

Chapter 3 The Effect of Physiological Detail on Ecosystem Models II:

Models of Chesapeake Bay and Port Phillip Bay

Abstract

Bay Model 2 (BM2) is a biogeochemical ecosystem model. The model formulation uses general assimilation equations rather than intensive physiologically based equations to characterise the biomass dynamics of the modelled groups. The model was developed as a part of a larger study considering the effects of formulation detail on model behaviour.

The behaviour of the generic form of BM2 indicates that it can capture general system properties and behaviour (chapter 2). Consideration of its behaviour when applied to specific systems indicates that it can usually reproduce large scale patterns and levels of biomass that match those of the real system fairly well. However, its performance is not as good for some of the poorly known groups (like infauna) or when environmental conditions undergo extreme change. While BM2 requires retuning if there are very large changes in loadings on the system or when applied to new systems (a new bay), even without tuning the model is capable of predicting outcomes that are qualitatively correct. Thus, as in the generic case, the performance of BM2 is sufficiently sound to justify its use of simpler model equations (in comparison with total system models that use extremely detailed physiological equations, such as IGBEM). This supports the finding in chapter 2 that high levels of physiological detail are not always required to achieve realistic dynamics and system responses in ecosystem models, especially for the purposes of system understanding or general guidance of management decisions.

Keywords

biogeochemical, model, ecosystem, ERSEM, IGBEM, BM2

3.1 Introduction

Much of the scepticism about ecosystem models generated by the earliest such models (mainly from the International Biological Program of the early 1970s) stemmed from the fact that their complexity often saw the available resources channelled into the development and maintenance of the models not their application (Watt 1975). This failure of the IBP models to cost effectively reproduce the dynamics of the systems to which they were applied (O'Neill 1975, Patten et al. 1975, Watt 1975, Halfon 1979) lead to the belief that complex total system models failed to match reality when applied to specific systems (Silvert 1981). As a result it was decided that it was much easier, more efficient and more productive to build simpler models that dealt with fewer processes and tighter scopes (Silvert 1981). However, as ecosystem and ecological theory advance it is hard to compare results across systems if they are built on differing premises and assumptions (Halfon 1979). Consequently, 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 I and II (ERSEM I and ERSEM II) (Baretta et al. 1995) have been applied in 18 locations.

Bay Model 2 is a biogeochemical ecosystem model built as part of a wider model study considering the effects of model structure and formulation on model behaviour. As the study is concerned with considering the effects of model structure in general rather than modelling a specific bay much of the work done is set in a hypothetical generic system (e.g. chapter 2). Generic models are very useful devices for

developing theory and general system understanding, but in most circumstances models are applied to specific locations. Moreover, investigations of generic model behaviour will not necessarily answer concerns regarding applications to specific systems. Thus, a thorough evaluation of the effects of model complexity should consider model performance for specific systems as well as generic behaviours and predictions. It is this aspect of the work on the effect of formulation detail on model behaviour that is presented here. The results in a generic setting can be found in chapter 2.

3.2 Methods

Bay Model 2 (BM2) is a biogeochemical ecosystem model that uses a formulation framework based on general assimilation equations rather than intensive physiologically based equations (chapter 2). This model was compared with empirical observations from a number of real bays as well as the predicted values from another ecosystem model (the Integrated Generic Bay Ecosystem Model) run under the same environmental conditions. The Integrated Generic Bay Ecosystem Model (IGBEM) is very similar to BM2 with regard to the food web, interactions and general processes incorporated, but it includes much more explicit physiological detail. Comparing the performance of these models to each other and to empirical values from real bays should help to identify the level of detail required to capture system dynamics in specific circumstances.

The runs of BM2 considered here cover a 20 year time period and use a combination of linear and quadratic mortality, a Holling type II functional response for grazing, constant recruitment and prescribed fish movement.

The standard form of BM2 uses a spatial geometry configured for Port Phillip Bay, Australia (see Figure 2.1). Three other temperate bays (Figure 3.1) with similar physical conditions (tidal range and relative size of opening to the sea) provided a

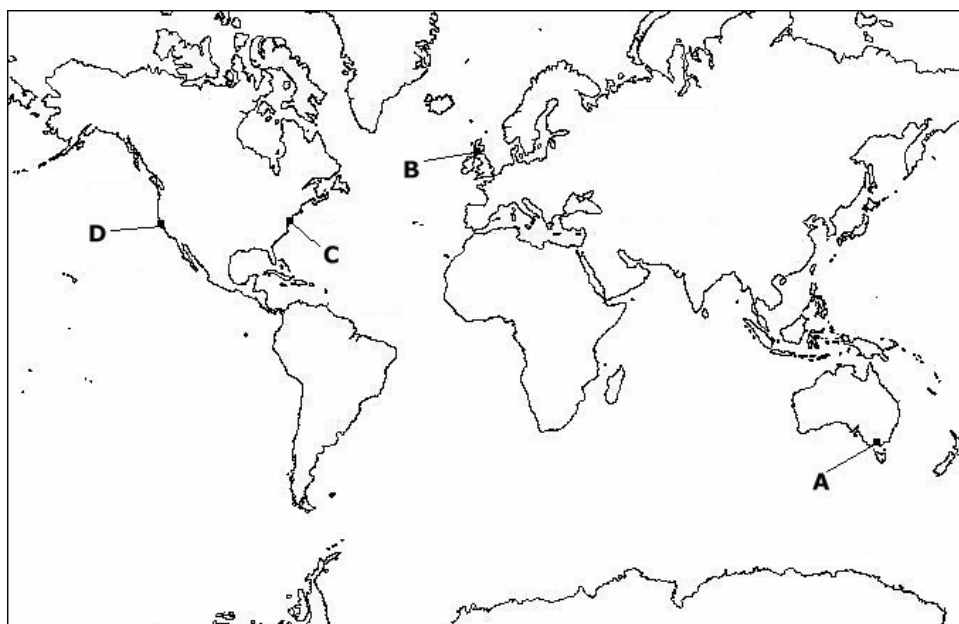


Figure 3.1: The specific bays chosen to set alternative nutrient load scenarios for BM2.

A is Port Phillip Bay, B is the Firth of Clyde, C is Chesapeake Bay and D is San Francisco Bay.

foundation from which to evaluate the performance of BM2 under varying conditions and to identify how well the model replicates the behaviour of particular natural systems. Unfortunately, there is only enough available biological information to give a full assessment, comparing the entire set of values of a specific bay with those for the corresponding model, for the Chesapeake Bay and Port Phillip Bay (PPB) runs. These runs will be referred to as CM and PM respectively. The results for the other bays contribute to the findings on the generic behaviour of BM2 in chapter 2.

To reproduce the nutrient loadings in the three other bays considered, the nutrient forcing files for BM2 were scaled so that the new values matched the area-corrected inputs (from Monbet 1992) for each of the chosen bays. No attempt was made to replicate the geometry of the other bays and the hydrodynamics also remained unchanged, but the levels of inflowing nutrient were altered in an attempt to capture the state of the other bays. The biological parameters used in BM2 and IGBEM are not

changed across the various runs as there is not enough information to recalibrate to local species, or functional groups, in all cases. As the standard parameter set for BM2 is not parameterised to match the species composition of any particular bay (the parameters were based on species from temperate bays around the world), the absence of retuning for each location (i.e. with each change in nutrient loading) is justified. As part of a related piece of research (chapter 7) the parameters in BM2 and IGBEM were tuned to represent the actual species composition of PPB rather than a generic temperate fauna and flora. This work is referred to here briefly and is the only research mentioned in this paper where the standard (generic) parameter sets are not used.

The same range of measures (biomasses and system indices) and pooled trophic sets (chlorophyll a, zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos and detritus) that were used to judge general performance in chapter 2 were also used here to judge performance in the PM and CM runs.

3.3 Results and Discussion

3.3.A BM2 vs IGBEM and real bays

Biomasses

Comparison of empirical measures for each pooled trophic set in Port Phillip Bay and Chesapeake Bay with the predicted values of BM2 and IGBEM under corresponding nutrient load levels indicated good performance of BM2 (Table 3.1). In most cases the values predicted by BM2 are within interannual variation of the field values. However, there are some exceptions. The predicted biomass of meiobenthos is high for both the CM and PM runs (Table 3.1), but meiobenthos is difficult to sample (Schwinghamer 1981) and slight increases in the empirical estimates would see the predicted values fall within interannual variation. It is likely that a limitation term for crowding in the meiobenthos is also needed in BM2.

Table 3.1: Average value for each trophic set observed in Port Phillip Bay (PPB) and Chesapeake Bay (CB) and predicted by the associated runs (PM and CM respectively) of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). DIN stands for dissolved inorganic nitrogen. The values used to determine the ranges and averages for the trophic sets observed in CB and PPB are taken from Appendix A.

Set	Units	PPB	PM-BM2	PM-IGBEM	CB	CM-BM2	CM-IGBEM
Chlorophyll 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*	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*	99.17
Microphytobenthos	mg Chl a m ⁻²	38.35	3.05*	5.13*	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*	0.15	1.41	2.31*	0.84
Detritus	g AFDW m ⁻²	2953.37	3720.62	1771.96*	10417.00	7156.19*	6041.44*
DIN	mmol DIN m ⁻³	1.00	1.472	1.49	19.49	20.20	13.50

*Outside the range of interannual variation observed in the field.

The macrophyte group in the CM run is also high (Table 3.1) and this probably reflects the need to retune BM2 with substantial changes in nutrient loads. However, 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 dynamic can be traced back to the differing behaviour of phytoplankton in BM2 and IGBEM under an increase in nutrients (chapter 7). 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 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).

Another symptom of the need to retune BM2 is that the dynamics of change are dissimilar under differing parameter sets. For example, with increasing nutrients the macroalgal biomass grows more than that of the microphytobenthos if the standard parameters are used, but if the parameter set employed in chapter 7 is used the situation is reversed. Although these effects are caused by the same pelagic dynamic, the final form of the effect is dependent upon the parameter set chosen.

The problems with the microphytobenthos in BM2 go beyond those already mentioned. As with IGBEM, 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 3.1). 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 (chapter 1). Similarly, the low levels of detritus predicted for the CM run by BM2 (Table 3.1) 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 is that the predicted zooplankton biomass in the PM run is high compared to recorded values from PPB (Table 3.1). Water column modelling is well developed and usually results in very good fits to reality (Fransz et al. 1991). The failure in this case reinforces the suggestion 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. Regardless, when using standard parameters, BM2 tends to overestimate zooplankton biomass under low nutrient conditions. This result indicates that the standard parameter set does not work equally well over all nutrient conditions. Notably, calibrating BM2 to the dominant species in Port Phillip Bay (PPB) results in predictions much closer to values measured in PPB and to the output of IGBEM (Figure 3.2). It is likely that, unlike IGBEM which performs well across a wide range of nutrient conditions without requiring additional tuning, BM2 may require tuning to particular sites. If so, then there are important ramifications in

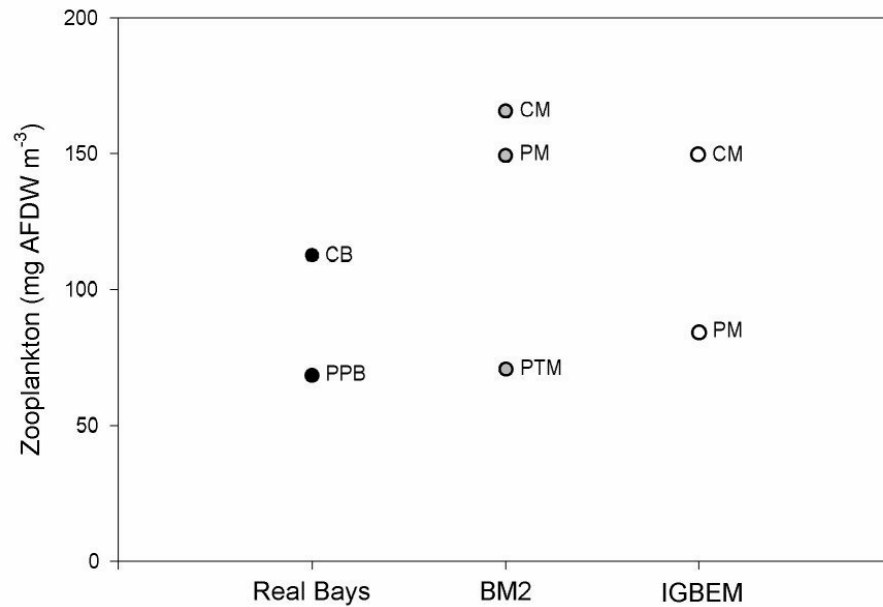


Figure 3.2: Average value for the zooplankton in Bay Model 2, in comparison with values for this trophic set in the field and in the output of the Integrated Generic Bay Ecosystem Model (IGBEM). The values used to determine the averages for the real world sets are taken from Appendix A. CB stands for 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.

applying BM2 in situations where there are large changes in nutrient loads. It was found (chapter 7) that under changing nutrient levels, there is qualitative agreement between the system-level dynamics of BM2 and those predicted by IGBEM and ECOSIM (Christensen and Pauly 1992, Walters et al. 1997). However, quantitatively there is some divergence in the models, with biomass predictions for BM2 the least sensitive to changes in nutrient loading and productivity. This implies that BM2 is capable of correctly indicating the direction of change of a system under pressure, but it may not indicate the true magnitude of this change. This failure suggests that BM2 is not as robust as IGBEM against changes in species composition, as it is more sensitive to shifts in parameter values that would probably accompany such changes in composition.

Based on the improvement in performance of BM2, relative to empirical values, when it is tuned to PPB (chapter 7), at least some of the discrepancies noted for the standard parameter set will disappear if BM2 is tuned when applied to a specific location. However, the problems identified above for microphytobenthos and meiobenthos may persist regardless of such tuning. While site-specific parameterisation of as many functional groups as possible is best, the key groups to focus on appear to be the zooplankton, zoobenthos (primarily the epifaunal carnivores) and the benthic primary producers (in particular the seagrass and microphytobenthos). The deposit feeders and meiobenthos can be sensitive to the parameter settings used, but this is more likely the result of the omission of a crucial limiting factor (e.g. the availability of space) for these groups.

Community composition

The relative composition of communities (in terms of biomass) is another informative comparison, particularly for the fish and benthic groups. This comparison is only possible for the PM run (Table 3.2) and shows that BM2 well represents patterns

Table 3.2: Comparison of the community composition for the fish and benthic groups observed in Port Phillip Bay (PPB) and predicted by BM2 and IGBEM in the runs with conditions matching those in PPB. 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).

Functional Group	% 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

of relative abundance, particularly for the benthic groups.

Estimates of the fish community produced by the models indicate that the predictions of both models are reasonably close to the values from PPB and that neither model consistently out performs the other in this area. The estimates produced for BM2 are closer to the PPB values for the demersal fish groups, but the IGBEM estimates are closer for the pelagic groups. Results for the benthic groups reflect favourably on BM2. The predicted community composition reflects that observed in PPB and BM2 performs as well as or better than IGBEM for the majority of benthic groups. Despite minor divergences, our results show that BM2 captures the large-scale community level dynamics of the fish and benthic groups.

Production and Consumption

Levels of daily production and consumption can be informative for management and scientific purposes. Reasonably accurate predictions of these values by models not only indicate their usefulness for prognostic purposes, but are also a good indication of

whether the model represents the system in a faithful manner.

The majority of the production/biomass (P/B) and consumption/biomass (Q/B) values given by BM2 are reasonably close to the empirical estimate for PPB (Table 3.3). The only two values that are less than half the PPB estimates are the P/B ratios for planktivorous fish and macrophytes. Overall, both models perform equally well. In some cases the predictions given by both models are very close (such as those for zooplankton), while in others one or the other is much closer to the PPB estimate.

Table 3.3: Comparison of the estimates of the ratios of production:biomass and consumption:biomass for Port Phillip Bay (PPB) and the BM2 and IGBEM runs with conditions matching those in PPB.

Set	Production:Biomass			Consumption:Biomass		
	PPB	BM2	IGBEM	PPB	BM2	IGBEM
Phytoplankton	210.3	200.1	241.8	-	-	-
Zooplankton	2.1	1.7	1.8	3.4	2.7	2.9
Fish	3.1	1.9	4.0	21.7	30.0	13.5
Planktivorous	6.3	2.1	3.2	82.6	49.8	22.4
Piscivorous	2.0	3.6	2.6	8.2	11.0	5.9
Demersal	1.5	1.4	2.1	7.1	9.9	5.7
Demersal Herbivorous	1.2	1.9	3.1	9.6	12.1	7.0
Benthos	14.2	7.7	17.0	49.0	46.5	44.1
Epifauna	9.9	6.7	5.3	17.3	30.2	8.7
Infauna	17.6	14.0	31.1	85.1	68.4	86.6
Macrophytes	22.6	8.5	12.4	-	-	-
Microphytobenthos	6.3	5.1	5.2	-	-	-

The most notable P/B values (Table 3.3) are those for macrophytes. Values predicted by the models are only about a half of observed estimates. This is largely due to the formation of a “macrophyte-barrens” cycle in the models. This is a “boom-bust” cycle, of varying period, which involves the phytobenthos, demersal herbivorous fish and the benthic grazers. In chapter 2 it was found that this “macrophyte-barrens” cycle only occurs in the more marginal macrophyte habitat in BM2, whereas it is more widespread in IGBEM. This cycle will be discussed further in the section on spatial

dynamics.

System indices

Just as ecosystem models should conform to observed empirical relationships (such as size-spectra) they must also give realistic values for system-level indices. Several of these (after Christensen 1992) were used 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 3.4). Both models generally produce realistic values for the various indices. Though both models predict a total throughput that is outside the range given by the coastal systems summarised by Christensen (1992), 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 better matches the system-level indices estimated for PPB, with the predicted value of 7 of the 11 indices close to the PPB estimates (compared with 4 for IGBEM). The match of some of the indices improves if the standard parameter set is replaced with one tuned to the species composition of PPB (from chapter 7) (for example Biomass/Throughput drops from 0.025 to 0.015, which is very close to the 0.016 estimated for PPB). However, even when tuned, the System Omnivory Index remains too low, as does the Schrodinger ratio. This is in contrast to IGBEM, where the majority of indices match once the model is tuned to represent the flora and fauna of PPB. 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 (e.g. the System Omnivory Index).

Table 3.4: List of indices and their associated values for Port Phillip Bay (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). The “Maximum”, “Minimum” and “Averages” refer to values of these indices calculated for 8 coastal areas from around the world (from Christensen 1992).

System (or run) \ Index	Sum of flows (Throughput)	Primary Production / Biomass	Biomass / Throughput	Biomass Supported	System Omnivory Index	Dominance of Detritus	Average organism 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 baseline 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 x10)	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 baseline 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 x10)	50702	18.7	0.019	0.040	0.15	0.47	0.042	3.36	0.06	4.59	29.8

3.3.B Spatial structure

To consider the spatial dynamics of the PM and CM runs, the predicted average biomasses per box over the final four years of the runs were analysed to determine whether there are boxes with similar biological and physical properties. A two-dimensional non-metric Multidimensional Scaling (MDS) plot, derived from a Bray Curtis similarity matrix, was used to compare the average biomasses of all groups in each box to see whether there are groups of boxes with similar community structure. To ascertain which groups determined the clustering seen, the average values of the physical variables and the biomass per group was then evaluated using the SIMPER routine of the Primer software package. This analysis identified “areas” (boxes in the model sharing biological and physical characteristics) in the model output and any “areas” predicted to share communities (dominant biological groups) were pooled to produce “zones”. The general mechanisms producing the patterns are discussed in chapter 2 and will not be repeated here; only specific details pertinent to the PM and CM runs will be mentioned.

The two models contained a similar distribution of zones around the bay in both the PM and CM runs (Figures 3.3 and 3.4). More importantly, the PM run of each model also produces a set of zones broadly similar to those identified empirically in PPB (Figure 3.3), although zonation patterns of BM2 better represent those observed in PPB than do those from IGBEM.

The communities associated with the light grey zones (Figure 3.3) are “edge” communities associated with sand and rock substrata, and they are consistently found along the edges of the bay. Communities associated with the dark grey zones in the centre of the bay are in deeper water associated with a mud substratum. The composition of these communities (Table 3.5) show some overlap (primarily in the water column groups), but there are also clear differences (especially in the epibenthos).

Figure 3.3: Spatial distribution of the main communities identified in the PM run of (a) Bay Model 2 and (b) the Integrated Generic Bay Ecosystem Model, as well as (c) those recorded in Port Phillip Bay (from findings in Hall 1992, Poore 1992, Parry et al. 1995, Beardall et al. 1996, Nicholson et al. 1996, Beardall and Light 1997). Dark grey indicates a “central” community that features meiobenthos, microphytobenthos, bacteria and a discrete plankton assemblage (Table 3.5). Light grey (whether striped or solid) indicates an “edge” community that is usually dominated by one of two alternative plankton assemblages, along with fish, macrophytes and benthic macrofauna (Table 3.5). Note that for ease of comparison the edges of the zones for Port Phillip Bay have been matched to the boundaries of the boxes used in the models. The major landmarks of note in Port Phillip Bay are marked on (a) and the northern shore from A to B is known as the Geelong Arm.

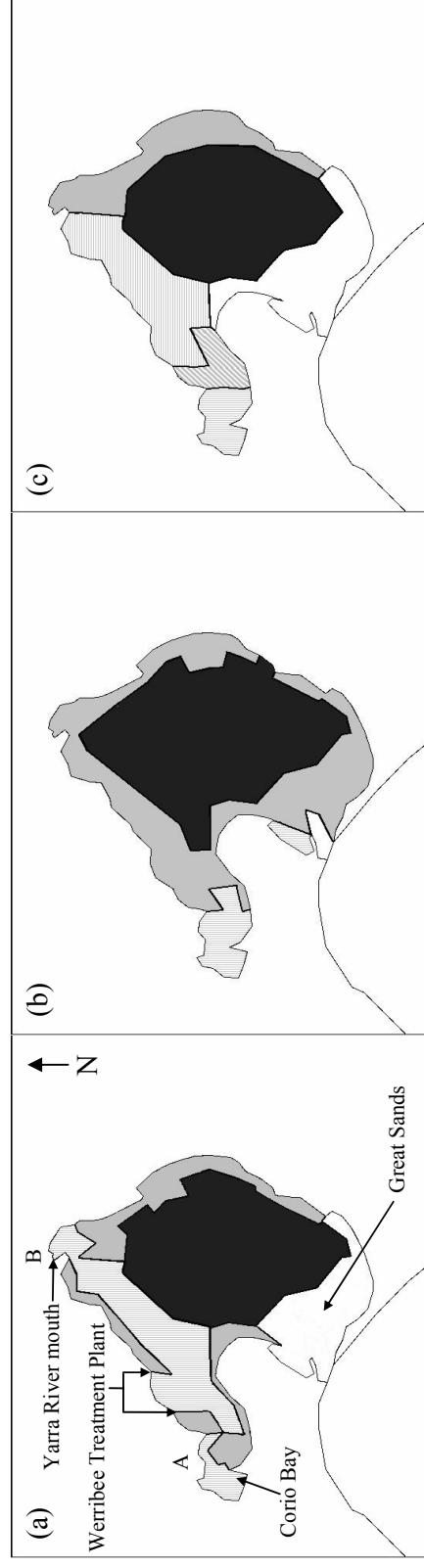


Table 3.5: Dominant groups distinguishing the “edge” and “central” communities. These groups are identified consistently in the output of both models (BM2 and IGBEM) and from field observations in Port Phillip Bay. The meaning of the codes for each of the biological groups mentioned here are given in Table 3.6. 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).

Community	Biological Components				Physical Characteristics	
	Planktonic	Fish	Epibenthic	Benthic	Macrophyte	Remin
Edge	PL, AF or PS, ZS	FP, FV, FD, FG	BF, BG, MZ	BD, BC	MA or SG	PB, DR ^b , DL ^b
Central	PS, AF, DF, HF, ZL, ZLC		BF, MZ ^a	OB, MB		

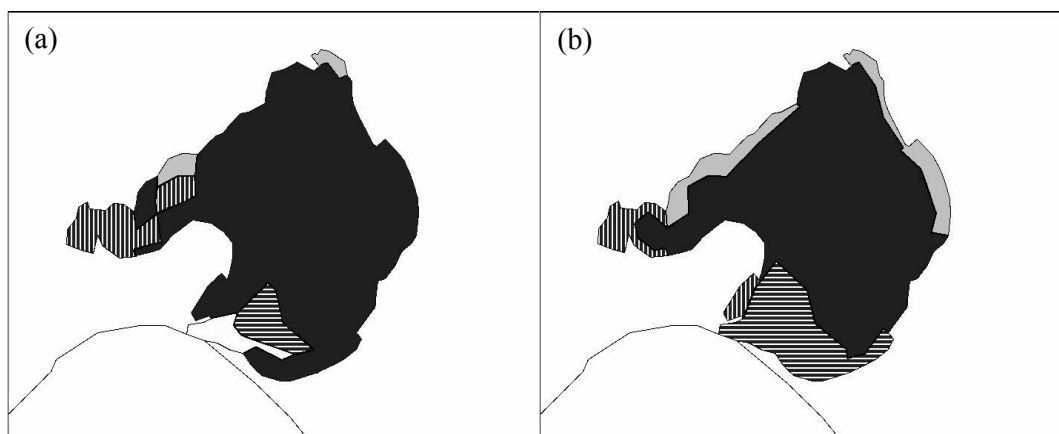
a. Not predicted by IGBEM

b. Only in the Geelong Arm of the bay (Figure 3.3).

Table 3.6: Meaning of the codes used in Table 3.5.

Code	Component
PL	Diatoms
AF	Autotrophic flagellates
PS	Picophytoplankton
DF	Dinoflagellates
PB	Pelagic bacteria (attached and free living)
HF	Heterotrophic flagellates
ZS	Microzooplankton
ZL	Large omnivorous zooplankton
ZLC	Large carnivorous zooplankton
FP	Planktivorous fish
FV	Piscivorous fish
FD	Demersal fish
FG	Demersal herbivorous fish
MA	Macroalgae
SG	Seagrass
MB	Microphytobenthos
MZ	Macrozoobenthos (epifaunal carnivores)
BG	Benthic (epifaunal) grazers
BF	Benthic suspension feeders
BC	Infaunal carnivores
BD	Benthic deposit feeders
OB	Meiobenthos
AEB	Aerobic bacteria
ANB	Anaerobic bacteria
DL	Labile detritus
DR	Refractory detritus

Figure 3.4: Distribution of the main communities distinguished in the CM run of (a) Bay Model 2 and (b) the Integrated Generic Bay Ecosystem Model. Dark grey indicates a “central” community. Light grey (whether striped or solid) or white indicates an “edge” community. The characteristics of these communities are as of Figure 3.3.



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 are 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 the highest densities of microphytobenthos along the north-west shore, from Corio Bay to the Yarra River (Figure 3.3), but reasonable levels exist throughout the bay north of the Great Sands (Figure 3.3). 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. 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.

3.3.C Strengths and weaknesses

Regardless of the degree of sophistication, no model is an exact replica of reality. Each model has its own idiosyncrasies, strengths and weaknesses. Both the strengths and weakness present in BM2 stem from its structure and relative simplicity.

Model calibration and stability

BM2 is more sensitive to parameter settings than IGBEM and it requires more tuning on a case-by-case basis. The best example of this is the zooplankton groups (Figure 3.2). For IGBEM the values are close to the observed values, while those for BM2 require tuning if they are to closely match empirical values over a range of conditions. This characteristic was noted in PPBIM (Murray and Parslow 1997) and may be a general feature of the kind of formulation used in PPBIM and BM2.

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 sufficient 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 standard 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.

The formulation of BM2 does have implications for the stability and biological

predictions of the model. Explosive growth and associated trophic cascades are not seen in IGBEM, but they are observed occasionally in BM2, primarily in the benthic groups. In particular, the benthic deposit feeders and microphytobenthos in BM2 are 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 (chapter 2). As benthic modelling matures it may be pertinent to include spatial limitation, even for mobile groups and those not confined to the sediment-water interface. 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 (chapter 6). In spite of these sensitivities and potential weaknesses, BM2 does capture the major changes seen in systems that are under pressure. Thus, even if only qualitatively, BM2 can give an indication of the likely consequences of a range of scenarios. Moreover, as there are fewer parameters in the model, the causes of “misbehaviour” are transparent and easily corrected.

Reduced complexity of detail is justified

Consideration of the relative performance of BM2 when applied to specific systems reinforces the conclusions drawn based on the investigation of its general dynamics (chapter 2). The output of BM2 often compares well with observations from Chesapeake Bay and Port Phillip Bay. Crucially, 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). However, the behaviour of BM2 is not as flexible as that of IGBEM when spanning

large changes in ecosystem forcing (e.g. large external inputs of nutrients). Moreover, BM2 occasionally produced anomalous behaviours and this should be used to guide its application on a site-by-site basis (particularly in oligotrophic conditions) and when extreme changes in ecosystem conditions are a matter of interest. Despite these warnings, 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. Thus it seems clear that simpler formulations are as capable of capturing the emergent properties and characteristics of marine ecosystems as larger models that include detailed physiology.

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 (this thesis) 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, chapter 1). 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, chapter 5). 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 coverage and resolution seems to be much more important than the level of detail incorporated in the formulation of these features.

3.4 Conclusions

As ecosystem approaches to resource management become increasingly common, general tools will be required and are beginning to appear (Walters et al. 1997, Sainsbury et al. 2000). Ecosystem models are becoming more widespread and some generic total system models are finding wide application (Christensen et al. 2000). As a consequence, evaluation of ecosystem models must include specific comparisons to particular systems in addition to more general analyses of performance and overall behaviour. Consideration of the biogeochemical model BM2 in this way indicated that its simpler structure was not as flexible as that of the more physiologically detailed model IGBEM. This means that while it requires more tuning on a site-to-site basis and may quantitatively break down under very large changes in nutrient loading, the qualitative predictions of BM2 do match those of other models that do not suffer any such degradation in performance with changing nutrient loads. Moreover, the model'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. Thus,

despite some weaknesses, BM2 can be applied successfully to coastal marine systems and without requiring as much information as some of the other extant ecosystem models, such as ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) or IGBEM (chapter 1).