ is the loss of PX due to lysis, $M_{nat,PX}$ is the natural mortality losses of PX when in the sediments and $P_{PX,i}$ are the losses of PX due to predation. The equations for the benthic primary producers are slightly different. The rate of change of microphytobenthos is given by:

$$\frac{d(MB_w)}{dt} = G_{MB_w} - M_{lys,MB_w} - \sum_{i=\text{water predator groups}} P_{MB_w,i} \tag{B.3}$$

$$\frac{d(MB_{sed})}{dt} = G_{MB_{sed}} - M_{nat,MB_{sed}} - \sum_{i=\text{sed predator groups}} P_{MB_{sed},i} \tag{B.4}$$

The macrophytes (MX) are restricted to the epibenthic layer and have no water column or sediment pools. The general form of their rate of change is as follows:

$$\frac{d(MX)}{dt} = G_{MX} - M_{MX} - \sum_{i=\text{predator groups}} P_{MX,i} \tag{B.5}$$

The process equations for primary producers are given below and modification to these equations due

to mixotrophy in dinoflagellates are noted in the main text.

B.1.2. Invertebrate consumers

Rate of change for a standard invertebrate consumer (CX):

$$\frac{d(CX)}{dt} = G_{CX} - M_{CX} - \sum_{i=\text{predator groups}} P_{CX,i}$$
$$- F_{CX} \tag{B.6}$$

$$s_{FX_i} = \begin{cases} U_{FX_i} \cdot \max(0, (Z_{FX} \cdot (1 + X_{RS}) \cdot FX_{i,s} - Y_{FX})), \\ U_{FX_i} \cdot \max\left(0, \begin{pmatrix} Z_{FX} \cdot (1 + X_{RS}) \cdot FX_{i,s} + (FX_{i,s} + FX_{i,r}) \\ -Y_{FX} - (1 + X_{RS}) \cdot FX_{i,s} \end{pmatrix}\right), \end{cases}$$

where F_{CX} stands for losses due to fishing on this group (this is set to zero in all standard runs of BM2). Invertebrate consumers are restricted to having only a water column or epibenthic or sediment pool and cannot have pools in multiple layers.

B.1.3. Fish consumers

The following are the rates of change for a fish group (FX):

$$\frac{d(FX_{i,s})}{dt} = G_{FX_{i,s}} \tag{B.7}$$

$$\frac{d(FX_{i,r})}{dt} = G_{FX_{i,r}} \tag{B.8}$$

$$\frac{d(FX_{i,d})}{dt} = T_{IMM,FX_i} - T_{EM,FX_i} - M_{FX_i}$$
$$- \sum_{j=\text{predator groups}} P_{FX,j} - F_{FX_i} \tag{B.9}$$

where the subscript i represents age group i (there is one equation for each age class included), s stands for structural weight (skeletal and other material that cannot be reabsorbed), r for reserve weight (fats and other tissues that can be broken down when food is scarce) and d for density. The T terms represent the movement of fish in to (T_{IMM,FX_i}) and out of (T_{EM,FX_i}) the cell. In addition there are short-term spawning and recruitment events which effect the various FX pools. At the same point each year (the exact day dependent on the fish and with a window of ± 14 days) the fish spawn

and the materials required to do this is removed from the reserve weight of FX. At this point all fish are aged one age class and the oldest age class leaves the bay (this is used in place of a plus group as it is more representative of the dynamics of PPB, Gunthorpe et al., 1997). Sometime later (the exact period dependent on the group) the recruits settle out and their weights and density are assigned to the youngest age class.

The amount of reserve weight (mg N per individual) that is used up during spawning is given by:

$$\begin{matrix} FX_{i,s} + FX_{i,r} > (1 + X_{RS}) \cdot FX_{i,s} \\ \\ FX_{i,s} + FX_{i,r} < (1 + X_{RS}) \cdot FX_{i,s} \end{matrix}$$
$$\tag{B.10}$$

where U_{FX_i} is the proportion of age group i that is reproductively mature, Z_{FX} is the fraction of the weight of FX used in spawning, Y_{FX} is the spawning function constant and X_{RS} is the ratio of structural to reserve weight in well fed fish.

B.1.4. Inanimate pools

Rates of change for ammonia (NH) in the water column is:

$$\frac{d(NH_w)}{dt} = \sum_{i=PX_w} P_{NH_w,i} - P_{NH_w,MB_w} - P_{NH_w,MA}$$
$$- P_{NH_w,PFB} + \sum_{i=CX_w,BF} E_i + \sum_{i=FX} E_i$$
$$+ \sum_{i=\text{pelagic bacteria}} E_i - S_{NIT,PAB} + R_{NET,w}$$
$$\tag{B.11}$$

and in the sediment:

$$\frac{d(NH_{sed})}{dt} = R_{NET,sed} - S_{NIT,sed} - P_{NH_{sed},MB_{sed}}$$
$$- P_{NH_{sed},SG} + \sum_{i \neq BF,CX_w} E_i \tag{B.12}$$

where $P_{NH,XX}$ is the uptake of NH by the autroph XX, E_{CX} is the production of NH by the consumer CX, $S_{NIT,XB}$ is the amount of NH lost due to nitrification by the bacteria XB, R_{NET} is the amount of NH produced by denitrification.

The rates of change for nitrate (NO) in the water column is given by:

$$\frac{d(\text{NO}_w)}{dt} = \sum_{i=\text{PX}_w} P_{\text{NO}_w,i} - P_{\text{NO}_w,\text{MB}_w} - P_{\text{NO}_w,\text{MA}} + S_{\text{NIT},\text{PAB}} \tag{B.13}$$

and in the sediment:

$$\frac{d(\text{NO}_\text{sed})}{dt} = S_{\text{NIT},\text{sed}} - S_{\text{DENIT},\text{sed}} - P_{\text{NO}_\text{sed},\text{MB}_\text{sed}} - P_{\text{NO}_\text{sed},\text{SG}} \tag{B.14}$$

The rates of change of dissolved silicate (Si) in the water column is:

$$\frac{d(\text{Si}_w)}{dt} = R_{\text{DSisol},w} - \sum_{i=\text{PL}_w,\text{MB}_w} P_{\text{Si}_w,i} \tag{B.15}$$

and the rate of change of detrital silica (DSi) in the water column is given by:

$$\frac{d(\text{DSi}_w)}{dt} = X_{\text{SiN}} \cdot \left(\sum_{i=\text{PL}_w,\text{MB}_w} \left(M_{\text{lys},i} + \sum_{j=\text{CX}_w} P_{i,j} \right) \right) - R_{\text{DSisol},w} \tag{B.16}$$

where X_{SiN} is the Redfield ratio of silicon and nitrogen (set at 3.0, Murray and Parslow, 1997) and R_{DSisol} is the amount of detrital silica remineralised. Note that the equations for Si_sed and DSi_sed are as for (B.16) and (B.17) except that CX_sed is used in the place of CX_w and MB is the only PX present in the sediment that uses Si.

The rates of change for dissolved oxygen (O_2) in the water column is given by:

$$\frac{d(\text{O}_{2,w})}{dt} = X_{\text{ON}} \cdot \left(\sum_{i=\text{PX}_w} G_i + G_{\text{MB}_w} + G_{\text{MA}} + \frac{G_{\text{SG}}}{2} \right. $$
$$ - \sum_{i \neq \text{infauna},\text{MZ},\text{BG}} E_i - \sum_{i=\text{FX}} E_i $$
$$ \left. - \sum_{i=\text{pelagic bacteria}} E_i - R_{\text{DON},w} \right) \tag{B.17}$$

and in the sediment:

$$\frac{d(\text{O}_{2,\text{sed}})}{dt} = X_{\text{ON}} \cdot \left(G_{\text{MB}_\text{sed}} + \frac{G_{\text{SG}}}{2} \right. $$
$$ \left. - \sum_{i=\text{infauna},\text{MZ},\text{BG}} E_i - R_{\text{DON},\text{sed}} \right) \tag{B.18}$$

where X_{ON} is the Redfield ratio of oxygen and nitrogen (set at 16.0, Murray and Parslow, 1997) and R_{DON} is the DON lost due to remineralisation.

The rates of change of dissolved organic nitrogen (DON) in the water column is:

$$\frac{d(\text{DON}_w)}{dt} = W_{\text{DON},w} - R_{\text{DON},w} - P_{\text{DON},\text{PFB}} \tag{B.19}$$

and in the sediment:

$$\frac{d(\text{DON}_\text{sed})}{dt} = W_{\text{DON},\text{sed}} - R_{\text{DON},\text{sed}} \tag{B.20}$$

where W_{DON} is the DON produced by bacteria, R_{DON} is the DON lost due to remineralisation and $P_{\text{DON},\text{PFB}}$ is the DON taken up by pelagic free bacteria (PFB).

The rates of change of labile detritus (DL) in the water column is:

$$\frac{d(\text{DL}_w)}{dt} = \sum_{i=\text{CX}_w} W_{\text{DL}_w,i} + \sum_{i=\text{FX}} W_{\text{DL}_w,i} $$
$$ + \sum_{i=\text{pelagic bacteria}} W_{\text{DL}_w,i} $$
$$ + \sum_{i=\text{PX}_w} M_{\text{lys},i} + M_{\text{lys},\text{MB}_w} $$
$$ + M_{\text{MA}} - P_{\text{DL}_w,\text{PAB}} - P_{\text{DL}_w,\text{BF}} \tag{B.21}$$

and in the sediment:

$$\frac{d(\text{DL}_\text{sed})}{dt} = \sum_{i=\text{PX}_\text{sed}} M_{\text{nat},i} + M_{\text{nat},\text{MB}_\text{sed}} $$
$$ + M_{\text{lys},\text{LB}_\text{sed}} + M_{\text{SG}} $$
$$ + \sum_{i=\text{infauna}} (W_{\text{DL},i} - P_{\text{DL}_\text{sed},i}) $$
$$ + \sum_{i=\text{epifauna}} (W_{\text{DL},i} - P_{\text{DL}_\text{sed},i}) $$
$$ - \sum_{i=\text{FX}} P_{\text{DL}_\text{sed},i} \tag{B.22}$$

where $W_{DL,CX}$ is the amount of DL in the waste products from consumer CX and $P_{DL,CX}$ is the DL consumed by CX.

The rates of change of refractory detritus (DR) in the water column is given by:

$$\frac{d(DR_w)}{dt} = \sum_{i=FX} W_{DR_w,i} - \sum_{i=CX_w} P_{DR_w,i} - P_{DR_w,PAB} - J_{DR} \tag{B.23}$$

and in the sediment:

$$\frac{d(DR_{sed})}{dt} = \sum_{i=infauna} W_{DR_{sed},i} - \sum_{i=infauna} P_{DR_{sed},i} + J_{DR} \tag{B.24}$$

where $W_{DR,CX}$ is the DR in the wastes of consumer CX, $P_{DR,CX}$ is the amount of detritus consumed by CX, infauna includes sediment bacteria and J_{DR} is the amount of DR transferred from the water column to sediment pool due to the feeding activities of the benthic filter feeders.

B.2. Process equations

B.2.1. Growth of primary producers
$$G_{PX} = \mu_{PX} \cdot \delta_{irr} \cdot \delta_N \cdot \delta_{space} \cdot PX \tag{B.25}$$

with μ_{PX} is the maximum growth rate, the nutrient limitation factor due to nitrogen is given by:

$$\delta_N = \frac{DIN}{\kappa_{N,PX} + DIN} \tag{B.26}$$

where $DIN = NH + NO$ except for those primary producers which are also limited by the availability of

$$\delta_{space} = \begin{cases} 1 - \dfrac{(CX - \theta_{CXlow})((CX - \theta_{CXlow})/(CX - \theta_{CXlow} + \kappa_{CXsat}))}{(CX - \theta_{CXlow})((CX - \theta_{CXlow})/(CX - \theta_{CXlow} + \theta_{CXsat})) + \kappa_{CXthresh}}, & CX = BF \text{ and } CX > \theta_{CXlow} \\ 1, & \text{otherwise} \end{cases} \tag{B.34}$$

Si then nutrient limitation is given by:

$$\delta_N = \min\left(\frac{DIN}{\kappa_{N,PX} + DIN}, \frac{Si}{\kappa_{Si,PX} + Si}\right) \tag{B.27}$$

and light limitation is given by:

$$\delta_{irr} = \min\left(\frac{IRR}{\kappa_{irr,PX}}, 1\right) \tag{B.28}$$

with the κ representing the half saturation constants for the respective processes, and space limitation as follows:

$$\delta_{space} = 1 - \frac{PX}{\theta_{PX,max}} \tag{B.29}$$

Using the above formulations for growth and nutrient limitation the nutrient uptake functions for the primary producer PX are given by:

$$P_{NH,PX} = G_{PX} \cdot \frac{NH}{\kappa_{NH,PX} + NH} \cdot \frac{\kappa_{NH,PX} + DIN}{DIN} \tag{B.30}$$

$$P_{NO,PX} = G_{PX} \cdot \frac{NO}{DIN} \cdot \frac{\kappa_{NH,PX}}{\kappa_{NH,PX} + NH} \tag{B.31}$$

where $\kappa_{NH,PX}$ is the half saturation constant for the uptake of NH. In addition, for PL and MB there is the uptake of Si as follows:

$$P_{Si,PX} = X_{SiN} \cdot G_{PX} \tag{B.32}$$

B.2.2. Growth of consumers
The growth of an invertebrate consumer (CX) is given by:

$$G_{CX} = \left(\varepsilon_{CX} \cdot \sum_{i=living\ prey} P_{i,CX} + \sum_{j=DL,DR} P_{j,CX} \cdot \varepsilon_{CX,j}\right) \cdot \delta_{space} \cdot \delta_{O_2} \tag{B.33}$$

where ε_{CX} is the growth efficiency of CX when feeding on live prey, $\varepsilon_{CX,j}$ the efficiency when feeding on detritus (DL treated separately to DR), space limitation given by:

where θ_{CXmax} is the maximum biomass per area allowed for CX, θ_{CXlow} is the crowding lower threshold, κ_{CXsat} is the crowding half saturation level, and $\kappa_{CXthresh}$ is the crowding threshold (this formulation is based on that of ERSEM II, Blackford, 1997). The oxygen limitation in the standard runs of BM2 is given by:

or $\delta_{O_2} = \begin{cases} \dfrac{\gamma_{O_2}}{\gamma_{O_2} + \kappa_{CX,MO_2}}, & \text{if epifauna or infauna} \\ 1, & \text{if pelagic} \end{cases}$ (B.35)

where γ_{O_2} is the depth of the oxygen horizon and κ_{CX,MO_2} is the half oxygen mortality depth.

The growth for each fish group, is calculated by equation of the same form as (B.34), but per age group of each fish, the result is then apportioned to structural and reserve weight increases such that:

$$G_{FX_{i,s}} = \Lambda \cdot G_{FX,i}$$ (B.36)

$$G_{FX,i} = (1 - \Lambda) \cdot G_{FX,i}$$ (B.37)

where

$$\Lambda = \begin{cases} \dfrac{(1/X_{RS}) + X_{pR,FX} \cdot (-FX_{i,r}/(X_{RS} \cdot FX_{i,x}))}{(1/X_{RS}) + (FX_{i,r}/(X_{RS} \cdot FX_{i,x}))}, \\ \quad \text{if} > 0 \text{ and } G_{FX,i} > 0 \\ 0, \\ \quad \text{otherwise} \end{cases}$$ (B.38)

with X_{RS} the maximum ratio of reserve to structural weight FX can have and $X_{pR,FX}$ is the relative degree to which FX concentrates on replenishing reserves rather than undergoing structural growth when underweight.

In the standard form of BM2 presented here the grazing term is given by:

$$P_{prey,CX} = \frac{CX \cdot k_{CX} \cdot p_{prey,CX} \cdot prey}{1 + k_{CX} \cdot \left(\left(\varepsilon_{CX} \cdot \left(\sum_{j=\text{live prey groups}} p_{j,CX} \cdot j \right) + \varepsilon_{CX,DL} \cdot p_{DL,CX} + \varepsilon_{CX,DR} \cdot p_{DR,CX} \right) / \mu_{CX} \right)}$$ (B.39)

where 'prey' is the group being consumed by CX, k_{CX} is the clearance rate of CX and $p_{prey,CX}$ is preference (or availability) of that prey for the predator CX. This last parameter is similar to the 'vulnerability' parameters in ECOSIM (Christensen et al., 2000) and represents the fact that the entire prey population will not be available to the predators at any one time (some may be hiding for instance). The availability of the food is further modified if the spatial range of the predator and prey do not completely overlap (and so explicit spatial refuges exist). The available fish in cohort i of fish group FX (FX$_i$), for the fish eating cohorts of piscivorous (FV) and demersal (FD) fish (FY$_j$), is given

by:

$$A_{FX_i} = \begin{cases} \sum p_{FX_i,FX_j} \dfrac{(FX_{i,x} + FX_{i,r}) \cdot FX_{i,d}}{\text{cell\_vol}}, \\ \quad \Theta_{low,FY} \cdot FY_{j,s} \le FX_{s,i} \le \Theta_{up,FY} \cdot FY_{j,s} \\ 0, \\ \quad \text{otherwise} \end{cases}$$ (B.40)

where $\Theta_{low,FY}$ is the lower prey selection size limit for FY and $\Theta_{up,FY}$ is the upper prey selection size limit. The availability of benthic prey to their predators (fish and invertebrate alike) is calculated in a slightly different way and is as follows:

$$A_{prey} = prey \cdot d_{prey}$$ (B.41)

where, if aerobic

$$d_{prey} = \begin{cases} 0, & \gamma_{CX} < \gamma_{top} \\ \dfrac{\gamma_{CX} - \gamma_{top}}{\gamma_{O_2} - \gamma_{top}}, & \gamma_{top} < \gamma_{CX} < \gamma_{O_2} \\ 1, & \gamma_{top} < \gamma_{O_2} < \gamma_{CX} \end{cases}$$ (B.42)

and if anaerobic

$$d_{prey} = \begin{cases} 1, & \gamma_{CX} < \gamma_{top} \\ \left(1 - \dfrac{\gamma_{CX} - \gamma_{top}}{\gamma_{O_2} - \gamma_{top}}\right), & \gamma_{top} < \gamma_{CX} < \gamma_{O_2} \\ 0, & \gamma_{top} < \gamma_{O_2} < \gamma_{CX} \end{cases}$$ (B.43)

where γ_{CX} is the depth in the sediment that the predator CX can forage down to and γ_{top} is set to zero for all standard runs (as only one sediment layer).

B.2.3. Mortality and loss functions

The mortality terms for invertebrate consumers and autotrophs are in terms of lost biomass while those for fish refer to the number of individuals lost. Nevertheless the general form of the equations is the same (but the units of the coefficients obviously differ between the fish and other groups). The natural mortality term for group XX is given by:

$$M_{XX} = m_{lin,XX} \cdot XX + m_{quad,XX} \cdot XX^2 \\ + (1 - \delta_{O_2}) m_{O_2,XX} \cdot XX + m_{special,XX} \cdot XX \\ + m_{top,XX} \cdot XX$$ (B.44)

where $m_{\text{lin,XX}}$ is the coefficient of linear mortality for XX, $m_{\text{quad,XX}}$ is the coefficient of quadratic mortality for the group XX, $m_{\text{O}_2,\text{XX}}$ is the coefficient of oxygen-dependent mortality and $m_{\text{special,XX}}$ is the special (additional) loss rate for XX. This rate of 'special' mortality is usually set to zero, except in the following cases:

$$m_{\text{special,MA}} = \text{STRESS} \cdot m_{\text{STRESS}} \tag{B.45}$$

$$m_{\text{special,SG}} = \text{DIN} \cdot m_{\text{DIN}} \tag{B.46}$$

where m_{STRESS} and m_{DIN} are the coefficient of mortality due to mechanical stress and fouling by epiphytes, respectively. Lastly:

$$m_{\text{special,XX}} = \begin{cases} \dfrac{m_{\text{strave,FX}} \cdot \theta_{\text{strave}} \cdot (1 + X_{\text{RS}}) \cdot \text{FX}_{i,s} - (\text{FX}_{i,s} + \text{FX}_{i,r})}{(1 + X_{\text{RS}}) \cdot \text{FX}_{i,s}}, & \text{if} > 0 \\ 0, & \text{otherwise} \end{cases} \tag{B.47}$$

with $m_{\text{starve,FX}}$ is the threshold ratio of reserve to structural weight at which death due to starvation is likely. The final term of Eq. (B.44) was adopted from ERSEM (Bryant et al., 1995) to represent the impact of seabirds and other top predators and is given by:

$$m_{\text{top,XX}} = m_{\text{seabird,XX}} + m_{\text{shark,XX}} \tag{B.48}$$

While all the groups in the standard run of the model had a linear mortality term, some groups (the fish and higher trophic level zooplankton and benthic groups) suffered mortality described by a quadratic term. This quadratic term represents predation due to groups not explicitly represented in the modelled web. Only benthic consumers had oxygen-dependent mortality, the macrophyte and fish groups had special mortality as shown above and m_{top} is only applied to the fish groups.

Fishing is another process that is only applied to fish in the standard runs. The amount caught at time t is given by:

$$F_{\text{FX},t} = C_{\text{eff}} \cdot (\text{FX}_{s,i} + \text{FX}_{r,i}) \cdot \text{FX}_{d,i} \cdot q_{\text{FX}_i} \tag{B.49}$$

where q_{FX_i} is the catchability of the ith age group of FX and

$$C_{\text{eff}} = \begin{cases} m_{\text{FC,FX}}, & \text{standard runs} \\ \dfrac{m_{\text{FCmax,FX}}}{1 + e^{(-m_{\text{FCa,FX},i,t-1})}}, & \text{effort model on} \end{cases} \tag{B.50}$$

with $m_{\text{FC,FX}}$ is the coefficient of fishing mortality for FX, $m_{\text{FCmax,FX}}$ is the maximum fishing mortality allowed for FX and $m_{\text{FCa,FX}}$ is the coefficient of spread for the fishing mortality of FX. As indicated by (B.50) and (B.51) the fishing implemented for standard runs is a simple catch equation.

The final loss term is one that is applied to the microscopic primary producers only and it represents lysis. The losses of a primary producer (PX) to lysis is formulated as follows:

$$M_{\text{lys,PX}} = \frac{m_{\text{lys,PX}} \cdot \text{PX}}{\delta_{\text{N}} + 0.1} \tag{B.51}$$

where $m_{\text{lys,PX}}$ is the rate of lysis.

B.2.4. Waste processes

The production of waste products by invertebrate consumers and fish are handled in the same way, but in the case of fish the mortality term has to be converted from a density to a biomass before being used in the following equations. The production of labile detritus (DL) by consumer group XX is given by:

$$\begin{aligned} W_{\text{DL}} = \Bigg(& (1 - \varepsilon_{\text{XX}}) \cdot \Gamma_{\text{XX}} \cdot \sum_{i=\text{living prey groups}} P_{i,\text{XX}} \\ & + (1 - \varepsilon_{\text{XX,DL}}) \cdot \Gamma_{\text{XX,DL}} \cdot P_{\text{DL,XX}} \\ & + (1 + \varepsilon_{\text{XX,DR}}) \cdot \Gamma_{\text{XX,DR}} \cdot P_{\text{DR,XX}} \\ & + \varphi_{\text{XX}} \cdot M_{\text{XX}} \Big) \cdot f_{\text{XX,DL}} \end{aligned} \tag{B.52}$$

where φ_{XX} is the proportion of mortality losses assigned to detritus, Γ_{XX} is the proportion of the growth inefficiency of XX when feeding on live prey that is sent to detritus, $\Gamma_{\text{XX,DL}}$ is the proportion of the growth inefficiency of XX when feeding on DL that is sent to detritus, $\Gamma_{\text{XX,DR}}$ is the proportion of the growth inefficiency of XX when feeding on refractory detritus (DR) that is sent to detritus and $f_{\text{XX,DL}}$ is the proportion of the total detritus produced that is of the type DL. The same equation is used for the production of DR (W_{DR}), except that the final multiplication of the brackets by $f_{\text{XX,DL}}$ is replaced by multiplication by $(1 - f_{\text{XX,DL}})$.

The other main waste product is excreted ammonia. The general formulation used for the production of ammonia by a consumer XX (invertebrate or fish) is as follows:

$$
\begin{aligned}
E_{XX} &= (1 - \varphi_{XX}) \cdot M_{XX} + (1 + \varepsilon_{XX}) \cdot (1 - \Gamma_{XX}) \\
&\quad \cdot \sum_{i=\text{living prey groups}} P_{i,XX} + (1 - \varepsilon_{XX,DL}) \\
&\quad \cdot (1 - \Gamma_{XX,DL}) \cdot P_{DL,XX} + (1 - \varepsilon_{XX,DR}) \\
&\quad \cdot (1 - \Gamma_{XX,DR}) \cdot P_{DR,XX}
\end{aligned}
\tag{B.53}
$$

B.2.5. Physical processes

The only physical processes in BM2 that differ from those in PPBIM (detailed in Murray and Parslow, 1997; Walker, 1997) are bioturbation, bioirrigation (detailed in the main text and IGBEM) and the calculation of the light attenuation coefficient. The formulation of the coefficient used in IGBEM is adopted in BM2 and it is an expanded form of the one used in PPBIM. The coefficient is given by:

$$
n = n_w + n_{DON} \cdot DON + n_D \cdot (DL + DR) + n_P \\
\cdot \sum_{i=PX} PX + n_{susp} \cdot SUSP
\tag{B.54}
$$

where n_w is the background extinction coefficient, n_{DON} is the contribution due to DON, n_D is the contribution due to detritus, n_P is the contribution due to phytoplankton (PX) and n_{susp} is the contribution due to suspended sediments (SUSP).

Appendix C. Equations for the dinoflagellates and mixotrophy

The formulation for the rate of change of dinoflagellates is:
$$
\frac{d(DF)}{dt} = G_{DF} - M_{DF} - \sum_{i=DF,ZL} P_{DF,i}
\tag{C.1}
$$

where M_{DF} describes losses due to lysis suffered by the dinoflagellate pool (DF); $P_{DF,i}$ are predation losses suffered by the dinoflagellate pool; and the total growth (G_{DF}) is given by:

$$
G_{DF} = G_{phs,DF} + \varepsilon_{DF} \cdot G_{phag,DF}
\tag{C.2}
$$

where photosynthetic growth ($G_{phs,DF}$) is given by:

$$
G_{phs,DF} = \mu_{DF} \cdot \delta_{irr} \cdot \delta_N \cdot DF
\tag{C.3}
$$

while the phagotrophic contribution ($G_{phag,DF}$) to total growth is given by:

$$
G_{phag,DF} = \min \left(\sum_{\text{prey groups}} P_{i,DF}, \frac{\mu_{DF}}{\varepsilon_{DF}} \cdot \delta_{irr} \right. \\
\left. \cdot (1 - \delta_N) \cdot DF \right)
\tag{C.4}
$$

ε_{DF} is the assimilation efficiency of the mixotrophic dinoflagellates (set at 0.6); μ_{DF} is the temperature-dependent maximum daily growth rate of the dinoflagellates (set at 0.5 mg N per day, Murray, personal communication), δ_{irr} is the light limitation factor, δ_N is the nutrient limitation factor and $P_{i,DF}$ is the amount of prey group i grazed by the predator DF, which is calculated in the same way as for all other grazers in BM2. The light and nutrient limitation factors were largely calculated as for the pure autotrophs in BM2. Since there is strong evidence that dinoflagellates show an increase in efficiency at low light levels (Jeong et al., 1999; Li et al., 1999), there were some modifications made to the formulation of light limitation for this group. The modification is based on general observations that, due to increased efficiency at low light levels, mixotrophic growth rates are two- to threefold higher than those of strict phototrophic growth under identical (low light) conditions (Skovgaard, 1996; Legrand et al., 1998; Li et al., 1999). The final form of the light limitation factor (δ_{irr}) is:

$$
\delta_{irr} =
\begin{cases}
\min(IRR \cdot 0.01 + 0.018, 1), & 0 < IRR \le 0.1 \\
\min \left(\dfrac{IRR}{\kappa_{irr,DF}}, 1 \right), & \text{otherwise}
\end{cases}
\tag{C.5}
$$

and the nutrient limitation factor as

$$
\delta_N = \frac{DIN}{\kappa_{N,DF} + DIN}
\tag{C.6}
$$

where DIN represents the total inorganic nitrogen pool (made up of ammonia and nitrate).

Appendix D. Equations for bacteria and the sediment chemistry

The general formulation for the dynamics of aerobic attached bacteria (where XB stands for pelagic at-

tached bacteria (PAB) or sediment bound aerobic bacteria (AEB)) is:

$$\frac{d(XB)}{dt} = G_{XB} - M_{XB} - \sum_{i=\text{consumer groups}} P_{XB,i}$$
(D.1)

where the growth of the group of bacteria (G_{XB}) is given by:

$$G_{XB} = \mu_{XB} \cdot XB \cdot \max(0, (1 - \rho_{XB})^{\psi})$$
(D.2)

and

$$\rho_{XB} = \frac{XB}{(\tau_{DL,XB} \cdot DL + \tau_{DR,XB} \cdot DR) \cdot \delta_{O_2} \cdot \delta_{stim}}$$
(D.3)

with μ_{XB} representing the maximum temperature-dependent daily growth rate for the group XB. XB is the current pool of bacteria and DL and DR are the labile and refractory detrital pools (all in mg N m^{-3}); $\tau_{DL,XB}$ and $\tau_{DR,XB}$ represent the maximum possible biomass of XB per biomass of that grade of detritus; ψ is the exponent dictating the reduction in growth as the bacterial pool approaches its maximum attainable levels (set to 3 in all standard runs) and δ_{O_2} is the oxygen limitation factor, which is given by:

$$\delta_{O_2} = \begin{cases} \dfrac{\gamma_{O_2}}{\gamma_{O_2} + \gamma_{XB}}, & XB \text{ benthic} \\ 1, & \text{otherwise} \end{cases}$$
(D.4)

where γ_{XB} is the half oxygen mortality depth for XB, and the oxygen horizon (γ_{O_2}) is given by:

$$\gamma_{O_2} = \frac{2 \cdot O_{2,sed} \cdot \gamma_{sed}}{O_{2,bw}}$$
(D.5)

with $O_{2,sed}$ is the concentration of oxygen in the sediments, $O_{2,bw}$ is the concentration in the bottom water and γ_{sed} is the depth of the sediment layer considered in the model. Finally, δ_{stim} indicates the degree of stimulation of the bacteria by bioturbation and it is calculated as follows:

$$\delta_{stim} = \begin{cases} \dfrac{\delta_{te} \cdot 250 \cdot (POR - 0.225)}{193.75}, & XB \text{ benthic} \\ 1, & \text{otherwise} \end{cases}$$
(D.6)

Use of a compound effect of enhanced bioturbation (δ_{te} calculated in the same way as for IGBEM—Fulton et al., this volume), and porosity (POR) is based on

observations by Alongi (1998) and the relationship detailed by Blackburn (1987). Using Eqs. (D.2)–(D.5), the utilisation of labile detritus by aerobic bacteria is given by:

$$P_{DL,XB} = G_{XB} \cdot \frac{\rho_{XB} \cdot \tau_{XB,DL} \cdot DL}{XB \cdot \varepsilon_{XB,DL}}$$
(D.7)

where $\varepsilon_{XB,DL}$ is the assimilation efficiency of the bacteria on labile detritus. The uptake of refractory detritus is calculated similarly. The natural mortality term (M_{XB}) is as for the other invertebrates (Appendix B), but the term representing predation losses to predator group i ($P_{XB,i}$) is given by:

$$P_{XB,i} = P_{DL,i} \cdot \rho_{XB} \cdot \tau_{XB,DL} + P_{DR,i} \cdot \rho_{XB} \cdot \tau_{XB,DR}$$
(D.8)

The waste handling equations for bacteria are also different to those for other invertebrates since wastes are channelled into DON not DL. All of the equations for the anaerobic bacteria (ANB) are as for XB here, except that any δ_{O_2} factors in the equations are replaced by $(1 - \delta_{O_2})$. Adopting these equations for the attached bacteria made it easier to identify a method of introducing dynamic flexibility to the empirical nitrification–denitrification model proposed by Murray and Parslow (1999a) for PPBIM.

To integrate a more interactive form of the processes governing nitrification and denitrification into BM2, the empirical sediment chemistry model used in PPBIM (Murray and Parslow, 1999a) is linked directly to the activities of sediment bacteria and infauna. The amount of ammonia produced by the remineralisation of DON (R_{DON}) is handled as in PPBIM, that is:

$$R_{DON} = \Phi \cdot DON \cdot POR$$
(D.9)

where Φ is the temperature-dependent rate of breakdown for DON (set at 0.00176 per day, Murray, personal communication). In PPBIM, equations similar to (D.9) were used to calculate the production of ammonia due to the breakdown of DL and DR (Murray and Parslow, 1997). This is not the case in BM2, where the production of the remainder of the ammonia is dependent upon the activity of sediment dwelling fauna and flora. Thus, the total ammonia available for nitrification and denitrification (R_{NET}) is:

$$R_{NET} = \max(0, R_{DON} + E_{AEB} + E_{ANB} + \xi$$
$$\cdot (E_{OB} + E_{BD}) - P_{NH,MB})$$
(D.10)

where $P_{NH,MB}$ is the uptake of NH by MB (see equations for autotrophs in Appendix B), E_{XX} is the ammonia released by XX and ξ is the fraction of the excreted NH by infauna that contributes available nitrogen for nitrification and denitrification (set to 0.95 in the standard runs). The form of E_{XX} for OB and BD is of the general form given for heterotrophs in Appendix B, but that for AEB and ANB is slightly different and is given by:

$$E_{XB} = P_{DL,XB} \cdot (1 - \varepsilon_{XB,DL}) + P_{DR,XB}$$
$$\cdot (1 - \varepsilon_{XB,DR}) + M_{XB} - W_{DON} - W_{DR}$$
(D.11)

where E_{XB} is the release of NH by XB, $\varepsilon_{XB,DX}$ is the efficiency of XB on the detritus fraction DX, and the production of DON (W_{DON}) and DR (W_{DR}) are calculated as follows:

$$W_{DON} = (P_{DL,XB} \cdot (1 - \varepsilon_{XB,DL}) + P_{DR,XB}$$
$$\cdot (1 - \varepsilon_{XB,DR}) + M_{XB}\varphi_{XB}) \cdot f_{XB,DON}$$
(D.12)

$$W_{DR} = (P_{DL,XB} \cdot (1 - \varepsilon_{XB,DL}) + M_{XB}\varphi_{XB})$$
$$\cdot f_{XB,DR}$$
(D.13)

where φ_{XB} indicates the fraction of the losses of XB due to natural mortality that are not released as NH and $f_{XB,DX}$ is the fraction of the products of growth inefficiency and mortality directed to the detritus fraction DX. Using Eq. (D.10) the processes of nitrification and denitrification were completed using the form of the empirical model of Murray and Parslow (1999a), giving nitrification (S_{NIT}) as:

$$S_{NIT} = R_{NET} \cdot \theta_{DMAX} \cdot \max\left(0, 1 - \frac{R_{NET} \cdot \gamma_{SED}}{\theta_{r0}}\right)$$
(D.14)

and denitrification (S_{DENIT}) as:

$$S_{DENIT} = S_{NIT} \cdot \min\left(1, \frac{R_{NET} \cdot \gamma_{SED}}{\theta_{rD}}\right)$$
(D.15)

where θ_{DMAX} is the maximum rate of denitrification (set at 0.25, Murray, personal communication), θ_{r0} is the temperature-dependent minimum rate of

respiration that supports nitrification (set at 200, Murray and Parslow, 1997) and θ_{rD} (set at 10, Murray and Parslow, 1997) is the peak of the nitrification–denitrification curve (as defined by, Murray and Parslow, 1999a). This general form is adopted from PPBIM due to its demonstrated performance and robustness (Murray and Parslow, 1999a; Fulton et al., this volume).

The more interactive representation of sediment processes lead to a minor modification to the bioirrigation equations. The formulation remained unchanged from that of PPBIM (Walker, 1997) and IGBEM (Fulton et al., this volume) for the majority of groups, but for oxygen it became:

$$O_{2,bw,t+1} = \frac{(O_{2,bw,t} \cdot VOL_{bw} + O_{2,sed,t} \cdot VOL_{por})}{VOL_{bw} + VOL_{por}}$$
$$+ e^{-\phi_{irr} \cdot ((1/VOL_{bw}) + (1/VOL_{por}))}$$
$$\times \left(O_{2,bw,t} - \frac{(O_{2,bw,t} \cdot VOL_{bw} + O_{2,sed,t} \cdot VOL_{por})}{VOL_{bw} + VOL_{por}}\right)$$
(D.16)

$$O_{2,sed,t+1} = O_{2,sed,t} - \frac{VOL_{bw}}{VOL_{por}}$$
$$\cdot (O_{2,bw,t+1} - O_{2,bw,t})$$
(D.17)

where ϕ_{irr} is the exchange rate due to irrigation (calculated as for IGBEM, Fulton et al., this volume), $O_{2,sed,t}$ is the concentration of oxygen in the sediment at time t, $O_{2,bw,t}$ is the concentration of oxygen in the bottom water at time t, VOL_{bw} is the volume of the bottom water layer and the pore water volume above the oxygen horizon is given by:

$$VOL_{por} = POR \cdot \frac{\gamma_{O_2} \cdot \chi_{cell}}{VOL_{sed}}$$
(D.18)

with VOL_{sed} being the volume of the entire sediment layer and χ_{cell} is the area of the cell. All other parts of the transport model were as implemented in IGBEM (Fulton et al., this volume).

Appendix E. Equations for fish movement

Fish movement (in terms of the density d of fish group FX, age class i, in cell j) in the default set-up of BM2 is given by:

$$FX_{i,d,j} = \begin{cases} FX_{i,tot} \cdot (\vartheta \cdot (FDEN_{j,qrt+1,FX} - FDEN_{j,qrt,FX}) + FDEN_{j,qrt,FX}), & qrt < 4 \\ FX_{i,tot} \cdot (\vartheta \cdot (FDEN_{j,1,FX} - FDEN_{j,qrt,FX}) + FDEN_{j,qrt,FX}), & qrt = 4 \end{cases}$$
(E.1)

where $FX_{i,tot}$ is the total number of FX in age class i in the entire system (that is the sum over all cells), ϑ is the proportion of the current quarter of the year which has already passed, $FDEN_{j,qrt,FX}$ is the proportion of the population of FX found in cell j in the qrt quarter of the year.

For the forage and density-dependent fish movement scheme, the following formulation is used:

$$G_{FX,i,j,\text{potential}}$$
$$= \begin{cases} g_{\text{roc\_mult}} \cdot G_{FX,i,j}, & G_{FX,i,j} > g_{\text{thresh}} \\ \dfrac{G_{FX,i,j}}{g_{\text{roc\_mult}}}, & \text{otherwise} \end{cases} \quad (E.2)$$

$$G_{FX,i,\text{tot}} = \sum_{\text{all } j} G_{FX,i,j} \quad (E.3)$$

$$FX_{i,d,j} = \frac{FX_{i,\text{tot}} \cdot G_{FX,i,j,\text{potential}}}{G_{FX,i,\text{tot}}} \quad (E.4)$$

where $G_{FX,i,j,\text{potential}}$ is a measure of the potential attractiveness of the cell j based on the available forage, $G_{FX,i,j}$ is calculated as of G_{CX} in equation B.34, $g_{\text{roc\_mult}}$ is a constant reflecting how much more attractive a sight with forage sufficient to support FX_i is over a site with poor food resources and g_{thresh} is the potential growth rate (as an index of the quality of the resources) where FX_i switch from finding the site desirable to undesirable.

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