Chapter 2 The effect of physiological detail on ecosystem models I: The generic behaviour of a biogeochemical ecosystem model

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 bay, Bay Model 2 (BM2), was constructed. It is a trophically diverse biogeochemical model built using the general framework from a model of Port Phillip Bay, Australia. BM2 captures the essential features of real marine systems as well as another similar but more complex ecosystem model (IGBEM), which contains much more physiological detail. It is capable of reproducing realistic levels of biomass and conforms with known ecological relationships. Novel handling of bacteria, as colonisers rather than as consumers, and the inclusion of mixotrophy for the dinoflagellates lead to more realistic dynamics for these groups. These dynamics represent a substantial improvement in predictions for these components in comparison with IGBEM. The behaviour of BM2 indicates that, with regard to capturing common system dynamics, high levels of physiological detail are not always required in ecosystem models.

Keywords

biogeochemical, model, ecosystem, ERSEM, Port Phillip Bay, IGBEM, BM2

2.1 Introduction: ecosystem models and physiological detail

The evolution of ecosystem models has seen a proclivity for 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. However, with no clear indication as to the effects of complexity on model performance, the "complex model" has once again seen an upswing in support. It is clear that the effect of model complexity on model performance is an important issue begging immediate attention.

A powerful approach to the issue of complexity is to begin with a highly detailed model and make systematic comparisons with simpler models. It may seem an unusual beginning to start off with a complex model when their worth is still controversial (Hedgpeth 1977, Silvert 1996a, Murray and Parslow 1999b), but this method has been used extensively and successfully in fisheries (e.g. Ludwig and Walters 1981). Moreover, as the models discussed here were to play a part in a much broader examination of the effects of model structure, it was decided that the models needed to incorporate some of the known complexities of the real world and be amenable to, potentially extensive, simplification. Insight gained during the construction of the Integrated Bay Ecosystem Model (IGBEM), a large generic bay ecosystem model, 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 complexity. Thus, this paper discusses 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 2.1). IGBEM (chapter 1) 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.

Table 2.1: Comparison of the underlying assumptions and formulations of the standard implementations of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Feature	BM2	IGBEM
General features		
Biomass units	mg N/m3	mg/m3 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	entire biomass pool of the functional group in the cell	entire biomass pool of the functional group in the cell
Resolution of the formulation used for the fish groups	biomass (structural and reserve weight) of the "average individual" for the functional group in the cell and the number of individuals in the cell	biomass (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 (autotrophs, invertebrate consumer, vertebrate consumer, bacteria, inanimate)	eight general sets of rate of change equations used (microautotrophs, macrophytes, small zooplankton, large zooplankton, fish, zoobenthos, bacteria, inanimate)
Formulation detail	general: only growth, mortality and excretion explicit.	physiological: 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	9 age classes	9 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

2.2 Building BM2

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 of acronyms and their meanings is given in Table B.1 of Appendix B.

BM2 is a process model that tracks the nitrogen and silicon pools of twenty-five living, two dead, four nutrient, six physical components and a gaseous component (Table B.2, Appendix B). The spatial geometry is made up of 59 polygons (boxes), which correspond to the geographical form of Port Phillip Bay. The area and shape of the polygons reflect the speed with which physical variables change within particular parts of the bay (Figure 2.1). This geometry was developed for the Port Phillip Bay Integrated Model (PPBIM, Murray and Parslow 1999a, Walker 1999), which was used as a base for the development of BM2. BM2 also uses the 3 layer (water column, epibenthic, sediment) vertical resolution and daily time-step common to IGBEM (chapter 1) and PPBIM. As a result, like PPBIM and IGBEM, BM2 is driven by seasonal variation in solar irradiance and temperature, as well as nutrient inputs from point sources, atmospheric deposition of dissolved inorganic nitrogen (DIN) and exchanges with the Bass Strait boundary box. BM2 retains the bioirrigation components used in PPBIM (Walker 1997), and the enhancements made to the transport model during the development of IGBEM (chapter 1). Hence, BM2 is identical to IGBEM with regard to the physical parts of the system, with the exception that the rate of sediment burial out of the modelled sediment layer is greatly reduced based on observations made during the validation of IGBEM (chapter 1).

The major differences between IGBEM (full details of its formulation can be found in chapter 1) and BM2 are in the biological aspects of the model system (Table 2.1). During the construction of BM2 the general form of the process equations

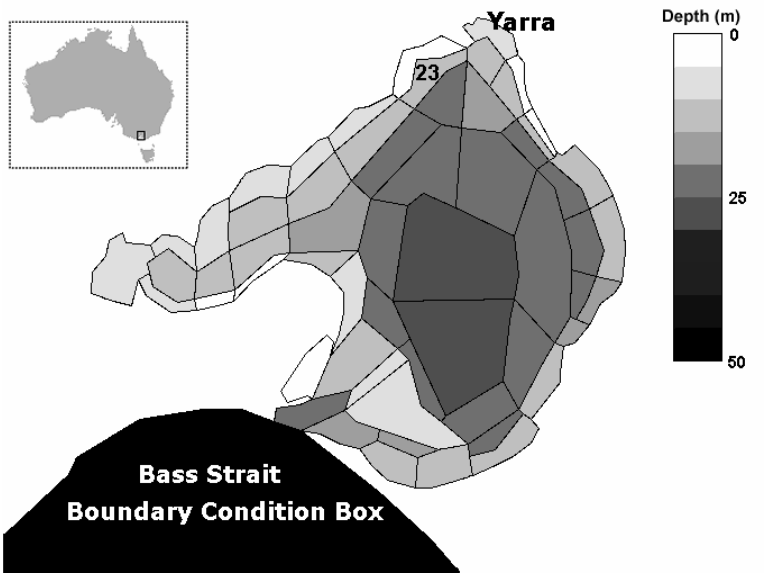
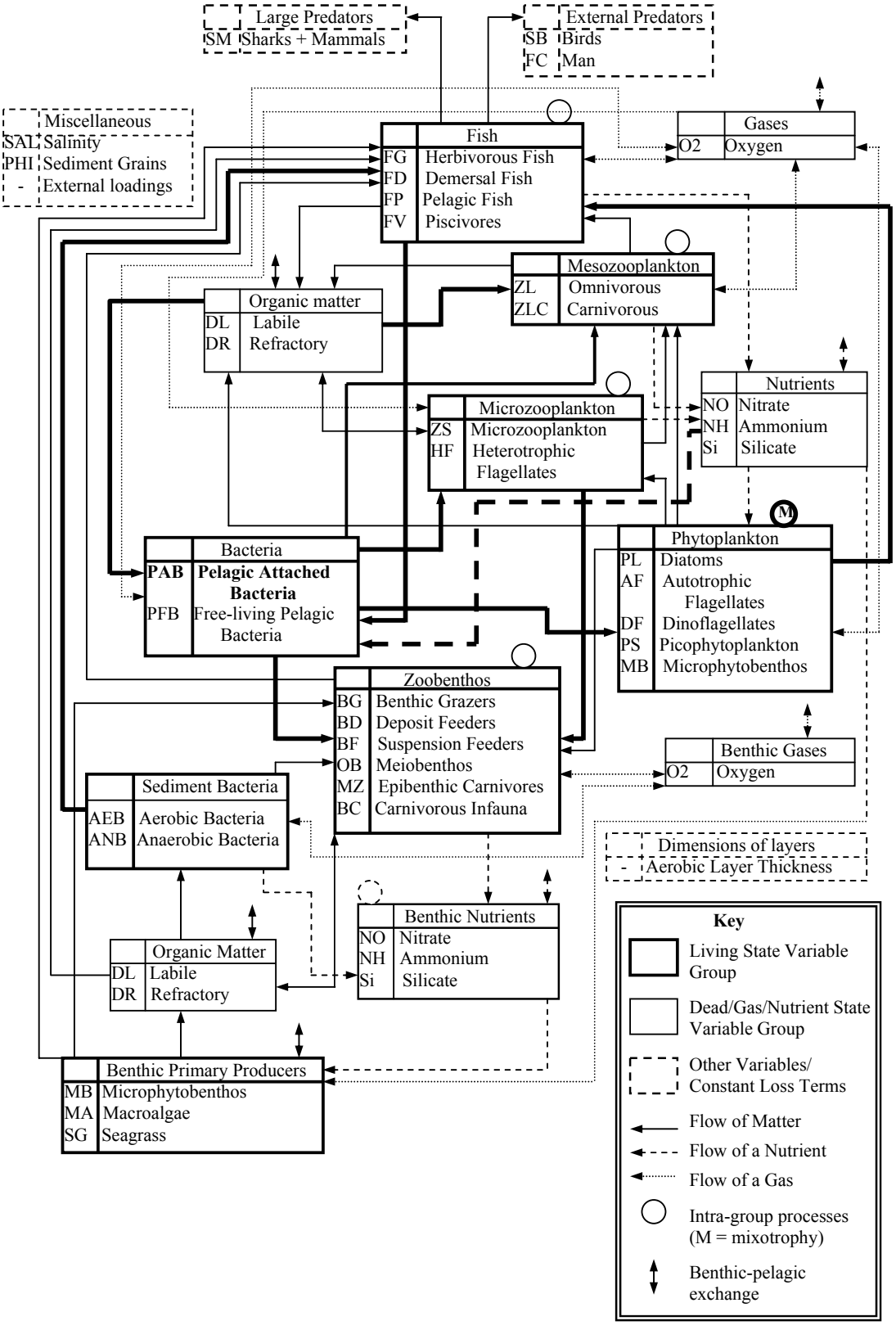


Figure 2.1: Map of the geometry used for the standard runs of Bay Model 2 (BM2). It represents Port Phillip Bay, Melbourne, Australia (location marked on map inset). The Bass Strait boundary condition box, the entry point of the Yarra River (the river the city of Melbourne is built around) and box 23 (referred to in Figure 2.10) are marked on the map.

implemented for the biological components in PPBIM (Murray and Parslow 1997) were replicated and extended (and modified where necessary) to cover all of the invertebrate groups listed in Table B.2 of Appendix B. This differs from IGBEM, which is built around a similar list of groups, but used the ERSEM 'standard organism' concept (Baretta et al. 1995, chapter 1). The fish groups in BM2 are much closer to the "average individual" model used in IGBEM, but the grazing and excretion processes are simplified 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 C.

The groups used in IGBEM and BM2 are 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 Figure 2.2). In BM2 the pelagic

Figure 2.2: Biological and physical interactions between the components used in Bay Model 2 (BM2). The pelagic attached bacteria and flows (arrows) in bold were built specifically for BM2 and do not appear in the Integrated Generic Bay Ecosystem Model (IGBEM). The figure is modified from that for the European Regional Seas Ecosystem Model (Blackford and Radford 1995).



bacteria are 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 are 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 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. In the past this reflects that 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). 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. The dinoflagellates in question had previously been considered pure autotrophs and, apparently, only displayed 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 Strickney et al. (2000) were used as a guide during the formulation of the mixotrophic dinoflagellates in BM2 (given in Appendix D).

The other part of the system treated unconventionally 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) are equated to the availability of colonisable substrata (the detrital groups) rather than to more grazer-like consumption of prey resources. The formulations used for bacteria and their integration with the nitrification-denitrification submodel are given in Appendix E.

Parameterising BM2

The number of 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.

Optional submodels

BM2 is part of a wider study of ecosystem models and so many alternative submodels were built into various parts of the main model. These were generally chosen to correspond to those of IGBEM and include forage and density dependent fish movement, a fisheries effort model, fishing induced mortality on non-target groups, functional group invasions and multiple alternative functional responses and mortality schemes. The majority of these are not discussed here, but some will be addressed in other chapters (e.g. chapter 6). The submodels included here are outlined in the following section.

2.3 Model runs

The standard runs of BM2 cover a 20 year time period, with output being recorded every 14 days. This run length and record step matches that of IGBEM, and the rationale for these choices may be found in chapter 1. One hundred year runs are also undertaken to check for long period cycles and to verify that the model has reached a representative state at the end of the 20 year period. Looping of the forcing files for the physical transport model is necessary, as the files only span four years, and this is done in the same manner as for IGBEM (chapter 1). The majority of the groups in the modelled food web have a linear natural mortality term, but for those groups on the upper edge of the web an additional quadratic mortality term is also imposed. This second term represents predation due to groups not explicitly represented in the

modelled web. This combination of linear and quadratic mortality terms is used in all standard runs of BM2, and the functional response employed in these runs is the one used in PPBIM (a Holling type II). In the standard form of BM2 the recruitment of fish is constant and fish migration is prescribed (as in IGBEM, chapter 1).

The assumptions underlying the formulations for the recruitment and movement of fish are some of the weakest in BM2. Thus, to explore model behaviour under alternative assumptions, runs that used alternative fish movement and recruitment relationships were undertaken. Forced migration and constant recruitment of fish, as employed by ERSEM II, was adopted initially, and this facilitates comparisons with IGBEM. 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 F). The alternative recruitment formulations include a lognormal distribution, a Beverton-Holt stock recruitment curve, and a recruitment relationship which uses primary production (as a proxy for larval resource availability) to dictate the number of recruits settling out in each cell (Table 2.2). These recruitment relationships are parameterised such that, if there is a constant stock size and no environmental changes, the average number of recruits returned matches that of the initial state of the system.

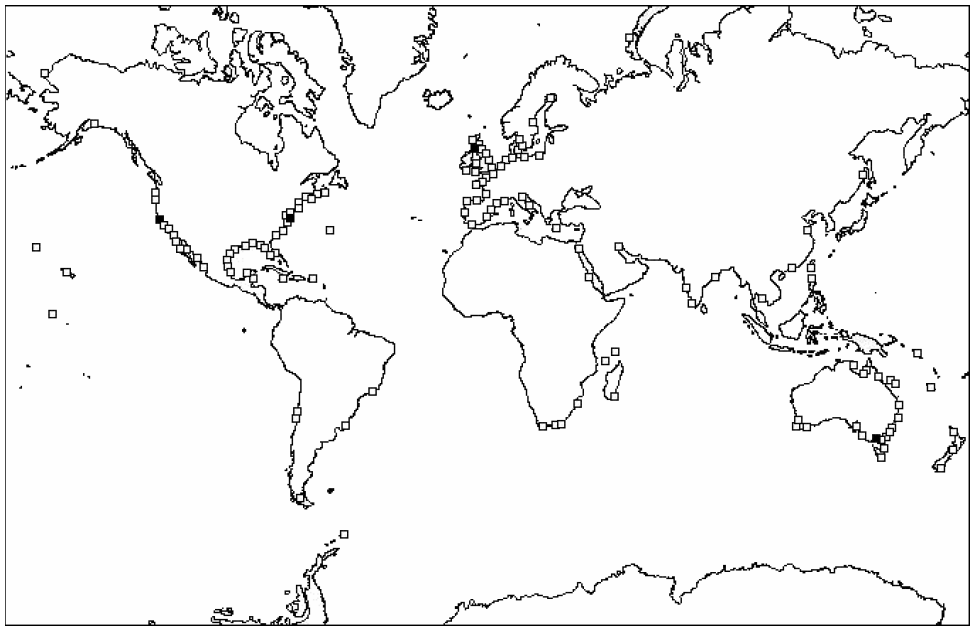
To evaluate the performance of BM2 under varying conditions and to judge how well the model replicates the behaviour of natural systems, the nutrient forcing files for BM2 were scaled so that the new values matched the area-corrected inputs (from Monbet 1992) for three other bays from around the world (Figure 2.3). The geometry and hydrodynamics remained unchanged, but the levels of inflowing nutrient were altered in an attempt to capture the state of other bays. In an effort to produce a generic system rather than one tied to specific circumstances, the parameter set used in

Table 2.2: The recruitment relationships available in BM2. The number of recruits added to box *j* at time *t* is represented by b_{tj}. Note that the number of recruits produced by the Beverton Holt recruitment relationship is calculated at the beginning of the recruitment period, but is delivered evenly across the recruitment period rather than being delivered in a single pulse on the first day.

Recruitment Regime	Formulation	Definition of Specific Terms
Standard	$b_{tj} = J_t$	J_t = element t of the recruitment vector (constant spatially and temporally)
Beverton-Holt stock-recruit relationship (distributed evenly across the recruitment period)	$b_{tj} = \frac{\left(\frac{\alpha \cdot L_{tj}}{\beta + L_{tj}}\right)}{t_x}$	α = Beverton-Holt α for the fish group β = Beverton-Holt β for the fish group L_{tj} = biomass of larvae in box *j* at time *t** t_x = total length of recruit period
Proportional to Primary Production	$b_{tj} = \frac{\eta_{FX} \cdot CHL_{j,t}}{\eta_{chl}}$	η_{FX} = recruitment coefficient for fish group FX $CHL_{j,t}$ = water column chlorophyll in box *j* at time *t* η_{chl} = reference level of chlorophyll (1.5)
Lognormal distribution	$b_{tj} = \frac{\lambda_{FX}}{y \cdot \sigma \cdot \sqrt{2 \cdot \pi}} e^{\left(\frac{-(\log y - \mu)^2}{2 \cdot \sigma^2}\right)}$	λ_{FX} = recruitment multiplier for fish group FX $y \sim U(0,1)$ $\sigma = 0.3$ $\mu = -0.5$ $\pi = 3.141592654$

* See equation B.11 in Appendix C.

Figure 2.3: Map of the world showing the bays used to evaluate the performance of Bay Model 2 (BM2). Symbols mark the locations of all the systems for which marine biomass or production estimates are 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.



BM2 with baseline ecosystem conditions is not parameterised to match the species composition of any particular bay. Instead the parameters used are based on species from temperate bays across the globe and so there is no retuning with each change in nutrient loading. This approach is also used with IGBEM (chapter 1) and proved to be robust. A range of measures, including levels of chlorophyll a (chl a), DIN, biomasses and system indices, are used to judge the model performance against available data across the entire set of bays shown in Figure 2.3.

2.4 Results and discussion

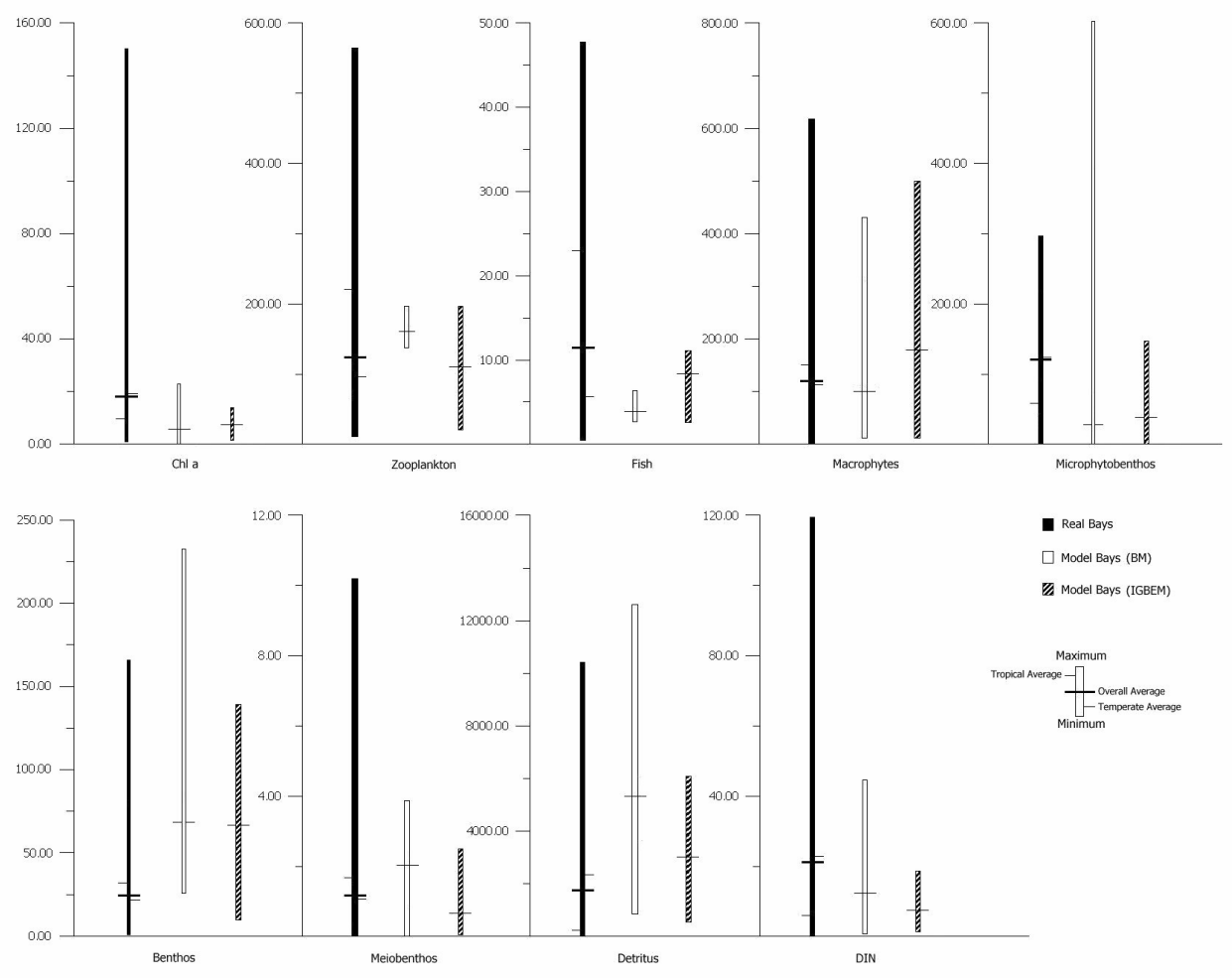
2.4.A BM2 *vs* IGBEM and real bays

The groups in BM2 and IGBEM are identical and both use the same spatial resolution and track the nitrogen content of the biomass pool, but aggregation of model output is necessary for comparison with data from real bays, which is not available at the same resolution. The pooling and nomenclature adopted during the analysis of IGBEM (chapter 1) is adopted here. The pooled outputs refer to the trophic sets: chlorophyll a (chl a) (as a proxy for total phytoplankton), zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos (all the other benthic consumer groups) and detritus (labile and refractory).

Range in biomass

Comparison of the range in biomass (for each trophic set) in real bays with that predicted by the models indicates that BM2 performs satisfactorily (Figure 2.4). For the majority of trophic sets the range of values produced by BM2 under different levels of nutrient forcing is within the range of empirical values from bays around the world. However, some trophic sets deviate from real world values. Ranges for the water column trophic sets for BM2 are all much smaller than their real world counterparts, whereas those for many of the benthic groups are as large (or larger) than those seen in

Figure 2.4: Range and average value for each of the main trophic sets of BM2 compared with values from empirical observations and from the output of 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 values from the empirical observations are taken from Appendix A.



the field. With respect to the ranges for biomass produced by IGBEM, the ranges generated by BM2 are comparable, though they do tend to be larger. The small range of values from the models for water column variables is not surprising given the very small range of nutrient inputs used to force the models. The simulations covered the cases from baseline loadings up to x30, whereas some real systems may reach as high as x1000 (e.g. Loire Estuary in France, Monbet 1992). Trying the model under the same range of loads as seen in nature is not possible, as sufficient biological and physical forcing data is only available for systems with loads up to x30. In contrast to the water column trophic sets, the predicted ranges of biomass for the benthic trophic sets often match or exceed the empirical ranges of biomass for these sets. Therefore, the ranges for biomass predicted for the models if loading were set to x1000 are unlikely to match those observed in reality unless the benthic groups in the model experience down turns when the nutrient forcing is raised above x30. There is some suggestion of this in the model dynamics with increasing nutrients, but further evaluations at higher nutrient loads would be necessary to confirm that the pattern of declines persists as nutrient loading reach extreme levels.

That so many of the trophic sets in BM2 have a wider range of values than in IGBEM suggests that the simpler process formulation used in BM2 is not as limiting as the use of explicit physiological formulations and 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 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 (e.g Fransz et al. (1991) identified 20 plankton models developed since the 1970s for the Atlantic Ocean and adjoining seas) and so the equations used have

been examined extensively and their limitations and associated remedies (e.g. model closure using quadratic mortality, see 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. Detailed tracking of flows in BM2 indicates that the dynamics of the benthic deposit feeder group is the primary cause of the large biomass ranges produced for benthic trophic sets. This suggests that this group may require some form of space limitation (via a crowding effect), similar to that applied to the benthic suspension (filter) feeders. Given that these animals 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. Overall, results for the ranges in biomass suggest that the water column components of BM2 function well, but that the benthic components can be refined further (see chapter 3).

Average biomass

Average values of the biomass for each trophic set and the values produced under specific conditions are also 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 (Figure 2.4). In all, 6 of the 9 trophic sets in BM2 were within 10% of the average empirical value for temperate bays and all were within 33%. The best match is by the macrophytes where the average biomass produced by BM2 is within 2% of the average of empirical observations. The worst fit is the microphytobenthos, where the difference between the model and empirical average is 32.5%. This performance is similar to that of IGBEM. More importantly, the performance of IGBEM is not consistently superior to that of BM2. Considering the 9 trophic sets in Figure 2.4, and using the average biomass as the performance measure, both models did equally well for chl a and benthic groups; the predictions of IGBEM are marginally better than BM2 for zooplankton, meiobenthos, detritus and microphytobenthos; while the performance of BM2 surpasses that of IGBEM for the fish, macrophytes and DIN. This lends further support to the view that the formulation of the water column components in BM2 is largely sufficient to capture their dynamics faithfully, while the sediment groups may require further attention if they are to behave as well as those in IGBEM.

The results for zooplankton (Figure 2.4) 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 (see chapter 3).

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

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 are pooled to match the size resolution used in the models, which converts the benthic size-spectrum from a "W" into a "U". The spectra calculated for BM2 match well with those of Sheldon et al. (1972) and Schwinghamer (1981), while those for IGBEM do not (Table 2.3 and 2.4). This is especially true for the microscopic classes, particularly in the benthos (Table 2.4). 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 (Schwinghamer 1981).

Table 2.3: A summary of the Sheldon spectra for the pelagic classes in the run of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) where the environmental conditions match those in Port Phillip Bay. Following the convention set by Schwinghamer (1981) the unit area biomasses are given in cm^3/m^2.

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

Table 2.4: A summary of the pooled Sheldon spectra for the benthic classes in the run of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) where the environmental conditions match those in Port Phillip Bay. The values given by Schwinghamer (1981) are included for comparison.

Class	BM2 (cm^3/m^2)	IGBEM (cm^3/m^2)	Schwinghamer (cm^3/m^2)
Bacteria	24.9	0.2	80.1
Meiobenthos and Microphytobenthos	5.63	0.7	6.1
Macrofauna	208.7	149.5	473.0

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 (>2m and <2m tidal range respectively) systems cluster separately, with little overlap (Port Phillip Bay is microtidal). Both BM2 and IGBEM comply with Monbet's relationship (Figure 2.5), but the performance of IGBEM is better than that of BM2 in which the response of chl a to DIN is flatter.

A final general relationship is that the maximum average biomass of meiobenthos decreases as the depth of the overlying water column increases (chapter 1). The biomass of meiobenthos given by the models reflects this relationship well (Figure 2.6), although those of BM2 tend to sit closer to the upper bound.

2.4.B Spatio-temporal structure and the effects of environmental change

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 Port Phillip Bay (PPB).

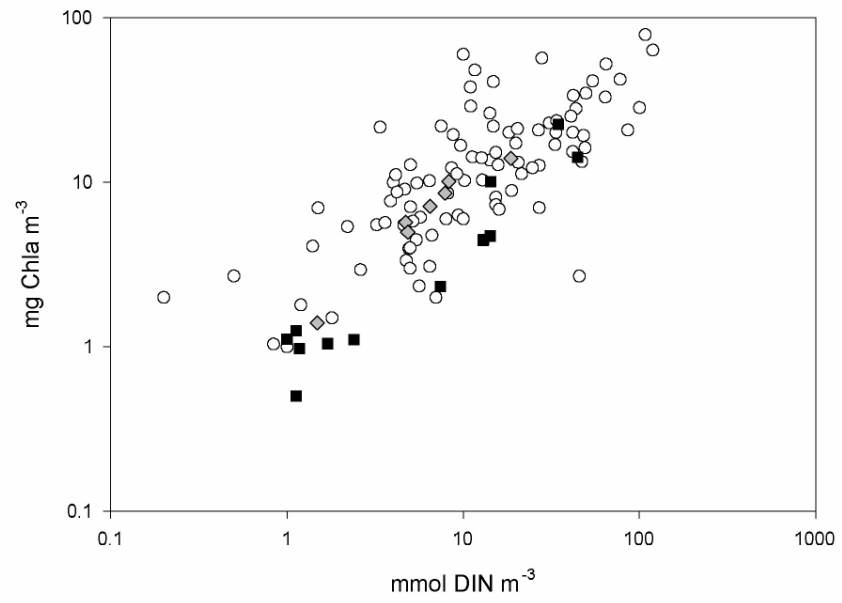


Figure 2.5: Comparison of the mean annual Dissolved Inorganic Nitrogen (DIN) against mean annual chlorophyll a (chl a) for real (open circles) microtidal marine systems (based on Monbet (1992) and additional values from the literature - see Appendix A), BM2 (black squares) and IGBEM (grey diamonds).

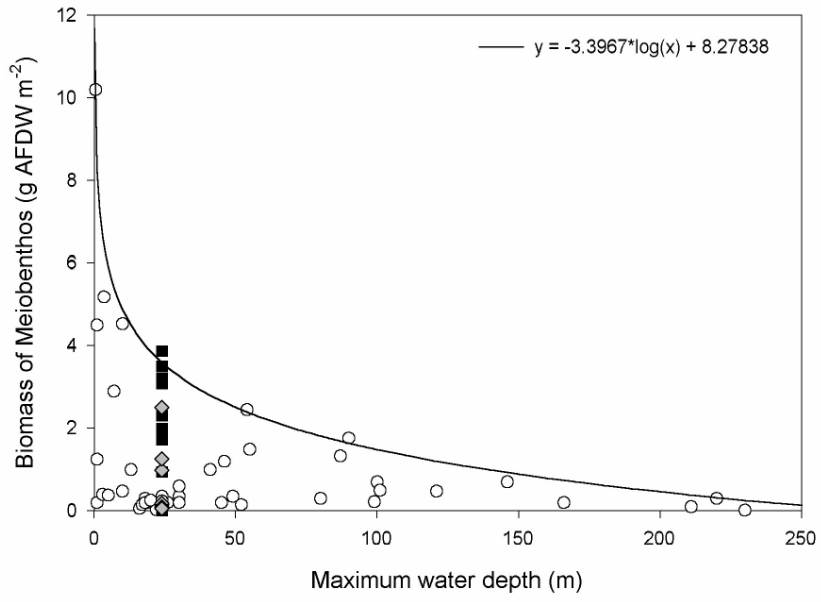


Figure 2.6: Plot of the average biomass of meiobenthos against maximum depth of the system for marine systems from around the globe (open circles), BM2 (black squares) and IGBEM (grey diamonds). The curve marking the upper bound was found by fitting the curve to the highest points in the plot (chapter 1), where y is the biomass of meiobenthos and x is the maximum water depth.

Spatial structure

The runs using the baseline nutrient loadings for Port Phillip Bay and Chesapeake Bay are designated PM and CM respectively. The predicted average biomasses per box over the final four years of the CM and PM runs, using both BM2 and IGBEM, were analysed to determine whether there are boxes that had similar biological and physical properties, which would suggest spatial patterns in the model output. 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) 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. Only the PM and CM runs are 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 two models contained a similar number of areas which are located in similar positions around the bay (Figures 2.7 and 2.8). Areas predicted to share communities (dominant biological groups) were pooled to produce "zones" and, as with the "areas", the two models showed a good deal of agreement (Figure 2.9). A number of factors produced this zonation 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. An important predator-prey interaction is that of the benthic grazers and macrophytes.

Figure 2.7: Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analyses of the runs using the loadings for Port Phillip Bay (the PM run) of BM2 and IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis. (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.

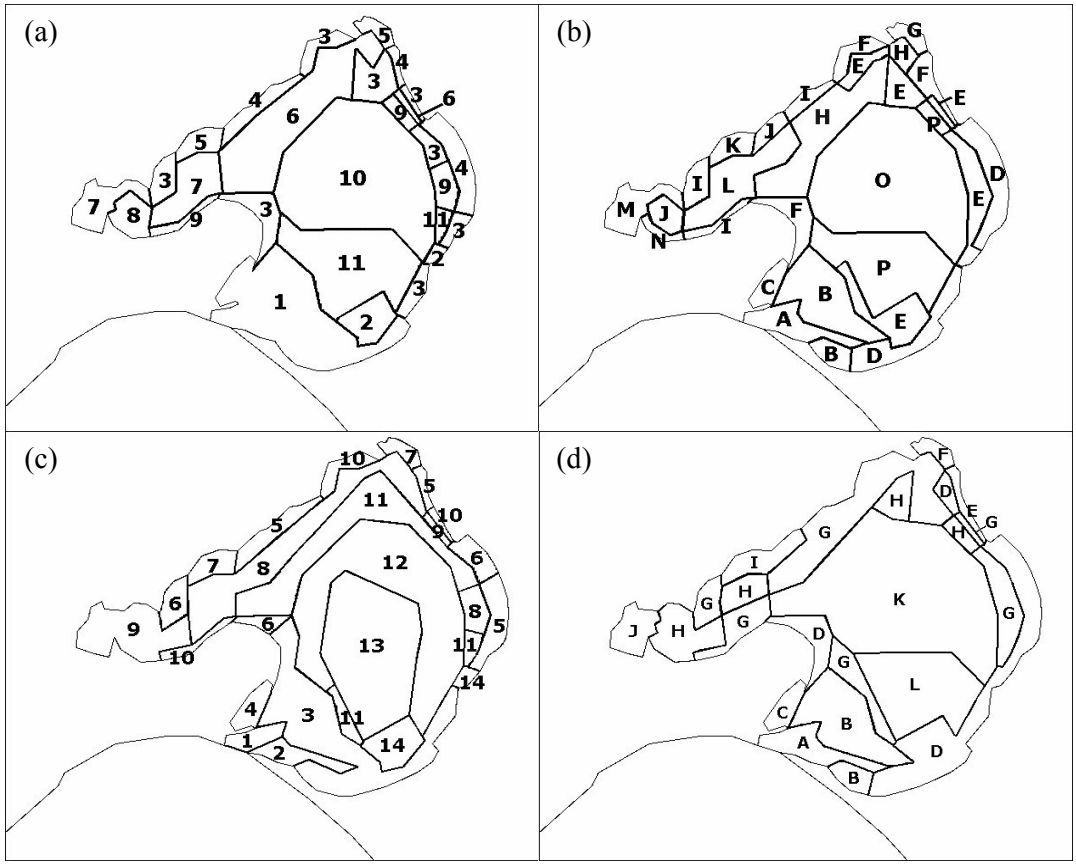


Figure 2.8: Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analyses of the runs using the loadings for Chesapeake Bay (the CM run) of BM2 and IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis and do not correspond to any of the numbers or letters in Figure 2.7. (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.

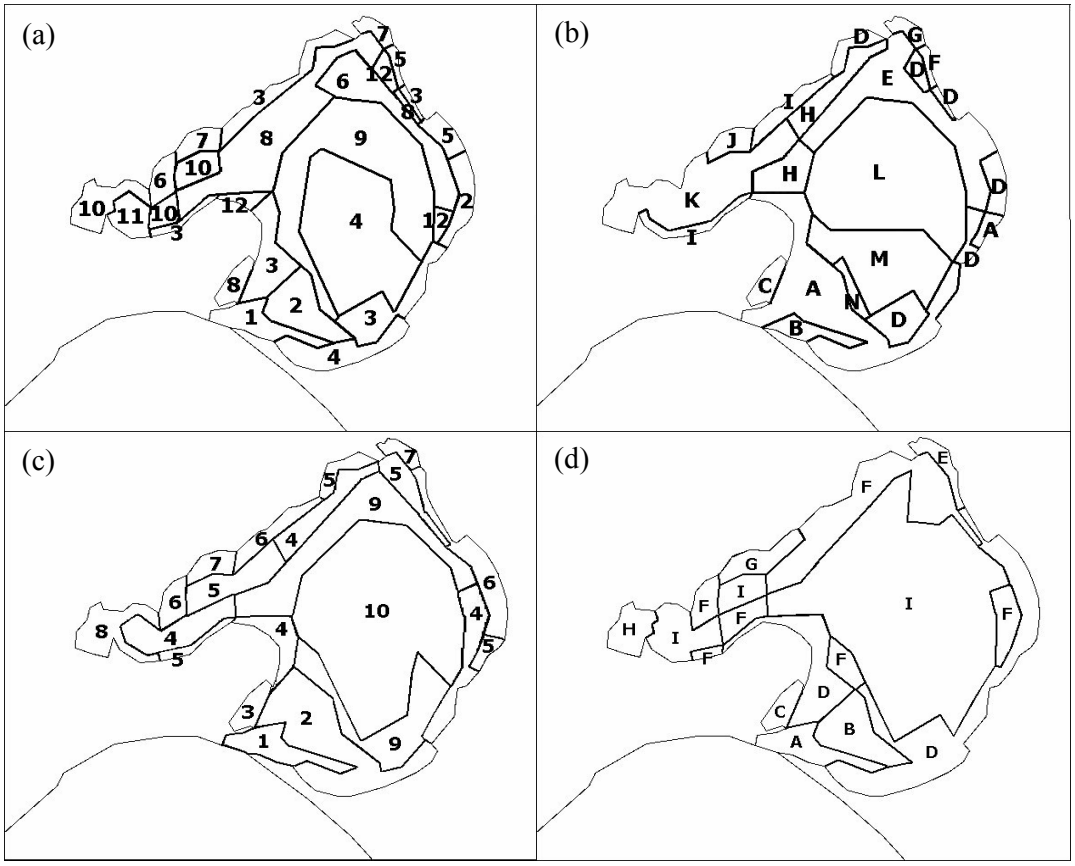
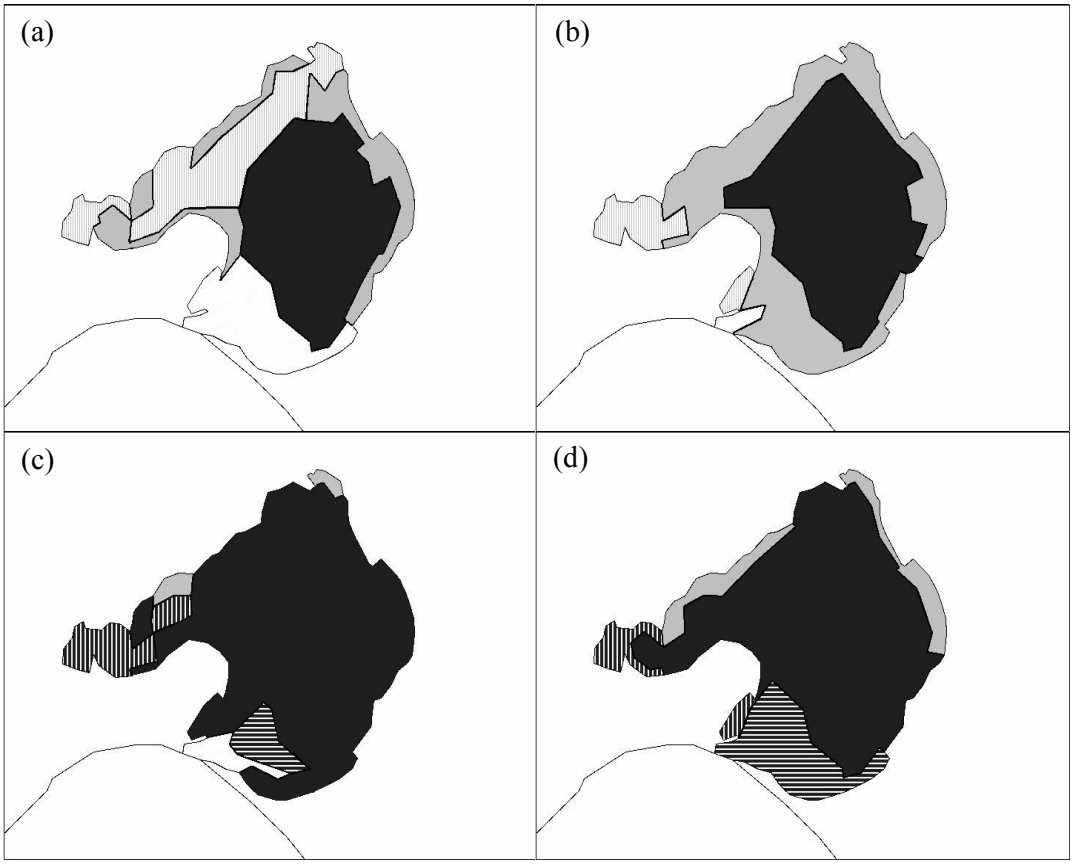


Figure 2.9: Distribution of the main zones identified in the output of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (a) PM run of BM2, (b) PM run of IGBEM, (c) CM run of BM2, and (d) CM run of IGBEM. The zones in white are part of Bass Strait or heavily influenced by it; the 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 large zooplankton), and well developed populations of meiobenthos, microphytobenthos, and bacteria.



Benthic grazers at high densities are only found in areas with persistent macrophyte populations. Further, the "macrophyte-barrens" cycle involving these groups (detailed below in the section on temporal dynamics) does not occur simultaneously around the edge but is sequential and driven, in part, by the total flows around the bay. This indicates that there is a refuge (macrophytes escape grazing) and pursuit (benthic grazers find new prey reserves) dynamic in action.

The clearest example of resource partitioning observed in the output of the models is within the detrital feeders and the effect is pronounced in BM2. The distribution of the meiobenthos and deposit feeders in BM2 show little spatial overlap and maintain healthy populations by spatial partitioning of their demands on shared food groups. If this spatial segregation is prevented by running the model on a coarser geometry (say 1 box instead of 59) then the model undergoes self-simplification and either the deposit feeder or meiobenthic group is lost (chapter 4). Usually it is the meiobenthos that goes extinct because it is both a competitor and prey of the deposit feeders. This result emphasises the importance of spatial context and differentiation in the model, as it provides a mosaic of spatial refuges and allows for emergent dynamics.

Competitive exclusion also arises in the benthic primary producer subweb, in which the macrophytes displace the microphytobenthos. The macrophytes potentially suffer from space limitation (if their biomass rises too high) and the effects of their physical environment (macrophytes are uprooted in rough conditions and epiphytes foul seagrass when nutrient levels are high). However, these factors arise only occasionally so that the macrophyte-microphyte interaction is largely driven by limiting nutrients. Because the microphytobenthos is limited by silica (Si), while the macrophytes are not, this allows the macrophytes to dominate the microphytobenthos when silica levels are low. However, the low light requirements of the microphytobenthos ensure its survival, though in reduced amounts, in the central parts of the bay where the light conditions do

not allow macrophyte growth.

Temporal dynamics

BM2 displayed many of the temporal dynamics previously reported for IGBEM (chapter 1). Both models demonstrate seasonal bloom dynamics, interannual variation and the long-term "macrophyte-barren" dynamics. However, in BM2 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, medium and long term (Figure 2.10). 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 (chapter 1) 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 Figure 2.10). These "events" were caused by the coincidental occurrence of conducive physical and biological conditions

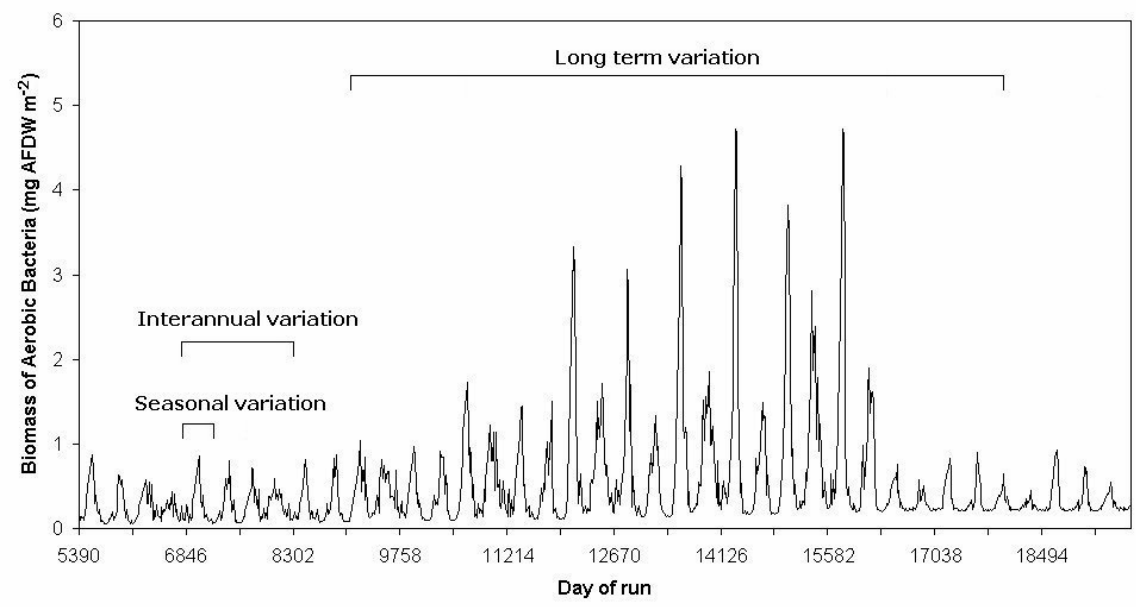


Figure 2.10: The biomass (mg AFDW m^{-2}) through time for the aerobic bacteria in box 23 (see Figure 2.1) of BM2. This time-series of biomass reveals examples of seasonal, interannual and long-term variation.

(primarily the densities of predators, prey and competitors). That both models suggest that physical and biological interactions, free from the impacts of escalating human activities, can cause substantial changes in biomass which 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.

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 (chapter 1) capture the major system changes 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) 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 Figure 2.9). 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 x10 or more, at which point productivity drops to between 20 to 50% of the original levels and biomass drops by more than half. This is in agreement with the results of IGBEM (chapter 1) 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. For example, IGBEM does not predict the increase in large phytoplankton with increasing nutrients, but it does indicate that the large zooplankton will be replaced by smaller groups (chapter 1). In contrast, BM2 correctly captures the changes in composition of all planktonic groups (Table 2.5). 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 Marshall 2000).

Table 2.5: 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 Port Phillip Bay (PM run) and Chesapeake Bay (CM run). Empirical values for Chesapeake Bay (CB) (Madden and Kemp 1996) and Port Phillip Bay (PPB) (Harris et al. 1996) are included for comparison.

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

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 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, which 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 standard 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. Because the flushing time for PPB is close to a year (Harris et al. 1996), and the storage capacity of the bay's sediments is immense, these conditions are not easily reversed. Thus, the detritus based, highly eutrophied state of the bay persists years after the model's nutrient input levels have been reduced below those used for the PM run. This hysteresis was also observed in PPBIM (Murray and Parslow 1999) and has not been diluted by addition of other trophic groups, or the modifications made to the sediment model (see Appendix E), during the construction of BM2.

The final observation of note reflecting the effects of eutrophication is that the change in the ratio of aerobic to anaerobic bacteria in BM2 mirrored that in IGBEM. The index fell from 3.50 to 0.38 as the nutrient inputs were increased to x30 baseline levels. This suggests that this index may be a robust indicator of system-level change.

2.4.C Strengths and weaknesses

No model can be a perfect representation of nature and so each has its relative strengths and weaknesses. The behaviour of BM2 in comparison to reality and IGBEM were used to give insight into the model's strengths and weaknesses. Aberrant or inaccurate behaviour is considered a weakness, while behaviour of a component that is close to matching reality is considered a strength (especially if it used a simpler formulation than employed in IGBEM). The weakest points in BM2 stem from its simplicity, and reduced form, and are shared by all models that make the same sets of assumptions and construction choices (such as PPBIM). Its greatest strengths also come

from its reduced form and the choices made during its development.

Nutrient limitation

The omission of limitation by phosphorus was a considered decision made early in the development of BM2. Under the conditions considered here, it is a sensible choice for bays such as Port Phillip Bay that have phosphorus in excess (Harris et al. 1996). However, this may not be true of all bay systems, such as the Bay of Seine, France (Guillaud et al. 2000)). It is sensible and straightforward to include phosphorus limitation of primary production in models of natural systems where it is known that phosphorous is limiting.

The implementation of nutrient limitation and flows in ecosystem models is made easier by the observation by Redfield et al. (1963) that the major chemical constituents (N:C:P) are maintained in a relatively constant ratio (around 16:90:1). 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 2.1). Under oligotrophic conditions the application of Redfield ratios and the use of external 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 particulate organic matter in these areas is preferentially remineralised and the resulting decline in dissolved inorganic carbon (DIC) over the growing season is much greater than predicted from a 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 runs using baseline ecosystem conditions 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 of nutrients facilitated by Droop-like equations is required if system-level behaviour is to be captured faithfully.

Recruitment and movement of fish

A theoretical shortcoming of BM2 is the implementation of recruitment, movement and mortality in the fish groups. Like IGBEM, the standard runs of BM2 use constant recruitment and prescribed fish movement. These formulations do not reflect particularly realistic assumptions regarding underlying processes. Consideration of alternative formulations is crucial for judging the general performance of the standard form of the model.

The effects on BM2 of the use of these features, or their alternatives, were similar in BM2 and IGBEM. Constant recruitment buffers BM2 against large-scale changes in productivity and especially against the effects of substantial changes in fishing pressure (chapter 7). Of the three alternative recruitment schemes tested (Table 2.2), the Beverton-Holt is the most effective at correcting for aberrant effects of constant recruitment. This is important as recruitment has a substantial impact on the potential size, persistence and behaviour of the fish stocks. The stocks did demonstrate more dynamic responses to changes in nutrients and fishing pressure when a Beverton-Holt recruitment scheme is used. For instance, when fishing pressure is raised fivefold for all harvested groups the constant recruitment for the fish groups in the standard run

buffered each group equally well so the decline and subsequent stabilisation of the biomass occurred at about the same pace in each. However, in the run with the Beverton-Holt stock recruit curves the planktivores did not decline at the same pace. This is because the reduction in the number of their predators allowed them some measure of release so enough adults remained (in spite of heavy fishing) to keep the stock from total collapse for a few more years than is the case for the other groups of fish (Figure 2.11). The steepness of the Beverton-Holt relationships used varied from 0.78 for the planktivores to 0.92 for the demersal herbivorous fish (Table 2.6). While these steepness values are representative of those for many fish species (Francis 1992, Koopman et al. 2000), they were derived here by tuning the parameters so that the average number of recruits matched the constant recruitment case. It is possible that if the Beverton-Holt stock recruit curve for each group had been taken from real fish, rather than just fitted, that the steepness values may have been much lower (there are cases where steepness is as low as 0.32 (Koopman et al. 2000)). If this were the case, then the effect of using this form of recruitment may have lead to a different outcome.

Table 2.6: Steepness values for the Beverton Holt stock recruit curves implemented for the fish groups.

Group	Steepness
Planktivorous Fish	0.78
Piscivorous Fish	0.81
Demersal Fish	0.79
Demersal Herbivorous Fish	0.92

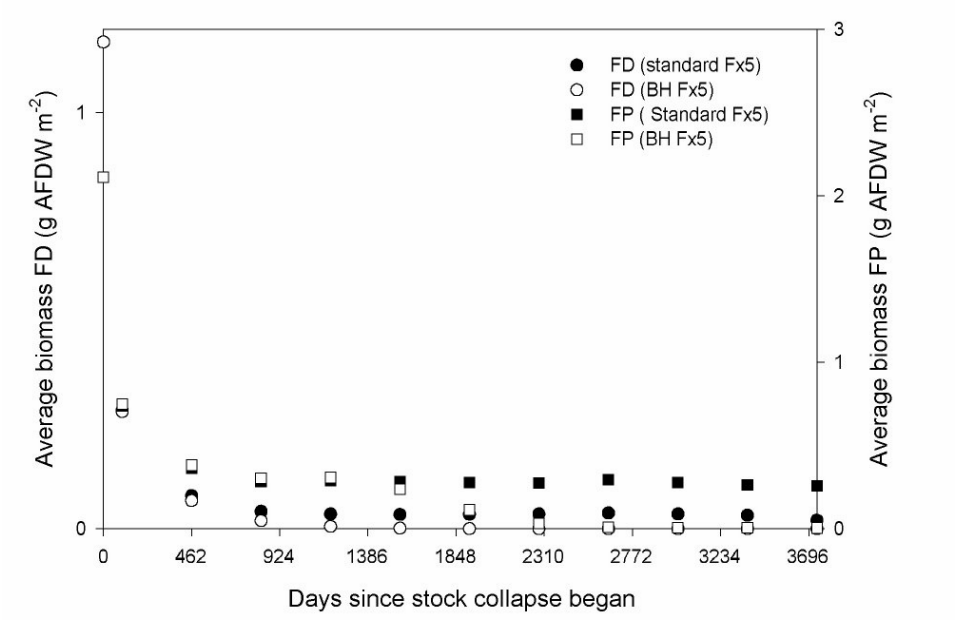


Figure 2.11: Declines in biomass of the demersal (FD) and planktivorous (FP) fish with an increase in fishing for the standard run of BM2 and the run using Beverton-Holt recruitment.

Recruitment as a function of primary production is more responsive in BM2 than in IGBEM and this is due to the greater amplitude and greater number of short period fluctuations in chl a in BM2. These fluctuations produced quite complex recruitment patterns, especially if the spawning window coincided with a spike or trough. However, the use of an index of total primary productivity as an index of recruitment is a problem in BM2, as in IGBEM, as it did not allow for a drop in recruitment with eutrophication. Use of this recruitment formulation requires the replacement of chl a (the index of total primary production used here) with a measure of abundance of a specific planktonic group as an index of year class strength.

Incorporating a random factor into recruitment, as well as density and forage dependent movement, can be used to explore broader theoretical aspects of overall model behaviour in BM2. Large recruitment and aggregation events are common in at least some harvested stocks (Samoilys and Squire 1994, Power and Atkinson 1998).

Using random recruitment or forage- and density-dependent movement to reproduce these events and consider their effects on the system as a whole could be instructive as a guide to understanding the implications of these phenomena in nature. That is not the aim of this model study though, so despite this potential they do not substantially change the existing conclusions regarding the performance of BM2.

Trophic closure

The mortality terms used for the highest trophic groups explicitly included in the model can have a substantial impact on model behaviour (Steele and Henderson 1992, Edwards and Brindley 1999). In BM2 each functional group has a linear mortality term representing the impacts of natural mortality, but ignoring the effects of higher predation. Experience with IGBEM lead to the inclusion of a quadratic mortality term for some functional groups in BM2. This quadratic term implicitly represents the effects of predation from groups not explicitly represented in the model, such as sharks, mammals and birds. Unfortunately, this did not completely correct for the problems of non-responsive higher trophic levels identified in chapter 7.

Considering the entire model food web, quadratic mortality terms are imposed on all groups that are at the edges of the web or link subwebs (such as the large zooplankton and macrozoobenthos). That is, quadratic mortality is imposed on those groups that had at least one predator not explicitly represented in the modelled web. This increased model stability and reduced the parameter space within which explosive growth is predicted, though it did not completely eradicate it across the range of parameter values that were trialled. Comparisons with IGBEM, which does not include quadratic mortality, indicates that system-level behaviours, biomasses and qualitative conclusions based on the models do not change markedly due to the inclusion of quadratic mortality. Though a more thorough sensitivity analysis may indicate

otherwise. This is a major concern within the literature discussing trophic closure in Nutrient-Phytoplankton-Zooplankton models (Steele and Henderson 1992, Edwards and Brindley 1996 and 1999, Murray and Parslow 1999b, Edwards and Yool 2000). There are problems with deducing the effects of quadratic mortality from a comparison of models built on differing premises. An investigation of the effect on model behaviour of linear and quadratic mortality on a single ecosystem model may lead to different conclusions. It was found (chapter 6) that the behaviour of BM2 with and without quadratic mortality enabled differed markedly under changing conditions and it was concluded that quadratic mortality is the most appropriate form of model closure as it allowed for realistic predictions across a range of conditions, whereas linear closure did not.

Mixotrophy

The implementation of mixotrophy in BM2 is effective as it successfully reproduced the main features of this behaviour recorded in laboratory studies. In a comparison of runs with and without mixotrophy, the biomass of dinoflagellates is increased tenfold if mixotrophy is allowed. Further, the rate of growth increased by 1.5 to 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).

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.

Even though the standard form of BM2 is a generic system rather than PPB in particular, the evaluation of the modifications made to the sediment chemistry model are best served by a comparison with the original form in the PPBIM model. The formulation used for attached bacteria in BM2 removes a weakness in the sediment chemistry of PPBIM. The original form of the empirical model used in PPBIM predicted an annual efflux from the sediments of PPB of about 11,000 to 16,000 t DIN. This is much higher than the sediment chamber estimates of Nicholson et al. (1996), which suggested the efflux is likely to be between 3,600 and 8,100 t DIN per year. The prediction by BM2 that the efflux is roughly 6,500 t of DIN per year matches this sediment chamber estimate well. Thus, the adaptation of the empirical nitrification-denitrification model of Murray and Parslow (1997, 1999) to include the dynamics of attached bacteria and infauna has preserved its strengths (such as the hysteresis discussed above), while correcting for its weaknesses.

Is less detail permissible?

The primary aim of the study presented in this chapter and chapter 3 is to evaluate whether the omission of physiological detail from an ecosystem model had a significant effect on model dynamics and the ability to represent reality. The performance of BM2 compares favourably with that of the far more detailed IGBEM. For the purposes of understanding system dynamics and at least qualitative responses to shifts in ecosystem forcing, BM2 is as capable of representing systems as accurately 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 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.

There is some anomalous behaviour, such as the almost exponential growth of the deposit feeders under certain parameterisations and nutrient conditions (chapter 3). The occurrence of this kind of behaviour should be used to guide the application of BM2 on a site-to-site basis and under extreme conditions of change and the model may benefit from the addition of space limitation for the benthic groups (chapter 3).

2.5 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. However, 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 II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) or IGBEM (chapter 1)). 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 does have some impacts on its performance in specific circumstances and this is explored in chapter 3. In many instances it would not take much effort to modify BM2 to include formulations (such as Droop-like equations) that would correct or temper these problems. 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, BM2 is instructive while requiring less information than other biogeochemical ecosystem models currently in use.