Chapter 1 An Integrated Generic Model of Marine Bay Ecosystems

Abstract

The Integrated Generic Bay Ecosystem Model (IGBEM) is presented. It is a coupled physical transport-biogeochemical process model constructed as a basis to explore the effects of model structure and complexity. The foundations for the model are two existing models, the European Regional Seas Ecosystem Model II (ERSEM II) and the Port Phillip Bay Integrated Model (PPBIM). Additional components (such as benthic herbivorous invertebrates) and certain sub-models (to do with sediment chemistry and mixing) had to be incorporated or modified to allow for extra factors of interest and a seamless amalgam of ERSEM II and PPBIM. The standard form of the entire model compares well with real systems, with similar physical features and of varying eutrophication schemes, from Chesapeake Bay through to Port Phillip Bay Australia. Furthermore, IGBEM conforms to general ecological checkpoints and produces spatial zonation and long term cycles characteristic of natural systems. Despite the model taking a generalised biomass per functional group form it captures crucial system resource dynamics well and allows for some exploration of the effects of ecological driving forces such as predation and competition.

Keywords

biogeochemical, model, ecosystem, ERSEM, Port Phillip Bay

1.1 Introduction: marine ecosystem models

There has been a proliferation of marine ecosystem models within the last two decades with literally hundreds, of varying scope and quality, in existence. Most are mass balance models, of Eulerian formulation, which typically concentrate on either end of the trophic chain, i.e. fish or nutrients and phytoplankton, but rarely both. Those that

couple physics and biology tend to do so by linking sub-models that approach the respective processes in quite different ways. Physical attributes are often dealt with via a number of common and well defined methods, including box models, specified (often Lagrangian) flows, prognostic dynamical flow models or general circulation models. The most common methodologies employed in the biological side of ecosystem models are pooled models (which conserve some biogeochemical currency within a chain, or small network, of compartments that represent functional groups or trophic levels), multispecies formulations (allowing for more realistic webs) and structured population models. Generally speaking, it emerges that box models and specified flows are the best way of considering biological processes in realistic flow environments, free of the complexity of directly calculating the flow itself. It is also apparent that pool models provide a useful framework for constructing a variety of models (Olson and Hood 1994). Models such as the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al. 1995) mix and match biological formulations based on trophic identity to capture the critical performance of the different components.

The felicitous history of reductionist physical models was probably one of the driving forces behind the bloom of highly detailed deterministic ecosystem models during the 1970s (Young et al. 1996). However, it became apparent that complicated models did not necessarily capture system dynamics well and there was a wide spread and rapid return to simpler or more circumscribed models. With the advent of more powerful computers and the push for an ecosystem perspective for resource and environmental management, detailed ecosystem models are again finding some measure of favour. While there is still debate about their usefulness for management, given their dependence on exceedingly large numbers of, often uncertain, parameter values, they are useful for locating gaps in our current understanding as well as learning about system behaviour and its determinants. It is in this context that the Integrated Generic

Bay Ecosystem Model (IGBEM) was constructed. Consequently, it is not intended as a simulated replica of any one system. For convenience it does utilise the physics of a particular Australian bay (Port Phillip Bay, Melbourne (Figure 1.1)), but it has the general biology and functional groups typical of most temperate bays.

IGBEM was constructed as a first step in understanding the effects of model structure and complexity on model behaviour and thereby deriving some guidelines to optimal model complexity. Though not a strict requirement, it was thought that such an exercise would benefit from being built upon a reference model that resembled reality as much as possible. Here we outline construction of the model and explore its capacity to reflect real world behaviours.

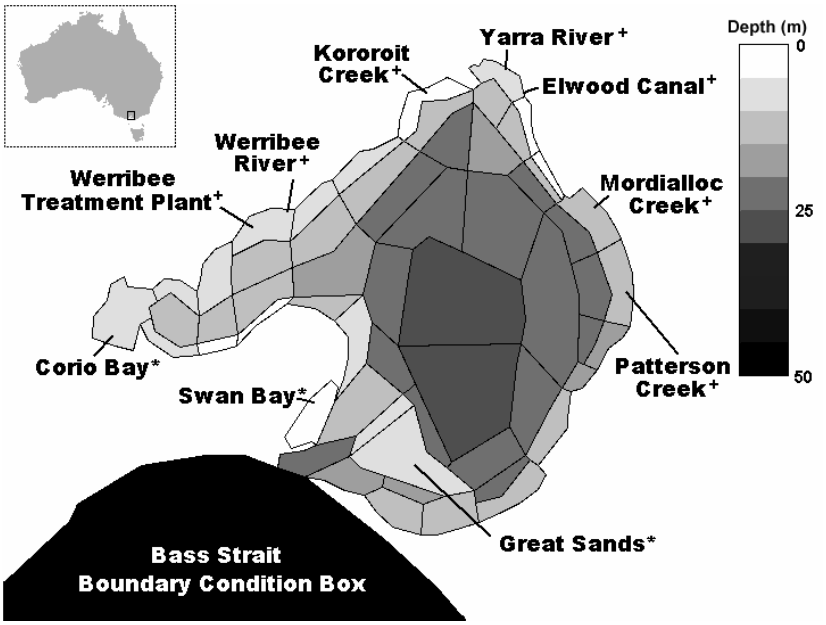


Figure 1.1: Map of box geometry used for the standard runs of the Integrated Generic Bay Ecosystem Model. It represents Port Phillip Bay, Melbourne, Australia (location marked on map inset). Important geographical features (marked with *) and point source-sinks used in the model (marked by +) are indicated.

1.2 Building IGBEM

Port Phillip Bay (PPB) has a number of features that make it an attractive site for learning. It is a large marine embayment, approximately 1930 km^2, that has over half its volume in waters less than 8 m (it is 24m at its deepest point). Only 8 drainage basins directly run off into the bay. Extensive sandbars form a tide delta in the southern end of the bay and these restrict exchange between the bay and the open waters of Bass Strait. This physically contained environment is therefore free of many of the often-worrisome issues that are associated with boundary conditions. Since approximately three million people reside within the urbanised portions of the bay's catchment area, the bay is also under some of the stresses faced by other major temperate bays. Accordingly it is a prime site to study ecosystem dynamics, human impacts and how they might best be modelled. Fortuitously it has also been the subject of intensive study over many years, which provides an extensive knowledge base to build from.

The biogeochemical model created as part of the most recent PPB study is both detailed and successful (Murray and Parslow 1999a). However, as it is based on the biogeochemistry of only the lower trophic levels it is not a suitable vehicle for the examination of the effects of ecosystem model complexity and formulation, when considering fisheries and eutrophication simultaneously. Since the Port Phillip Bay Integrated Model (PPBIM) by Murray and Parslow (1999a) does not cover enough faunal groups, it was necessary to use another model to extend PPBIM to produce a suitable generic model. The European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) is well suited to being grafted to PPBIM, as it is a marine biogeochemical boxmodel with a similar architecture and it includes more process detail than PPBIM and additional faunal groups. Between them, PPBIM and ERSEM II include most of the major groups and processes thought to be important in coastal marine systems and they represent state-of-the-art biogeochemical

models.

IGBEM was created by tying together the biological and physical sub-models of PPBIM (Murray and Parslow 1997 and 1999a) and the biological modules from ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997). The 4 submodels of PPBIM, 3 biological ones (water column, epibenthic, sediment) and a physical submodel, formed the framework for IGBEM and the various ERSEM II modules were translated and added directly to the appropriate sub-model. For those functional groups that are covered by both ERSEM II and PPBIM both formulations are included in IGBEM with a switch setting determining which is in use in any one run. Only the ERSEM II formulations were employed in the runs presented here.

The final form of IGBEM provides a spatially and temporally resolved model of nutrient cycles in an enclosed temperate bay. The model has twenty-four living components, two dead, five nutrient, six physical and two gaseous components (Table 1.1). These components are linked through both biological and physical interactions and the resultant network (Figure 1.2) is reminiscent of flow diagrams for real systems. The model is replicated spatially using the 3 layer (water column, epibenthic, sediment), 59-box geometry developed for PPBIM. Thus, the set of polygons and their bathymetry map a physical area that represents PPB (Figure 1.1). Temporally, a daily time-step is utilised for the standard runs of IGBEM as this best matches the transport model which underlies the physical sub-model of IGBEM, and is little different from that of PPBIM. The use of the transport model means that, like PPBIM, IGBEM is driven by seasonal variations 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. Further details of the transport model, the rationale behind its use and how it links into the biological submodels of PPBIM can be found in Walker (1999) and Murray and Parslow (1999a). The level of process detail used in the

IGBEM formulations and IGBEM's diet matrix are outlined in Tables 1.2 and 1.3 respectively.

Table 1.1: List of components in the Integrated Generic Bay Ecosystem Model (IGBEM) compared to those in the Port Phillip Bay Integrated Model (PPBIM) and the biological modules of the European Regional Seas Ecosystem Model II (ERSEM II). All living and dead components have C, N and P pools.

		Model		
Component	**Codename**	IGBEM	ERSEM II	PPBIM
Diatoms*	PL	Y	Y	Y
Autotrophic flagellates	AF	Y	Y	
Picophytoplankton	PS	Y	Y	Y
Dinoflagellates	DF	Y	Y	Y
Pelagic bacteria	PB	Y	Y	
Heterotrophic flagellates	HF	Y	Y	
Microzooplankton	ZS	Y	Y	Y
Large omnivorous zooplankton	ZL	Y	Y	
Large carnivorous zooplankton	ZLC	Y	Y	Y
Planktivorous fish	FP	Y	Y	
Piscivorous fish	FV	Y	Y	
Demersal fish	FD	Y	Y	
Demersal herbivorous fish	FG	Y		
Macroalgae	MA	Y		Y
Seagrass	SG	Y		Y
Microphytobenthos*	MB	Y		Y
Macrozoobenthos (epifaunal carnivores)	MZ	Y	Y	
Benthic (epifaunal) grazers	BG	Y		
Benthic suspension feeders	BF	Y	Y	Y
Infaunal carnivores	BC	Y	Y	
Benthic deposit feeders	BD	Y	Y	
Meiobenthos	OB	Y	Y	
Aerobic bacteria	AEB	Y	Y	
Anaerobic bacteria	ANB	Y	Y	
Labile detritus	DL	Y	Y	Y
Refractory detritus*	DR	Y	Y	Y
DON	DON	Y	Y	Y
DIP	DIP	Y	Y	Y**
Ammonia	NH	Y	Y	Y
Nitrate	NO	Y	Y	Y
Dissolved silicate	Si	Y	Y	Y
Dissolved oxygen	O2	Y	Y	Y**
Carbon dioxide	CO2	Y	Y	
Light	IRR	Y	Y	Y
Salinity	SAL	Y		Y
Sediment grain types	PHI	Y		Y
Bottom stress	STRESS	Y		Y
Porosity	PORE	Y		Y
Volume	VOL	Y		Y

* Also have an Si internal pool.
** Handled as nitrogen fluxes scaled by the Redfield ratio N:C:P:O:Si = 1:5.7:0.143:16:3 (from Murray and Parslow 1997)

Figure 1.2: Biological and physical interactions between the components used in the Integrated Generic Bay Ecosystem Model IGBEM). A '*' indicates those components from the Port Phillip Bay Integrated Model, and those in **bold** are components built specifically for IGBEM, while the remainder are from the European Regional Seas Ecosystem Model II (Blackford and Radford 1995). The code for each component is given by its name.

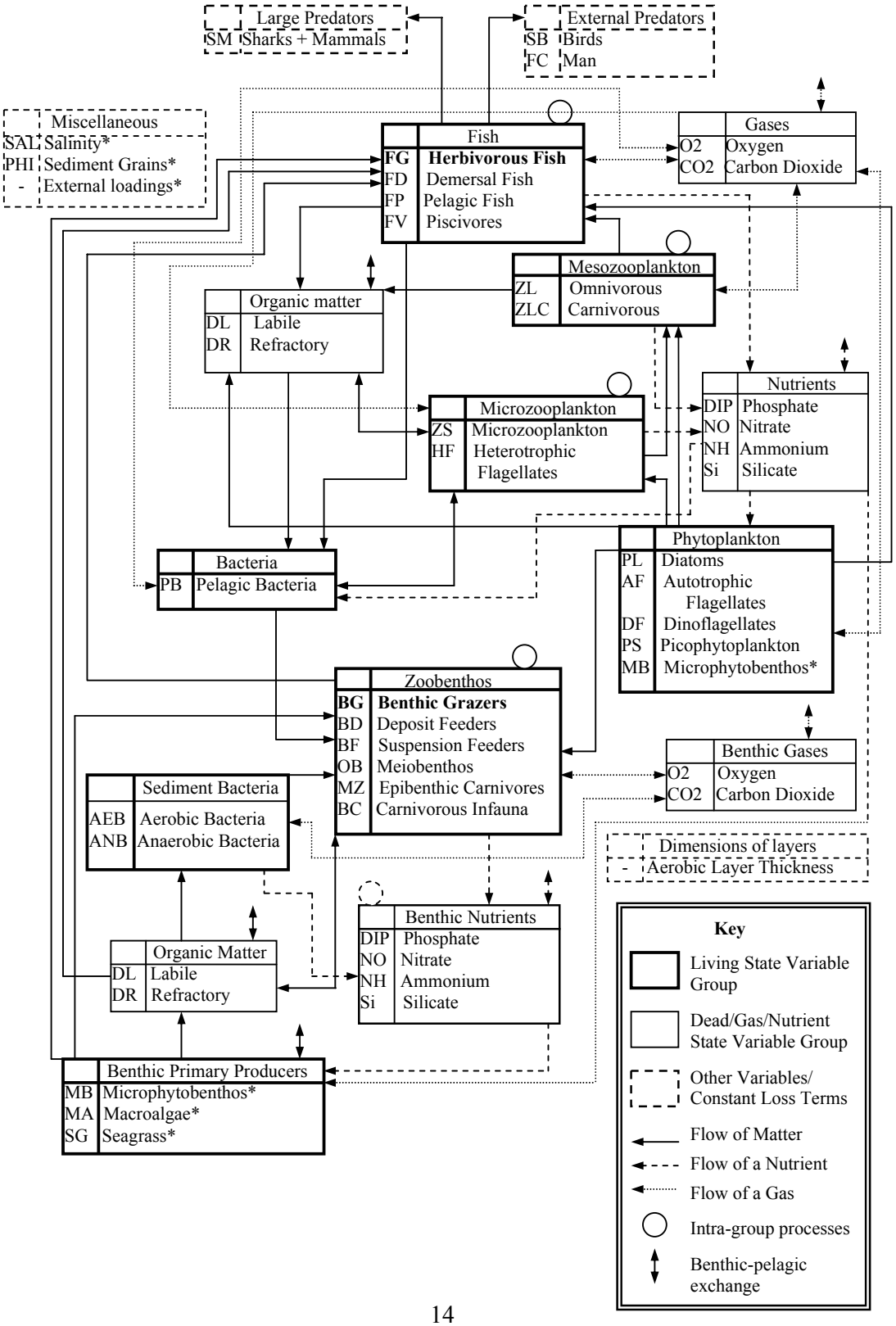


Table 1.2: Level of detail used in the model formulation for each of the processes carried out in a standard run of the Integrated Generic Bay Ecosystem Model. Component codes are as stated in Table 1.1 (except for C, N, P, Si which are Carbon, Nitrogen, Phosphorous and Silica respectively). The symbols indicate the formulation used for each process as follows: **a**ctivity; **b**asal; **c**onstant (not dynamic); **d**ynamic; DIN (**e**piphytic growth) effect; search and **h**andling times included; **i**nternal pool controls; **l**ight limitation; depth effect (**m**); **n**utrient effect; **o**xygen effect; **p**erforms this physical activity; **r**est; **s**tarvation; **t**emperature effect; cro**w**ding; assumed in formulation but not e**x**plicit; ph**y**sical bottom stress effect; present (+); absent (-). ** indicates that there is a flux of C from the static returns, but in the form of carbon dioxide.

Process	**Component**																	
Water Column	C	N	P	Si	PL	DF	AF	PS	PB	ZS	HF	ZL	ZLC	FP	FV	MB	DR	DL
Used by phytoplankton	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Used by bacteria	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Flux from excretion	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Mineralisation	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	+	+
Nitrification	-	+	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-
Oxygen production	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	+	-	-
Growth	-	-	-	-	lnt	lnt	lnt	lnt	ra	+	+	+	+	+	+	lnt	-	-
Respiration	-	-	-	-	ra	ra	ra	ra	o	ra	ra	ra	ra	ra	ra	ra	-	-
Lysis (nutrient stress)	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	+	-	-
Nutrient uptake	-	-	-	-	i	i	i	i	-	-	-	-	-	-	-	i	-	-
Predation losses	-	-	-	-	+	+	+	+	+	+	+	+	+	cd	cd	+	+	+
Cannibalism	-	-	-	-	-	-	-	-	-	+	+	+	+	-	+	-	-	-
Grazing (consumption)	-	-	-	-	-	-	-	-	-	+	+	h	h	h	h	-	-	-
Natural mortality	-	-	-	-	x	x	x	x	+	o	o	o	o	bs	bs	x	-	-
Excretion	-	-	-	-	i	i	i	i	i	i	i	i	i	i	i	i	-	-
Faeces	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-
Flux from static returns[1]	**	+	+	-	-	-	-	-	+	-	-	-	-	-	-	-	+	+

Sediment	C	N	P	Si	BD	BC	OB	AEB	ANB	PL	DF	PS	AF	MB	DR	DL
Used by microphytobenthos	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-

Process	Component															
	C	N	P	Si	BD	BC	OB	AEB	ANB	PL	DF	PS	AF	MB	DR	DL
Used by bacteria	+	+	+	-	-	-	-	-	-	-	-	-	-	-	ontm	ontm
Flux from excretion	+	+	+	+	-	-	-	-	-	-	-	-	-	-	+	+
Mineralisation	-	-	-	-	-	-	-	p	p	-	-	-	-	-	+	+
Nitrification	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Denitrification	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxygen production[2]	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Growth	-	-	-	-	ot	ot	ot	ra	ra	-	-	-	-	lnt[2]	-	-
Respiration	-	-	-	-	ra	ra	ra	otra[2]	otra[2]	-	-	-	-	ra	-	-
Nutrient uptake	-	-	-	-	-	-	-	ontm	ontm	-	-	-	-	i	-	-
Predation losses	-	-	-	-	+	+	+	+	+	-	-	-	-	+	+	+
Cannibalism	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
Grazing (consumption)	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-
Natural mortality	-	-	-	-	ot	ot	ot	+	+	+	+	+	+	+	-	-
Excretion	-	-	-	-	i	i	i	i	i	-	-	-	-	i	-	-
Faeces	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-
Impact upon bioirrigation/bioturbation	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-

Epibenthic	C	N	P	Si	MZ	BF	BG	MA	SG	FD	FG	DR	DL
Used by macrophytes	+	+	+	-	-	-	-	-	-	-	-	-	-
Flux from excretion	-	-	-	-	-	-	-	-	-	-	-	+	+
Oxygen production	+	+	+	-	-	-	-	-	-	-	-	+	+
Growth	-	-	-	-	-	-	-	+	+	-	-	-	-
Respiration	-	-	-	-	ot	ot	ot	lntw	lntw	+	+	-	-
Lysis (nutrient stress)	-	-	-	-	ra	ra	ra	x	x	ra	ra	-	-
Nutrient uptake	-	-	-	-	-	-	-	+	+	-	-	-	-
Predation losses	-	-	-	-	+	+	+	+	+	cd	cd	+	+
Cannibalism	-	-	-	-	+	-	-	-	-	+	-	-	-
Grazing (consumption)	-	-	-	-	+	+	+	-	-	h	h	-	-
Natural mortality	-	-	-	-	ot	ot	ot	by	be	bs	bs	-	-
Excretion	-	-	-	-	i	i	i	an	an	i	i	-	-
Faeces	-	-	-	-	+	+	+	-	-	+	+	-	-
Flux from static returns[1]	-	-	-	-	-	-	-	-	-	-	-	+	+
Impact upon bioirrigation and bioturbation	-	-	-	-	+	+	+	-	-	-	-	-	-

1. i.e. a % of the losses to fishing/seabirds/large predators
2. used to determine the oxygen horizon

Table 1.3: Diet matrix for the living components in a standard run of the Integrated Generic Bay Ecosystem Model. Component codes are as for Table 1.1. A "+" indicates a feeding link, "-" no link and a "0" is a potential link (implemented but the availability-preference parameter for that prey item is set to zero in the standard runs.)

	Grazer															
Prey	ZS	HF	ZL	ZLC	FP	FV	FD	FG	AEB	ANB	OB	BD	BC	BF	MZ	BG
PL	+	-	+	-	+	-	-	-	-	-	-	-	-	+	-	-
PS	+	+	0	-	-	-	-	-	-	-	-	-	-	+	-	-
AF	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-
DF	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
ZS	+		+	+	-	-	-	-	-	-	-	-	-	-	-	-
HF	+	+	+	0	-	-	-	-	-	-	-	-	-	-	-	-
ZL	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
ZLC	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
FP	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FV	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FD	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FG	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
PB	0	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AEB	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-
ANB	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
OB	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-
BD	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-
BC	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-
BF	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
MZ	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
BG	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
MB	+	-	0	-	-	-	-	+	-	-	+	+	-	+	-	-
MA	-	-	-	-	-	-	0	+	-	-	-	-	-	-	+	+
SG	-	-	-	-	-	-	0	+	-	-	-	-	-	-	+	+
DR	0	0	0	0	-	-	-	-	+	+	+	+	-	-	-	-
DL	-	-	-	-	-	-	-	+	+	+	+	+	-	+	-	+

Some components and processes in IGBEM do not feature in PPBIM or ERSEM II, or have been modified from their original formulation to enable synthesis of the two models. Important additions are components for epibenthic herbivorous scavengers and herbivorous fish. These were added to take advantage of the macrophyte food sources represented in PPBIM. These components were written by duplicating the general form of appropriate existing components (using ERSEM's 'standard organism' concept (Baretta et al. 1995)) and then adjusting diets and parameter values to those representative of herbivorous grazers. Consumption of these new groups by predatory groups within the model was also added (see the diet matrix, Table 1.3) based on diet data from the literature (Shepherd and Thomas 1982, Heymans and Baird 1995, Levinton 1995, Kuiter 1996, Gunthorpe et al. 1997).

Two biological components were modified in integrating PPBIM and ERSEM II. Microphytobenthos was included with minor modification after Blackford (1999). Also, the benthic suspension feeders of ERSEM II had their diets and habits modified slightly to better match those of PPBIM. This involved changing one of their dietary components from refractory to labile detritus and including an incidental transfer of refractory detritus from the water column to the sediment via suspension feeding.

A number of the original chemical and physical processes in PPBIM and ERSEM II required modification. The highly refractory detritus of ERSEM II, which has a very slow breakdown rate (on the order of a century or more) was omitted. The component referred to as refractory detritus in IGBEM is the equivalent of ERSEM II's “Slowly degradable organics”. The formulation of bioirrigation implemented in PPBIM was left intact for IGBEM, but it is tied to the dynamical sediment fauna via an “enhancement” term similar to that of ERSEM I (Ebenhöh et al. 1995). In contrast, bioturbation received more attention in IGBEM than in PPBIM. Bioturbation was considered during the formulation of PPBIM, but it was never implemented (Walker

1997), whereas it is a working part of ERSEM I (Ebenhöh et al. 1995). The inclusion of well-elaborated formulations of bioturbation (a good example being that of Francois et al. 1997) in an ecosystem model is no more feasible now then when ERSEM I was originally formulated (Ebenhöh et al. 1995), so simple approximations are necessary. IGBEM uses explicit sediment layers and includes the sediment mixing processes of particulate diffusion, expulsion (whereby material at depth is moved to the surface), and exchange (where material at the surface and at depth are exchanged). The only components (tracers) acted upon by bioturbation were those particulate tracers that were allowed in the sediments and were not macrobenthos. That is, sediment grains, settled phytoplankton, microphytobenthos, meiobenthos, detritus and sediment bacteria. The approximation used in IGBEM represents particulate diffusion, expulsion and exchange with the surface by transferring sediment between the appropriate layers of the model. Accordingly, the formulation implemented expresses the tracer concentration in the *i*th sediment layer (Ci(t)) at the end of a time step as:

$$C_i(t+\Delta t) = \frac{C_{i+1}(t)\cdot k_{i+1} + C_{i-1}(t)\cdot k_{i-1} + C_i(t)\cdot z_i - 2C_i(t)\cdot k_i - C_i(t)\cdot m_i - C_i(t)\cdot g_i + C_0(t)\cdot g_0}{k_{i+1} + k_{i-1} + z_i - 2k_i - m_i - g_i + g_0} \tag{1.1}$$

$$k_i = \frac{\psi\cdot\delta\cdot\tau\cdot\theta_i}{z_i} \tag{1.2}$$

$$m_i = \gamma\cdot\delta\cdot\tau\cdot\theta_i \tag{1.3}$$

$$g_i = \eta\cdot\delta\cdot\tau\cdot\theta_i \tag{1.4}$$

Where k_i represents the thickness transferred from i due to particulate diffusion, m_i is the thickness moved to the surface from layer *i* by expulsion and g_i is the thickness moved from layer *i* due to exchange with surface layers and z_i is the thickness of layer *i*. The thicknesses k_i, m_i and g_i only differ in a single parameter. For the parameters they share, δ represents the base density of biological activity; τ represents the modification to the baseline to reflect dynamic sediment fauna activity in the ecological sub-model

(calculated in much the same way as that of ERSEM (see Ebenhöh et al. 1995)); and θ_i is the depth dependence of the mixing process (this is a simple functional form, as of PPBIM, and though usually constant it is also possible to implement linear, parabolic and half-Gaussian forms (Walker 1997)). The parameter which does differ in the calculation of k_i, m_i and g_i is the base rate of each process - ψ is the rate of particle diffusion (m^2 per Δt per unit biomass of bioturbative benthos per m^2), γ is the rate of expulsion (m per Δt per unit biomass of bioturbative benthos per m^2) and η is the rate of exchange between the surface and deeper layers (m per Δt per unit biomass of bioturbative benthos per m^2). These simple representations minimise computational costs and perform satisfactorily for the amounts involved under the model geometry used in standard runs. A small amount of burial of sediments and associated detrital particles is also enabled in IGBEM.

The implementation of sediment chemistry in IGBEM also differed from that of ERSEM II and PPBIM. An attempt was made to make the empirical model of PPBIM (Murray and Parslow 1999a) more dynamic by incorporating more of the processes included in the calculation of ERSEM I's density profiles. This highlighted the crucial importance of the denitrification submodel. Blackford (1997) noted that ERSEM II underestimated the levels of bacterial biomass in the sediments and this was also very true of IGBEM. As a consequence any attempt to use bacterial activity to set levels of nitrification and denitrification failed and the model output took on a “eutrophied” form regardless of the levels of nutrient loading. In the short term this problem was solved by reverting to using Murray and Parslow’s (1999a) sediment chemistry model and retaining bacteria only as tracers (as they had inherent value as indicators of system state). All the runs presented here were completed in this way. In the long term a new way of considering bacteria was developed as part of a related ecosystem model (chapter 2).

Space precludes detailing the many other alternative settings that were built into the model. These alternatives included forage- and density-dependent movement of fish (in place of the prescribed movement of ERSEM II), invasions by specific functional groups, fishing induced mortality on non-target groups and a basic effort model for the fishery. Alternatives that were used in runs discussed here are identified below.

The parameter set used for IGBEM is based on the combined parameter sets of PPBIM and ERSEM II (corrected so that everything is at a reference temperature of 15 degrees Celsius and in mg m^{-3} (or mg m^{-2} if epibenthic)). Calibration of the model was required to ensure mass balance and to achieve stability. However, the large number of parameters (in excess of 775, disregarding those duplicated spatially or with age) means that a systematic sensitivity analysis is not possible. Thus, growth and mortality parameters and those associated with processes producing the greatest divergences or instability were calibrated until stability was achieved and all functional groups persisted. The restriction imposed on this calibration is that final parameter values must be within the range of values recorded in the available literature for that parameter.

1.3 Model runs

All functional groups are active in the standard run of IGBEM. Runs usually simulate a 20 year period, but a few simulate 100 years to allow consideration of long term cycles and to check whether the model has reached a representative state by the end of the usual 20 year run. The files containing the forcing for the transport model cover only 4 years and so are looped such that when the model reaches the end of a 4-year period it returns to the start of the forcing files and repeats them.

The standard run of IGBEM has fish migration as a forcing function, like ERSEM II (Bryant et al. 1995) and fish recruitment is identical in time and space from year to year, though the exact date of recruitment can vary by a few weeks. To check

the impact of these assumptions an alternative movement scheme and a number of alternative recruitment schemes were also tried. The alternative form of fish migration is forage- and density-dependent and fish are distributed among spatial cells based on available food resources in relation to metabolic requirements. The alternative recruitment formulations include a Beverton-Holt stock recruitment curve; a case where recruitment is related to primary production (used as a proxy for larval resource availability); and a random number drawn from a lognormal distribution, which simulates the often observed pattern of recruitment where there is the occasional very strong year class. Each of these alternative forms was parameterised such that the mean number of recruits returned would be very similar in each case and also very close to that given by the constant case in the initial state of the system (Table 1.4).

Table 1.4: Alternative regimes for fish recruitment implemented in the Integrated Generic Bay Ecosystem Model. Note b_{tj} is the number of recruits added to box j at time t.

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 $y \sim U(0,1)$ σ = 0.3 μ = -0.5 π = 3.141592654

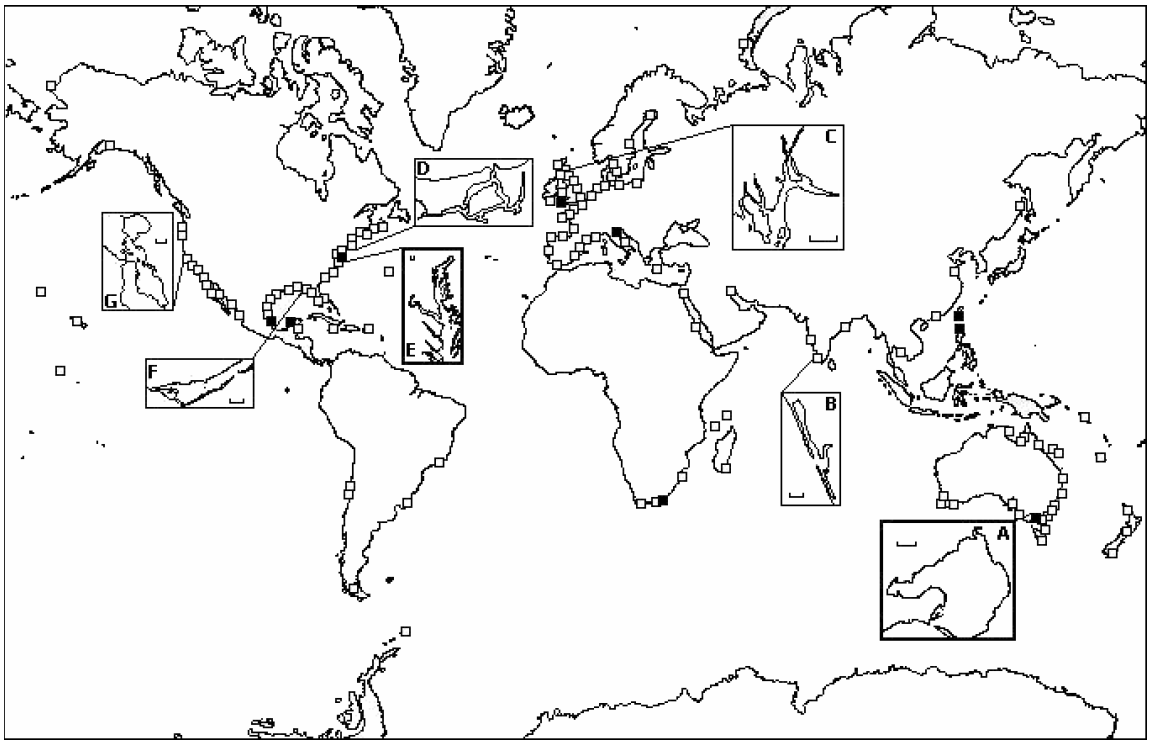
To evaluate how well the model replicates existing systems a number of other bays around the world that have similar physical conditions (tidal range and relative size of opening to the sea) (Figure 1.3) were identified. The inputs to these bays (from Monbet 1992) were then scaled based on the area of the bay relative to PPB and then the nutrient forcing files for IGBEM were adjusted to match. Thus, while the exact geography of the bay was not changed, nutrient conditions were altered to try and capture the state of several well-studied bays. Only minimal changes were made to the biological parameters of the system. Since the biological parameters for the run under baseline conditions have not been tuned to the species composition of any particular bay to begin with, but are based on species from temperate marine bays in many parts of the world, the decision not to tune the biological parameters in each case is justified. The ability to achieve a plausible representation of these other bays was based on the model's output values for chlorophyll a (chl a), DIN, biomasses and other measures identified from the literature.

1.4 Results and discussion

1.4.A IGBEM vs real bays

Information on each of the individual components present in the model is not generally available for real bays. Consequently output has to be pooled so that it matches the most common resolution of the data available in the literature. To differentiate between the individual functional groups of IGBEM and the pooled forms of the output, the latter are referred to as trophic sets. The list of trophic sets is made up of chl a (as a proxy for total phytoplankton), zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos (all the other benthic consumer groups, except bacteria) and detritus (labile and refractory).

Figure 1.3: Map of the world showing the bays used to evaluate the performance of the Integrated Generic Bay Ecosystem Model (IGBEM). Boxes mark the locations of all the systems for which marine biomass or production estimates are available for comparison with the output of IGBEM. The solid black boxes indicate systems for which complete biomass data are available. The inserts are maps of the particular estuaries or bays that were used to set the level of nutrient inputs for the test runs, they were: (A) Port Phillip Bay, (B) Cochin Backwater, (C) Firth of Clyde, (D) Flax Pond, (E) Chesapeake Bay, (F) Apalachicola Bay and (G) San Francisco Bay. The scale bar in each case represents 10km, Flax Pond has no scale bar as its total length (west to east) is approximately 600m. The two bays with a bold border (Chesapeake and Port Phillip Bay) have enough available information to allow for an intensive evaluation of the runs.



Biomasses

Empirical estimates of average biomasses for the trophic sets covered in IGBEM were obtained from the literature for 276 coastal marine systems (Figure 1.3; a list of the values and associated references is given in Appendix A). Estimates of the biomass of all major trophic sets is available for only 10 of these locations (black squares in Figure 1.3) and complete information of both inputs and the biomasses of the trophic sets is available only for Chesapeake Bay and PPB (inserts with bold borders in Figure 1.3). Thus the published values allow a very general consideration of model output across the various nutrient loadings, but a specific evaluation of performance is only possible for the case of baseline inputs (equated with PPB) and a tenfold increase in inputs (equated with Chesapeake Bay). Note that, there are insufficient data on the biomass of bacteria to include them in the general comparisons of biomass. The information that could be found shows that the values for biomass given by IGBEM for the pelagic bacteria are high and the values for the sediment bacteria are very low, something the model has inherited from ERSEM (Baretta-Bekker et al. 1995).

Range in biomass

Overall the model conforms well with the range of values seen in real systems, but the level of performance is not consistent across all measures or trophic sets. The biomass of each trophic set (Figure 1.4) is within the range of data from real bays. The model ranges are often smaller than the ranges from field data, but this is understandable given the small subset of possible nutrient inputs used (30x present loading was the highest loading used in model runs, but real inputs in some bays would reach as high as 1000x present loadings) and the use of geometry of a single bay (whereas the empirical data derive from bays of various topographical forms, from open coastal bays and shallow lagoons to deep, narrow fjords). Even though the model is of a

temperate bay, the sparse nature of empirical data for some trophic sets necessitates including data from tropical systems in the field data ranges. This would have little or no effect on the absolute ranges given for the field data for any trophic set with the exception of the fish (the maximum value would fall to 21.16 g AFDW m^{-2} if only data from temperate bays is included).

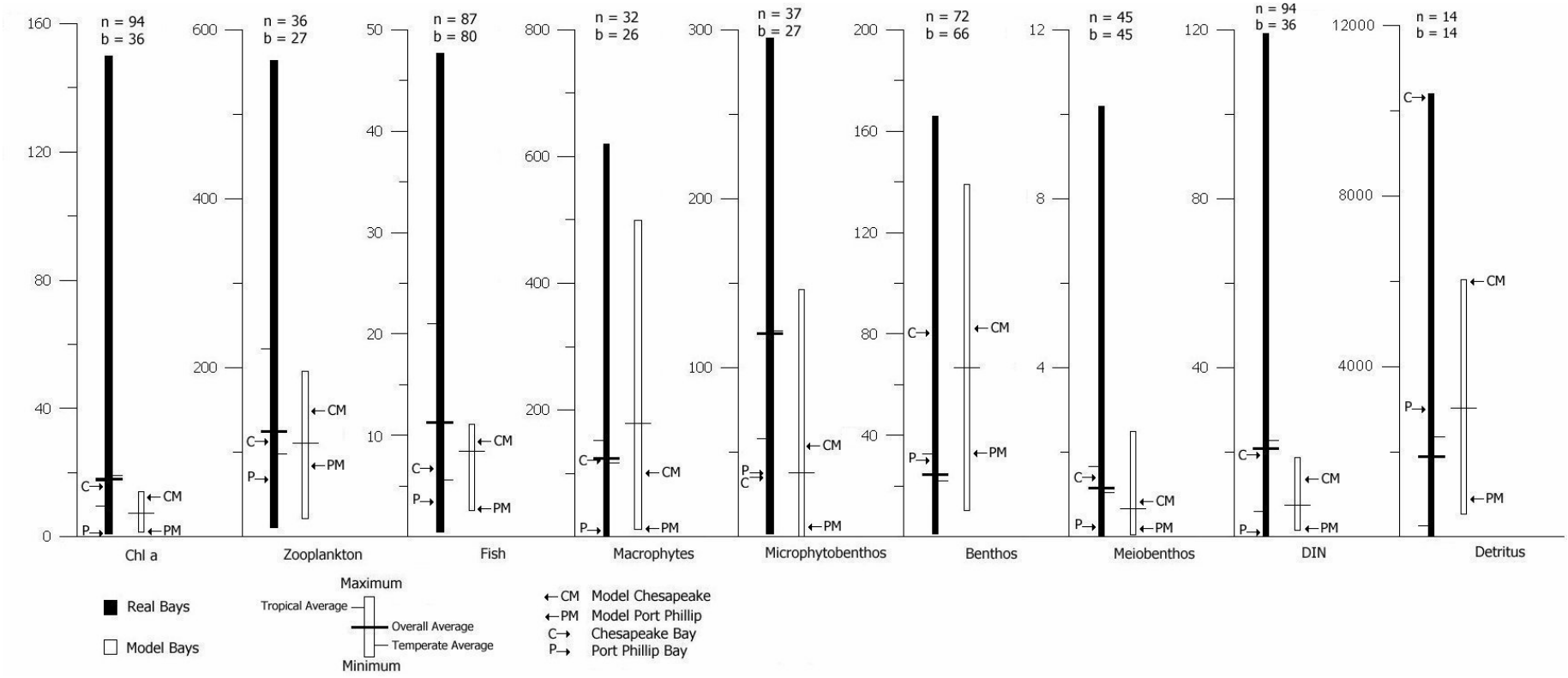
Average biomasses

The average biomasses indicate a more mixed, though still positive, performance. Given the magnitude of the range in field values, the average model values are not far from the average field values in most cases. Only three of the trophic sets have an average model value that is more than 10% of the range away from the average empirical value. Considering only the temperate average, the difference between the model and field average is 27% of the range for the benthic trophic set, 29% for the microphytobenthos and 13% for the DIN. The model also consistently yields detrital biomasses that are too low. That IGBEM does not include extremely refractory detritus, whereas the field data may, might account for this in part. However, it is also likely that estimates of the atmospheric component of detrital inputs to PPB are too low so overall inputs are too low (by about a third). Moreover, assimilation rates by deposit feeders are poorly known and may also be too high in the standard parameterisation; similarly, the burial of detritus out of the model system may be too fast.

Model biomasses in comparison with those of Port Phillip Bay and Chesapeake Bay

When the specific empirical values for the trophic sets in PPB and Chesapeake Bay are compared with the appropriate model values, the estimates for trophic sets from the model are usually within the bounds of empirical interannual variation, with the

Figure 1.4: Ranges and average values for the main sets of the model (IGBEM) in comparison with field values worldwide. The systems giving the maximum and minimum for the field data for each set are marked beside the reference in Appendix A. The model values come from the runs under different nutrient inputs based on inputs for real bays (A-G in Figure 4). 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}.



exception of the microphytobenthos and detritus. These trophic sets do not realise values within field measured levels of interannual variation and they are the only trophic sets where the difference in averages (model vs field) is more than 10% of the range in field values. The values for microphytobenthos are too low for the "Port Phillip Bay run" (PM), though it was at an acceptable level for the "Chesapeake run" (CM). There is also some suggestion that the predicted change in biomass of microphytobenthos with eutrophication is opposite to that observed empirically. The model average rose while the field values dropped marginally, if at all, given interannual variation in field values.

Microphytobenthos is the only component in the model that fails to follow the patterns of change with eutrophication that are predicted by field observations. The low levels of microphytobenthos in the baseline (PM) run are, at least in part, the result of two things. Firstly, this group competes with the large macrophyte pools, particularly the macroalgae. This causes it to be confined to the deep central parts of the bay, which have low light levels at the sediment surface. While low light levels in this area limit the microphytobenthos pool, limitation is not as pronounced as for the other benthic primary producers (the microphytobenthos light saturation is set at 3 W m^{-2} compared to 5 W m^{-2} for macroalgae and 60 W m^{-2} for seagrass). Also, as a result of very little available information on benthic interactions, the availability of the microphytobenthos to the deposit feeders and meiobenthos seems to be set too high. The efficiency of deposit feeders mentioned above exacerbates this problem. As a result of these factors the microphytobenthos is kept cropped to low levels. This facet could be improved by further calibration of the microphytobenthos part of IGBEM. However, more importantly, all aspects of the infauna and benthic microfauna in this, and other biogeochemical models (Silvert 1991), would benefit from an increased understanding of benthic interactions and ecology.

Community composition

Another biomass related comparison that can be made for the PM run is the relative make-up of the fish and benthic communities (Table 1.5). This level of detail was only accessible for PPB and so it is not possible to repeat the comparison for the runs under altered nutrient conditions. For both fish and benthic communities the relative compositions are similar to the community compositions observed in the field and well within the bounds required for "a generic system" status for the baseline run of IGBEM. However, with regard to the specific "fit" of the predicted communities to PPB, there is room for improvement.

Table 1.5: Comparison of the community composition for the benthic and fish communities determined from empirical estimates in the real Port Phillip Bay (PPB) (calculated from data in Wilson et al. 1993) and the PM model run. Bracketed values for the fish groups in PPB are the percentages when the relative community composition is restricted to the species used to parameterise the dynamic fish groups in IGBEM.

Functional Group	**PM (model) (% of total biomass)**	**PPB (empirical) (% of total biomass)**
Fish Community		
Planktivores	46.1	18.8 (31.2)
Piscivores	13.6	5.1 (8.5)
Demersal Fish	36.1	72.0 (50.3)
Demersal Herbivorous Fish	4.2	6.0 (10.0)
Benthic Community		
Macrozoobenthos (Epifaunal Carnivores)	4.3	1.1
Benthic (Epifaunal) Grazers	4.5	4.3
Benthic Suspension Feeders	45.8	50.0
Infaunal Carnivores	11.4	6.3
Benthic Deposit Feeders	34.0	38.3

The relative values for the fish community indicate that the IGBEM run over-emphasises the pelagic component of the fish community. However, the estimates of biomass for the pelagic groups in PPB are only tentative as the fish stocks of the bay have been primarily evaluated with trawls (which catch few if any of the pelagic

species) and so the currently available estimate of the relative contribution of the planktivores to the PPB community may be an underestimate. Further, the dynamic fish groups in IGBEM do not represent the entire fish population, but only part of it. One of the static closure terms imposed on the fish groups represents sharks and other large demersal fish. If the relative composition for PPB is recalculated, based only on the species-groups (for instance flatfish rather than all demersal fish) used to parameterise the fish groups dynamically included in IGBEM, the two compositions are much closer (bracketed values in Table 1.5). There is still an over representation of the pelagic groups at the expense of the demersal groups, but the model values are much closer to the field values. Thus, if the model is judged only on those groups it represents dynamically then the trophic compositions produced by IGBEM do compare favourably (though not perfectly) with those observed in PPB. However, as discussed below, the fish groups are one of the weaker parts of IGBEM and it may well be that the standard seed populations used do not produce the correct community composition in this case.

In contrast to the fish community, the relative composition of the benthic community in IGBEM is close to that observed in PPB (Table 1.5). There is some suggestion that the model may tend to favour the traditional primary production based food web over the detritus based web that dominates in PPB. This is indicated in that the contribution of both of the carnivorous groups is higher (by more than a factor of two), while that of the suspension and deposit feeders is slightly lower, in the PM run than in PPB. This tendency may be the product of two factors. Firstly, the static loss term imposed on epifaunal groups (to represent predation by fish groups not dynamically included in IGBEM), may not be high enough in the standard parameterisation to completely capture the benthic community structure observed in PPB. Secondly, there may be a mechanism in nature that influences the population dynamics that is not present in IGBEM. For example, some kind of burrow effect may

be appropriate (as it would lessen the impact of anoxic conditions in the sediment). Alternatively an index of habitat type (like the % of the area made up by hard substrata) may be necessary so that epifaunal groups restricted by crowding and available habitat in the wild are not inflated by the large homogeneous polygons used in the model. Nevertheless, the community compositions produced by the model are adequate with regard to IGBEM's role in generating data for a wider model study.

Standard relationships

While a good fit to biomasses across many trophic sets and under varying conditions is a positive attribute, it is not sufficient given that IGBEM is the foundation of a wider investigation of model structure and behaviour. Thus, the model output was checked to see if it complied with existing patterns and relationships observed generally in the field.

The work by Monbet (1992) indicates that there is a strong relationship between mg chl a m^{-3} and mmol DIN m^{-3} in the water column. As a further test of model performance the values of chl a versus DIN for the model runs under varying rates of nutrient forcing are plotted against values from real bays (Figure 1.5) (references for the real bays are in Appendix A) to examine whether the model conforms with the observed relationship. Only microtidal estuaries and bays (tidal range < 2m) are used in this comparison since PPB (and thus the model) is a microtidal system and Monbet showed that, relative to microtidal estuaries, macrotidal estuaries have much lower concentrations of chl a for the same levels of DIN. All of the model points sit well within the general relationship between chl a and DIN observed by Monbet (1992). On a more specific level the model values are compared against the values from the bays used to set the nutrient input levels for the various test runs (Figure 1.6). This serves to reinforce the strong performance of the model in this aspect, as all of the values are

within interannual variation measured in real bays.

Figure 1.5: The relationship between the mean annual concentration of dissolved inorganic nitrogen (DIN) and chlorophyll a (chl a) for real (open circles) and modelled (solid black circles) microtidal marine systems. See Appendix A for references used to give values for real bays.

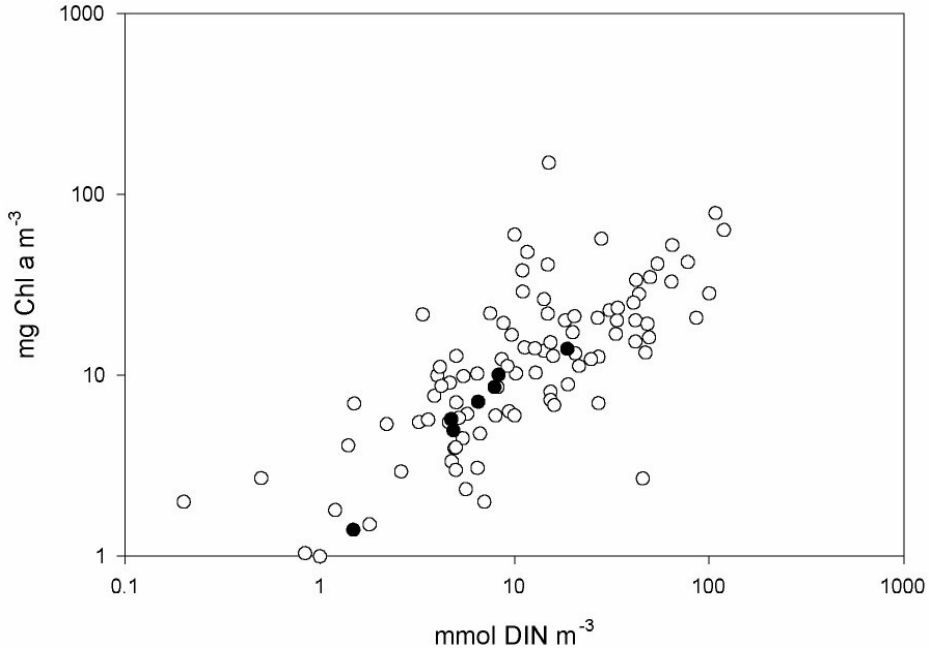
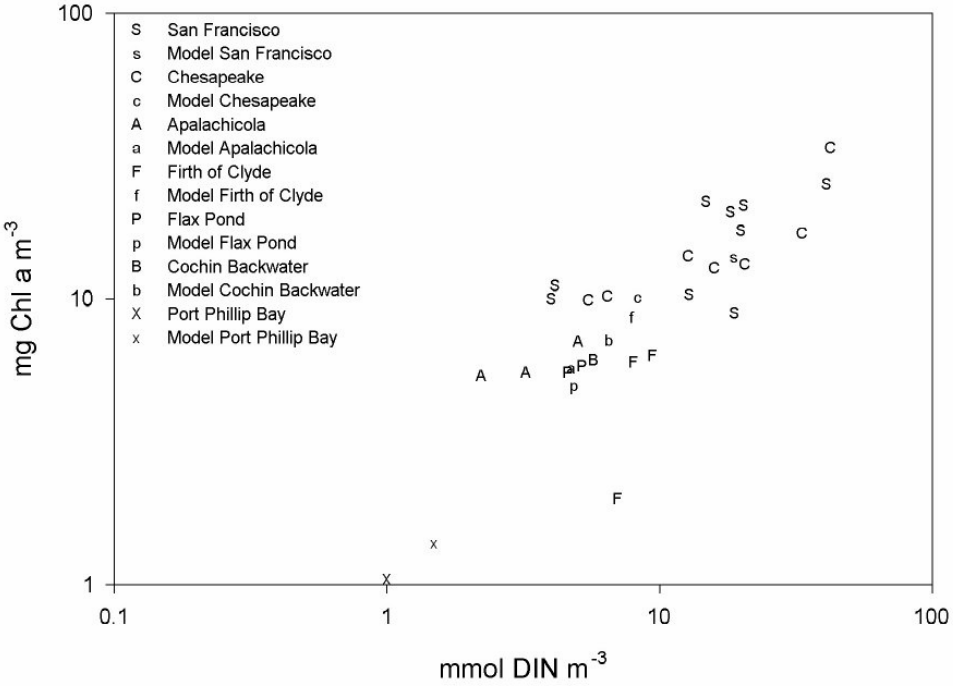


Figure 1.6: The relationship between the mean annual concentration of dissolved inorganic nitrogen (DIN) and chlorophyll a (chl a) for a selection of real and model microtidal marine systems. See Appendix A for references used to give values for real bays.



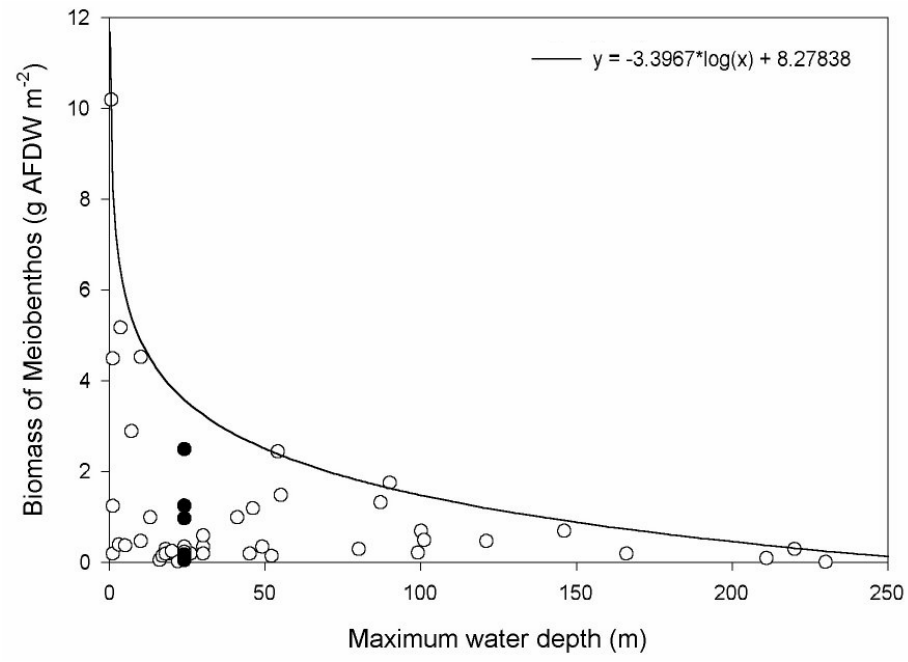


Figure 1.7: Relationship between the maximum depth and the average biomass of meiobenthos in the sediments of real (open circles) and modelled (solid black circles) coastal marine systems. See Appendix A for references for the real bays.

A general property to emerge from the empirical data is a curvilinear upper bound on the rate of decrease of the biomass of meiobenthos with increasing water depth. A curve fitted to the highest points in the plot (marked by a solid line in Figure 1.7, equation for the line given on the plot) gives an r^2 of 0.97. The model output was examined to see if it complies with this requirement (solid points in Figure1.7). As all the model points fall below the bound, it is judged that the model conformed with this relationship.

Beyond the relationships between certain groups and physical characteristics of a system, there are also relationships between relative biomasses within the biological components of systems. In marine systems two such relationships are the biomass spectrum, in logarithmic size classes, for benthic and pelagic communities. Sheldon et al. (1972) observed that marine pelagic communities appear to have similar biomasses

in all logarithmic size classes of organisms. That is the "Sheldon spectrum" is almost flat. In contrast, benthic communities have a "Sheldon spectrum" that is W-shaped (Schwinghamer 1981). Sheldon spectra for the benthic and pelagic components were obtained from the model and compared to observed empirical spectra. The spectrum for the pelagic components of IGBEM (Table 1.6) indicates that the model output does hold with Sheldon's finding that, over the entire size range of pelagic organisms, concentration varies by only an order of magnitude. Constructing the "Sheldon spectrum" is not simple for the benthic groups in IGBEM because the definitions of the groups are primarily trophic with only minor concessions to size structure. As a consequence it is necessary to use the totals per class (bacteria, microalgae and meiofauna, macrofauna) given by Schwinghamer rather than the specific values per size interval (converting the form or the "Sheldon spectrum" from a "W" into a "U"). In this case the spectrum (Table 1.7) indicates that the model does not conform well with field observations and that, using Schwinghamer's relationship as a guide, the smallest fauna in IGBEM (particularly bacteria) are under represented. The two larger classes (meiofauna/microalgae and macrofauna) are within the bounds given by Schwinghamer, but the bacteria are <2% of the field average.

Table 1.6: Summary of the Sheldon spectra for the pelagic classes in the run where nutrient loads were at the levels recorded in Port Phillip Bay (PM run) and Chesapeake Bay (CM run).

Class	PM (cm^3/m^2)	CM (cm^3/m^2)
Bacteria	40.5	149.3
Phytoplankton	10.0	75.6
Zooplankton	10.5	18.5
Planktivorous fish	5.5	23.3
Other (larger) fish	6.4	19.9

Table 1.7: Summary of the Sheldon spectra for the benthic classes in the baseline (PM) and nutrient load x10 (CM) runs of IGBEM. As a guide, the total mean biomass for each class after Schwinghamer (1981) are also provided.

Class	PM (cm^3/m^2)	CM (cm^3/m^2)	Schwinghamer (cm^3/m^2)
Bacteria	0.2	1.4	80.1
Meiobenthos and Microphytobenthos	0.7	4.3	6.1
Macrofauna	149.5	373.2	473.0

Production and consumption

Levels of daily production and consumption were obtained from the literature for comparison with the predicted values from IGBEM. Generally the model values compare favourably with the empirical field values of Production / Biomass (P/B) and Consumption / Biomass (Q/B) (Table 1.8), with some noteworthy discrepancies. Macrophyte production in the model is only a half of the field values and no easy explanation can be found for this. It may be due, at least in part, to a "macrophyte-barrens" which establishes itself in this particular run. This cycle is essentially a predator-prey cycle between the macrophytes and the benthic grazers, facilitated by the spatial and trophic structure of the model, and is discussed more fully below. Consideration of the fish on an individual functional group level rather than an overall pooled "fish" basis indicates that the P/B for the planktivores is much lower in the model output than given by the field estimates. Evaluation of the benthic components based on their habitat (epifauna vs infauna) rather than a single pooled value for all the benthos, also indicates some differences between the model and field estimates (Table 1.8). It is interesting to note that those P/B values that are considered to be substantially different between the field and the model show no consistent pattern, whereas Q/B values of the model are almost always lower than the field estimates. This suggests that while there may be multiple causes for the differences in production, the low consumption estimates are probably all due to assimilation being too efficient.

A final production related comparison is possible. The growth curves for the fish groups in the model were compared with those of real species used to parameterise the model groups (Figure 1.8). The growth curve for the individual planktivores and the herbivorous demersal fish are close matches to those for pilchards and mullet respectively. The curve for the piscivores is also a good match for the growth curve of barracouta and only the growth curve of individual demersal fish fails to fit its real-life equivalent (flathead) closely, falling short in the older fish. These older demersal fish have a diet that is primarily fish-based rather than invertivorous, and they experienced competition with the smaller piscivores. While further tuning would improve the match between the curve for the demersal fish group in IGBEM and flathead, the standard parameterisation is retained for the purposes of the wider model study as it adequately represents a demersal fish, even if it does not exactly match flathead.

Table 1.8: Estimates of primary and secondary production and consumption for Port Phillip Bay (PPB) and the PM run of the Integrated Generic Bay Ecosystem Model. Values for fish and benthos represent the pooled production or consumption value over the pooled biomass value.

Set	Production:Biomass		Consumption:Biomass	
	PPB (empirical)	**PM (model)**	**PPB (empirical)**	**PM (model)**
Phytoplankton	210.3	241.8	-	-
Zooplankton	2.1	1.8	3.4	2.9
Fish	3.1	4.0	21.7	13.5
Planktivorous	6.3	3.2	82.6	22.4
Piscivorous	2.0	2.6	8.2	5.9
Demersal	1.5	2.1	7.1	5.7
Demersal Herbivorous	1.2	3.1	9.6	7.0
Benthos	14.2	17.0	49.0	44.1
Epifauna	9.9	5.3	17.3	8.7
Infauna	17.6	31.1	85.1	86.6
Macrophytes	22.6	12.4	-	-
Microphytobenthos	6.3	5.2	-	-

System indices

Given the holistic nature of ecosystem studies, simple reductionist comparisons of biomasses, productivity and other ecosystem attributes are far from a sufficient summary of model performance. The fit of the model dynamics to system-level indices must also be considered. To this end a number of system indices were calculated for the baseline (PM) and nutrientsx10 (CM) runs of IGBEM. The most informative of these (based on the findings of Christensen 1992) were compared with values for the same indices calculated for 9 real marine systems (Table 1.9). The comparison indicates that the model conforms well with the real systems. For most of the indices the values for the model runs are within the range of the values calculated for the real systems. The value for the total throughput for the CM run is beyond the range given by the real bays, but this may be because the run is under a higher nutrient load (and is more eutrophic) than any of the real systems being considered.

On a specific level only 4 of the 11 indices given show a relatively close match between the values calculated for the PM run and PPB. The "System Omnivory Index", "Dominance of Detritus", "Path length" and "Relative Ascendancy" all suggest the real and modelled systems are quite similar, while the remaining indices suggest divergences. Much of this is due to the species used to parameterise IGBEM. The standard parameter set is based primarily on northern hemisphere species (as they make up the bulk of available information) and while the resulting model system does match the levels of biomass and productivity reported for PPB reasonably well, it does not do a consistently good job of matching higher level indicators. If the species used to set the parameter values are those resident in PPB, then the match between model and real system indices is vastly improved. The "BASE run" in Table 1.9 is based on parameters determined from species resident in PPB and the match between the model and real values is close for all but two of the 11 indices. Thus, the standard parameter set does a

Figure 1.8: Growth curves for fish groups as produced by the model (open circles) and the species their parameterisations are based on (solid black circles). (a) Pilchard *vs.* IGBEM planktivore, (b) Barracouta *vs.* IGBEM piscivore, (c) Flathead *vs.* IGBEM demersal, and (d) Mullet *vs.* IGBEM demersal herbivore.

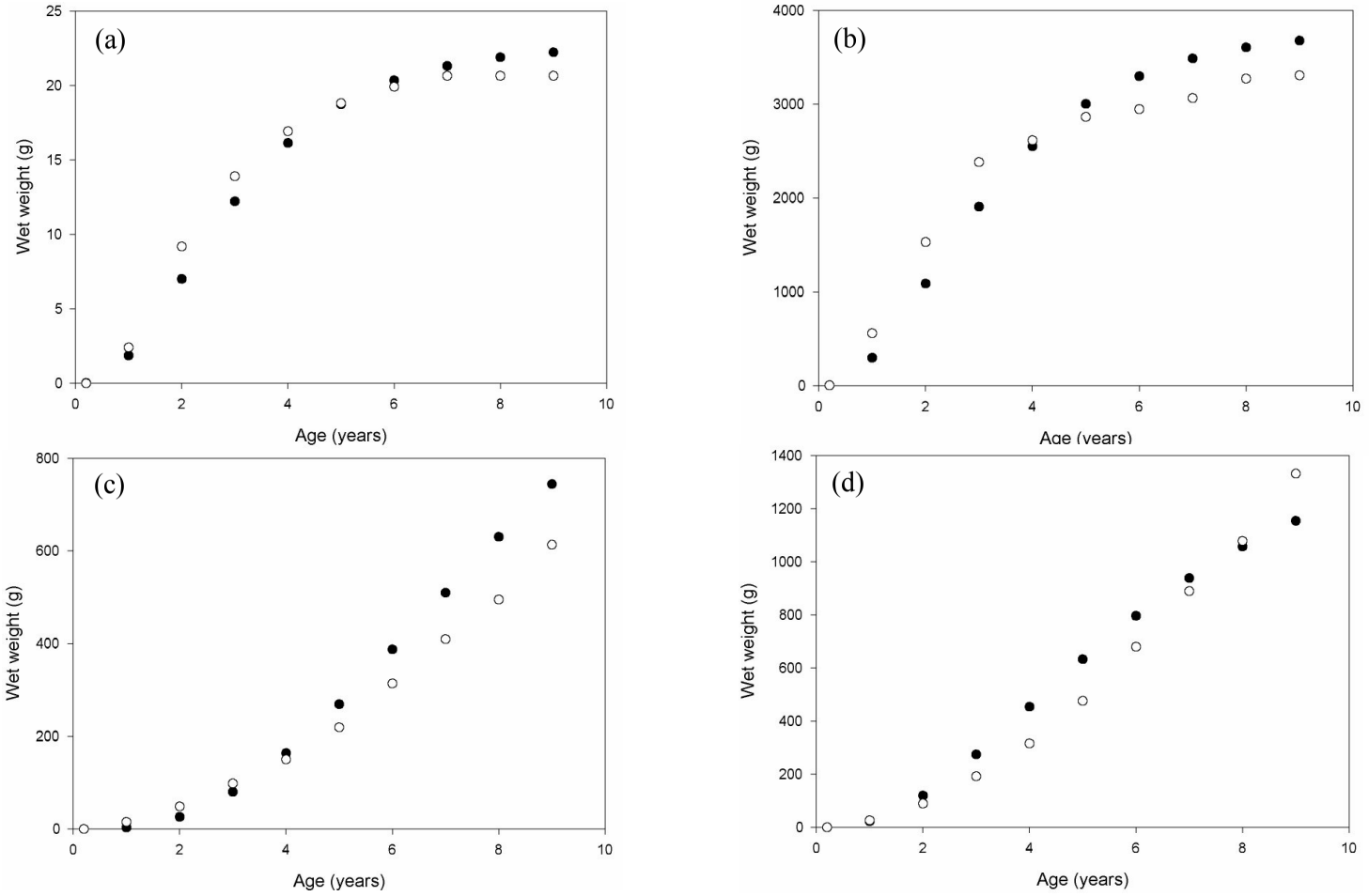


Table 1.9: System-level indices for a range of real coastal areas (values for the first 8 locations are from Christensen 1992) and three separate runs of the Integrated Generic Bay Ecosystem Model (IGBEM).

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
Mandinga Lagoon, Gulf of Mexico	3075	36.6	0.008	0.016	0.26	0.36	0.023	2.98	0.02	27.31	36.0
Tamiahua Lagoon, Gulf of Mexico	1444	9.6	0.018	0.041	0.13	0.65	0.076	3.16	0.06	14.62	25.4
Coast, Western Gulf of Mexico	17191	5.8	0.018	0.052	0.15	0.78	0.100	3.56	0.07	13.56	31.4
Campeche Bank, Gulf of Mexico	10327	5.5	0.042	0.08	0.21	0.49	0.124	3.28	0.14	7.01	26.2
Shallow area, South China Sea	11895	74.9	0.004	0.008	0.27	0.42	0.010	3.26	0.01	52.03	21.7
Lingayen Gulf, Phillipines	7198	14.6	0.013	0.037	0.15	0.63	0.041	5.14	0.07	12.46	31.1
Etang de Thau, France	41929	5.1	0.045	0.099	0.35	0.72	0.123	4.26	0.19	5.06	30.6
Schlei Fjord, Germany	2825	3.9	0.071	0.151	0.03	0.45	0.198	3.63	0.26	2.79	32.1
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
BASE run (IGBEM tuned to PPB)	13243	13.7	0.023	0.053	0.18	0.49	0.049	3.60	0.08	5.15	32.5
PM run (IGBEM baseline nutrients)	4702	4.6	0.051	0.13	0.14	0.62	0.128	4.21	0.21	3.16	32.3
CM run (IGBEM nutrients x10)	50702	18.7	0.019	0.04	0.15	0.47	0.0418	3.36	0.06	4.59	29.8

sound job of reproducing a generic coastal system while tuning can produce a close fit to the holistic form of a specific system.

1.4.B Spatial and temporal form of meso- and eutrophic runs

To complete the evaluation of the standard behaviour of IGBEM, the spatial and temporal dynamics are considered. This indicates that the model can produce a rich collection of responses, from competitive exclusion to predator-prey cycles and the formation of identifiable communities structured by biotic and abiotic factors.

Spatial structure

The predicted average biomasses per box over the final four years of the CM and PM runs were analysed to determine whether there were 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 examined (using the SIMPER routine of the Primer software package) to ascertain which groups determined the clustering. This analysis identified "areas" (boxes in the model sharing biological and/or physical characteristics) in the model output. Only the PM and CM runs were analysed in this way as they were considered representative of the "mesotrophic" and "eutrophic" states of the model output.

Fourteen biological areas (Figure 1.9a) and twelve geophysical areas (Figure 1.9b) exist in the output of the PM run. While there is some correlation between the two, the two sets of areas differ sufficiently that physical factors alone do not produce the form of the biological areas. Biological interactions are also important to the spatial patterning. For instance, certain functional groups consistently occur together with high

biomasses in the same cells, and these are called communities (Table 1.10). A comparison of the communities and attributes per biological area (Table 1.11) shows that Swan Bay (area 4) and Corio Bay (area 9) are distinct to the main bay. This is due to their shallow depth, large macrophyte communities and restricted connection with the main bay. Within the main bay a comparison of the biological areas reveals a depth-based zonation. The areas around the edge of the bay (areas 1 – 10) are usually distinguished by the presence of either one of two planktonic communities, as well as rich fish, epibenthic and macrophyte assemblages. In contrast the deep central sections of the bay (areas 11 – 14) all share a common planktonic community and the macrobenthic groups are largely replaced by microscopic communities able to tolerate the low light while exploiting the high levels of detritus. There is some seasonal and interannual variation in the composition of the communities and some switching between specific plankton communities expressed in the areas along the bay edge, especially within the planktonic communities 1 and 2. This is mainly as a result of responses to tidal forcing and the patterns of nutrient forcing within and across years. Nevertheless, the overall differences between the central and edge areas persists over time in the model output.

Figure 1.9: Maps of the location of the physical and biological areas identified in the output of the PM run. (a) The biological areas (sections of the bay in the same "biological area" are marked with the same number), and (b) the physical areas (sections of the bay in the same "physical area" are marked with the same letter).

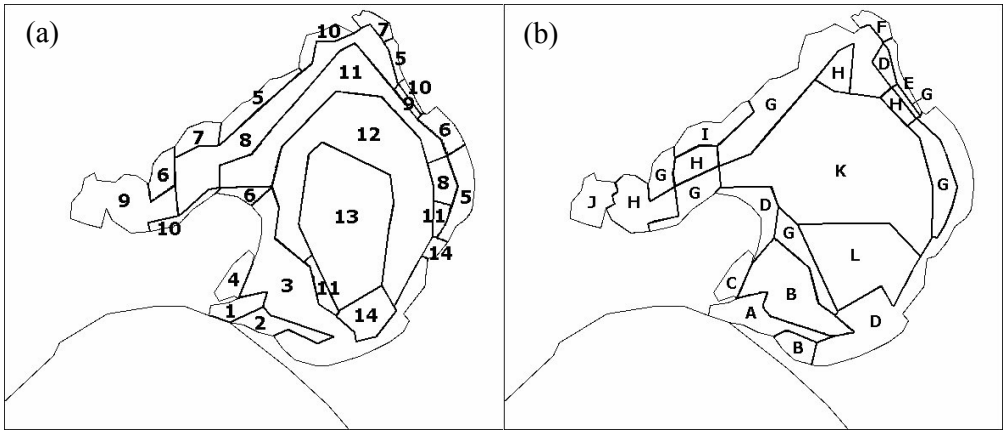


Table 1.10: Definitions for the various communities found in the output of the Integrated Generic Bay Ecosystem Model runs.

Community		Functional Groups Present
Planktonic	1	diatoms and autotrophic flagellates
	2	picophytoplankton and microzooplankton
	3	picophytoplankton, autotrophic flagellates, dinoflagellates, heterotrophic flagellates, large omnivorous zooplankton and large carnivorous zooplankton
	4	heterotrophic flagellates
Epibenthic	1	benthic suspension feeders
	2	macrozoobenthos (epifaunal carnivores)
Macrophyte	1	seagrass
	2	macroalgae and benthic (epifaunal) grazers
Fish	1	planktivores
	2	piscivores
	3	demersal herbivorous fish and demersal fish
	4	piscivores and demersal fish
Benthic	1	benthic deposit feeders and infaunal carnivores
	2	meiobenthos and microphytobenthos
Remineralisation (Remin)	1	pelagic bacteria, aerobic bacteria, anaerobic bacteria, labile and refractory detritus
	2	pelagic bacteria
	3	aerobic bacteria
	4	labile and refractory detritus

Table 1.11: Dominant communities and physical attributes characterising each biological area identified in the PM run. Codes for the functional communities are as for Table 1.10. For the biological communities a blank entry signifies that while a community of that kind may be present in the area it was not large enough (relative to their size in other areas) to significantly contribute to the definition of the area. A blank entry for a physical attribute signifies low to negligible levels for that attribute.

Area	Biological Communities						Physical Attribute				
	Planktonic	**Fish**	**Epibenthic**	**Benthic**	**Macrophyte**	**Remin**	**Tidal Influence**	**Bottom Stress**	**Light Levels**	**Depth**	**DIN Levels**
1	1	1					High	High		Moderate	
2	1,2		1				Moderate			Deep	
3		2			1			High	High	Shallow	
4					1				Very High	Very Shallow	Moderate
5	2	2	1							Shallow	High
6	2		1						Moderate	Shallow	
7	2	2,3	1,2	1		4				Shallow	Very High
8	1		1		2	4				Intermediate	Moderate
9			2		1,2				Moderate	Shallow	Moderate
10	1	1,2,3							High	Shallow	
11	3		1		2	1				Moderate	
12	3		1	2		1				Deep	
13	3		1	2		1				Very Deep	
14	3									Deep	

When the CM run is analysed only 10 distinct biological areas and 9 physical can be identified (Figure 1.10). The decline in the number of the physical areas results directly from changes in the levels of inputs and indirectly from changes in the biological components and their resultant effects on light, nutrients, detritus and bottom stress. The two sets of areas do show some overlap and the correlation is more pronounced than in the PM run, but it is still clear that abiotic factors alone are not the cause of the biological areas. As before, the mix of biotic and abiotic agents is thought to form the areas seen in the output. Once again there are clear differences between the areas along the edge and those in the middle of the bay (Table 1.12). However, the distribution of "central communities" is now much more widespread than in the PM run and they have taken over much of what was previously the domain of the "edge communities". An "edge community" still exists but it is restricted to the very edge of the northern parts of the bay. Moreover, the distinction between "edge" and "central" planktonic communities is less clear. Swan Bay and Corio Bay again stand out as being substantially different from the main bay, but the contrast is much sharper than for the PM run. Even though no functional groups disappeared from the run, some rose substantially at the expense of others which where depressed to low levels and restricted to much smaller areas. This suggests that the model is replicating the simplification of habitat and the reduction in diversity seen with eutrophication.

Temporal dynamics

Distinct temporal patterns are evident in the long-term output of the PM run, including seasonal, interannual and decadal cycles (Figure 1.11a-d). The cycles seen in fish biomass will not be discussed here as they are largely prescribed by the movement regime employed, with only minor amounts of variation occurring due to interannual variation in growth tracking their food supply (Figure 1.11e).

Table 1.12: Dominant communities and physical attributes characterising each biological area identified in the CM run. Codes for the functional communities are as for Table 1.10. For the biological communities a blank entry signifies that while a community of that kind may be present in the area it was not large enough (relative to their size in other areas) to significantly contribute to the definition of the area. A blank entry for a physical attribute signifies low to negligible levels for that attribute.

Area	Biological Communities						Physical Attribute				
	Planktonic	**Fish**	**Epibenthic**	**Benthic**	**Macrophyte**	**Remin**	**Tidal Influence**	**Bottom Stress**	**Light Levels**	**Depth**	**DIN Levels**
1	1, 4	1,2,3	1	2	1		High	High		Deep	
2		2		2				High	Moderate	Shallow	Moderate
3			1		1				High	Very Shallow	High
4	2,3	2	1,2			2				Shallow to Moderate	High
5	3	1,4	1		2	2				Shallow to Moderate	High
6	1,2	1,4	1	1						Shallow	Very High
7	1,2	4	1,2	1,2		3,4				Shallow	Very High
8			1		1,2				Moderate	Shallow	High
9	2,3		1	1,2		1				Moderate	High
10	2,3		1			1				Deep	High

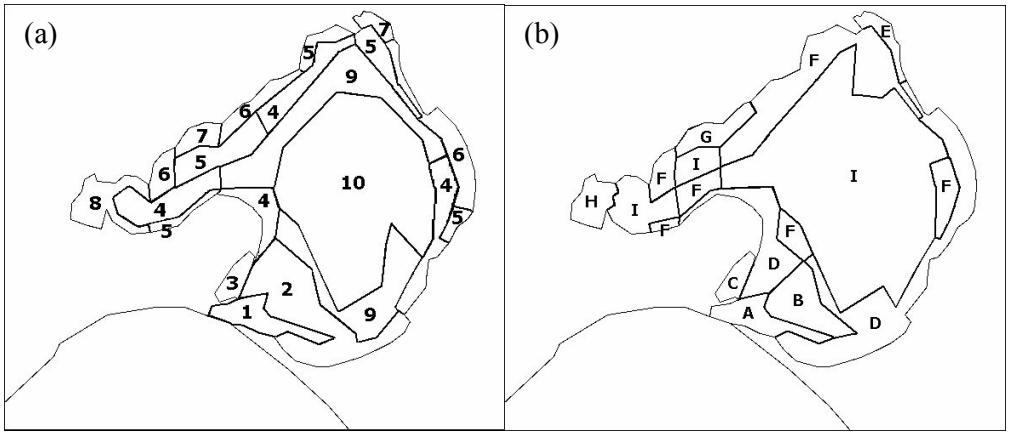


Figure 1.10: Maps of the location of the physical and biological areas identified in the output of the CM run. (a) The biological areas (sections of the bay in the same "biological" area are marked with the same number), and (b) the physical areas (sections of the bay in the same "physical area" are marked with the same letter). The letters and numbers used in this figure do not correspond to any of those in Figure 1.9.

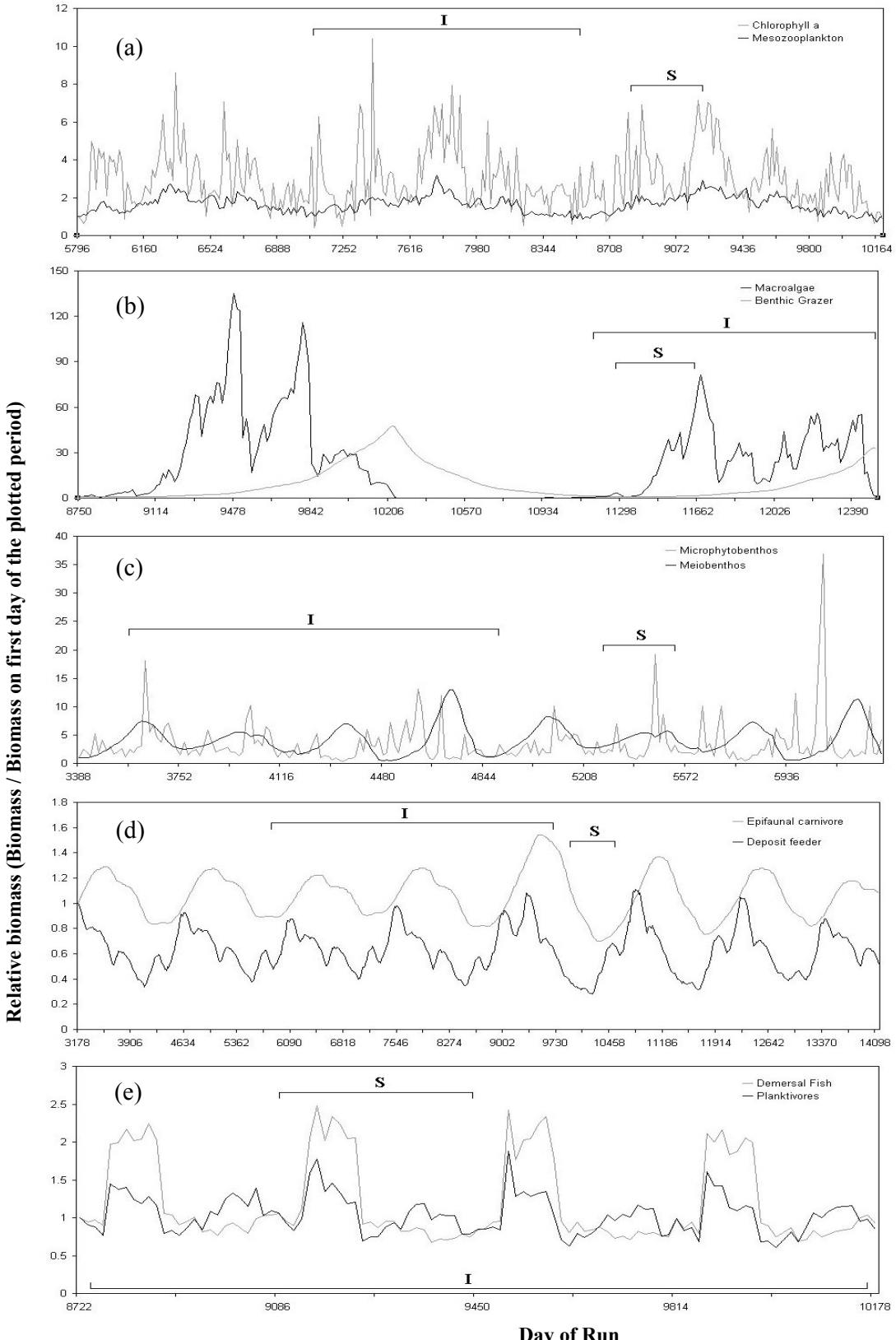
While there are high levels of short-term fluctuation in the phytoplankton groups, seasonal cycles within the planktonic groups are nonetheless clear (Figure 1.11a). This cycle is characterised by blooms in the planktonic communities associated with seasonal cycles in light levels, temperature, river flows and nutrient inputs provided by the forcing files. The build up in DIN over the winter months, particularly in the boxes fed by the two largest nutrient point sources (the Yarra River and the Werribee Sewage Treatment Plant, Figure 1.1), leads to bloom events in spring when light levels begin to rise. The form of the blooms is least stable in the Yarra and WTP boxes where local flows cause a lot of variation. Further away from the point sources, cycles are much more stable. Similar seasonal cycles can be seen in the benthic primary producers (Figure 1.11b, c) and the detritus based web fed by them (Figure 1.11d). The slow growing nature of the consumers in this set of cycles means that they show little, if any, of the short-term fluctuations which are common in the planktonic dynamics.

The looping of the hydrodynamic files (the same cycle of 4 years is continually repeated for the whole run) is apparent in the interannual variation. Many groups fall

into a steady repetition of interannual variation through time (Figure 1.11c, d) and this is due to the influence of the hydrodynamics on nutrient supply, advection of the water column communities and other food supplies. The strength of the impact of the cycle of hydrodynamic forcing differs between boxes and is strongest in the central parts of the bay, where boxes are distanced from point source inputs. The dependence of the behaviour of so many groups on the hydrodynamic cycle (either directly or via the impact of it upon their food and nutrient supplies) agrees with the findings of the developers of PPBIM (Murray and Parslow 1997) and ERSEM (Ebenhöh et al. 1995). It is interesting however, that even these cycles do not become regular bay-wide, as variation is evident in the amplitude and period of the cycles. This variation in amplitude and period would be lost within all the other forms of variation (and error) in the field, but its existence is intriguing. Apparently the extra variation is due to the effect of the point source impacts on prey groups in conjunction with the timing of the few stochastic components of the model (for example the exact day that recruitment begins in fish). The combination of bottom-up and top-down controls leads to noticeable variation in a pattern that could be expected to be extremely predictable given the cyclic nature of the forcing conditions.

The interaction of physical forcing and biotic interactions also underpins the more interesting long-term cycles (5 – 20 years). The two cycles in question are in the epibenthic groups. The first is a "macrophyte-barrens" cycle (example in Figure 1.11b) where the macrophytes are at high levels (equivalent to temperate kelp forests) for between 2 and 7 years before dropping to very low levels (<1 mg N m^{-3} in some cases) for between 2 and 9 years. The cycles have a shorter period (about 4 years for a complete cycle) in the areas with conditions conducive for macrophyte growth and are much longer (up to 15 years) in those parts of the bay with conditions less hospitable to macrophyte growth. The benthic grazers are also locked into this cycle, though the

Figure 1.11: Relative Biomass (Biomass / Biomass on first day of period shown) (y-axis) through time (x-axis) showing temporal patterns for representative groups in the PM run of the Integrated Generic Bay Ecosystem Model. The small spans marked by S are an example of seasonal variation, the large spans marked by I are examples of interannual variation. The entire period plotted in (c) and (e) are examples of decadal scale cycles. All but (d) are from edge boxes, while (d) is from the large central box.



amplitude expressed from one repetition of the cycle to the next is not necessarily constant, as it also depends on levels of their predators. This cycle may be a model artefact or a symptom of an instability as no such cycle has been recorded for PPB. However it does a very good job of simulating the impact of urchin barrens in a temperate system, a dynamic that has been widely reported and investigated (Hagen 1995, Leinaas and Christie 1996, Silvertsen 1997, Sala 1997). The whole cycle can be suppressed by adjustments to the growth rates of the main groups involved in the cycle (the macrophytes, benthic grazers and epifaunal carnivores) and by reducing the availability to predation of the macrophytes and the benthic grazers.

The other long-term cycle is related to the "macrophyte-barrens" cycle. The epifaunal carnivores show long term changes in the pattern of their interannual variation (Figure 1.11d) depending on which food web they are receiving most prey from. The amplitude of the cycle in their abundance is smaller if the detritus based web (infauna and suspension feeders) makes up most of their diet and the benthic grazers are only a relatively small part. If the contribution by the benthic grazers to the food supply of the epifaunal carnivores rises above 20% (which occurs if the barren cycle begins its decline slightly later in the year than normal) then the cycle switches to one with larger amplitudes. This cycle gradually slips back into the previous state (where the benthic grazers make up a smaller proportion of the diet) over time. These patterns (the "macrophyte-barrens cycle and the one seen in the epifaunal carnivores) indicate that long-term change in system dynamics and biomass may be a feature of systems that are under a mixture of bottom-up, top-down and abiotic control. Attempts to ascertain the impact of human actions under these circumstances would be problematic. Despite this, human actions do have the potential to cause widespread changes in system behaviour if they impact upon a crucial group or occur at a crucial time.

The patterns outlined here persist in runs with higher nutrient loadings. The

exact form and magnitude of the pattern often changes (in response to the higher levels of nutrients and eutrophication), and some change from a 4 year to an 8 year period (for example the microzooplankton in Corio Bay), but on the whole the cycles are still recognisable. The only cycle that disappears is the long-term one identified in the epifaunal carnivores. The contraction of the macrophyte community to only a handful of boxes means that the coincidence of events required to cause the change in the cycle of interannual variation in the epifaunal carnivores no longer occurs. This supports the view that anthropogenically induced changes can cause large alterations in system behaviour beyond simple reductions in diversity and shifts in biomass.

Effects of eutrophication

Monitoring studies have noted that as nutrients increase there is an initial increase in production and biomass, which is reversed (particularly in the benthic community) if the level of nutrients keeps rising (Harris et al. 1996). Studies have also shown that these changes in productivity and biomass are also associated with a general decline in species diversity and system complexity (Gray 1992). These findings are borne out in the output of IGBEM across a range of nutrient loadings.

If the various runs are considered as points along a continuum of nutrient increase, then within the water column there is a general increase in overall productivity (by a factor of five to ten) as nutrients rise. There is a concomitant change in community composition, with the larger phytoplankton and zooplankton groups dropping off and being replaced by the small rapidly growing groups. In comparison to the patterns observed in real systems suffering the effects of eutrophication, this result is not completely as expected. It has been found that as nitrogen loadings increase the composition of the phytoplankton shifts from one dominated by small cells to one centred on large cells (Murray and Parslow 1997). This is opposite to predictions of the

model where the proportion of the phytoplankton community made up by the diatoms and dinoflagellates fall by 5% with increasing nutrients in the water column. It has been very difficult to determine what changes in community compositions result with changes in nutrient levels for other ecosystem models, as results are usually given in terms of "phytoplankton" rather than specific size classes. However, the fact that ERSEM I and II consistently give ratios of small to large phytoplankton that are too high, despite the fact that field observations suggest the reverse is true for the North Sea (Varela et al. 1995, Ebenhöh et al. 1997), suggests that IGBEM has inherited this characteristic from ERSEM II. Another potential explanation is that the elevated nutrient loadings used moved the system to a state where the diatoms are silicate limited, and thus the proportional contribution of small phytoplankton increased, as predicted by Murray and Parslow (1997). In contrast with the phytoplankton dynamics, the 20% increase in the proportion of the zooplankton community made up of small size classes does match with relationships found in real estuarine systems (Park and Marshall 2000). Thus, the gross dynamics of the planktonic trophic levels in IGBEM do match field observations, but the exact form of the composition of the communities within those trophic levels are not always consistent with real systems and this suggests that the linkages and parameter values used need more consideration if the model is to be applied to a specific system for prognostic purposes.

Within the fish groups there is some increase in production and biomass (it increased by a factor of 3.5) with eutrophication, but it is not as pronounced as that in the planktonic groups. More interestingly there is a change in the average size of the demersal fish (it drops by up to 10%), so that the system is populated with more fish of a smaller size. This also concurs with observations made in the field (Tober et al. 1996). One thing to note at this point though, is that as nutrients rise to 30x baseline levels there is no collapse in the fish stocks as might be predicted based on the recruitment

failures observed in certain real systems under this level of pressure. This is due to two features. Firstly the system being modelled is shallow and vertically well mixed so there is no stratification or anoxia like that observed in the Baltic and deep parts of other coastal marine systems. As a result there is no substantial jump in the mortality of the fish groups as eutrophication sets in. Secondly, recruitment in the standard run is constant and so the population is buffered from negative reproductive impacts of the high nutrient levels.

The well-mixed nature of the model system also prevents a complete devastation of benthic groups by eutrophication-induced anoxia. However, they are not completely spared and the initial rises in productivity and biomass (to fourfold original levels) soon give way to declines (down to a third of the initial values) as conditions become increasingly stressful and the epifaunal groups all but disappear (dropping to 20% of the baseline biomass). Intense phytoplankton blooms in the water column starve the benthic primary producers of light and nutrients and so these dwindle (the seagrass density drops by an order of magnitude). A wide number of studies have observed this pattern of change with eutrophication in benthic flora (Walker and McComb 1992, Harris et al. 1996). This decrease in the benthic flora causes some reduction in the oxygenation of the sediments, though a weakness in the sediment chemistry model means that the impact of this is not as strong as it should have been. Further, it causes a drop in one of the major benthic food sources (as the benthic primary producers are food for the grazers, but also supply much of the detritus for the deposit feeders). The increase in detrital material coming from pelagic blooms more than compensates for the loss of detritus from the macrophyte groups, and so the infaunal groups increase with the nutrient inputs. It is anticipated that an improvement of the sediment chemistry model, or an application of IGBEM to a system that is deeper and not so well mixed, would see anoxia of the bottom sediments have a substantial impact on all the benthic groups. An

interesting result is that, despite the problems with the sediment chemistry model and the bacterial dynamics in general, as the levels of nutrients rise in the model the ratio of aerobic to anaerobic bacteria drops (from 2.8 to 0.14). Given that there is increasing pressure to identify reliable indicators of ecosystem health that are also easy to measure, identification of relationships such as this one could prove to be useful if they hold in the field.

No component of the model completely disappears with an increase in nutrients, but the change in relative compositions in all of the communities indicates a shift to smaller, faster growing more opportunistic groups with eutrophication. Further, as mentioned in the sections above, there is a simplification of habitat and a substantial expansion of the communities tolerant to low light, high nutrients and detritus. Thus, the model is showing a simplification of the overall system with eutrophication similar to that observed in the field (Harris et al. 1996). This agreement between the patterns of biomass, distribution of communities and productivity produced by the model and those observed in real systems indicates that the model does reproduce realistic system dynamics despite possible short comings of its current parameterisation.

1.4.C Weaknesses and alternative formulations

Closure at the top

The form of the mortality terms applied to the top-most groups explicitly represented in the modelled web is known as trophic closure or model closure (Murray and Parslow 1999b). There are a number of forms of model closure, but the two most common are linear and quadratic mortality terms and these have differing underlying ecological assumptions (Edwards and Brindley 1999, Murray and Parslow 1999b). The use of a linear term assumes that predation due to groups not explicitly included in the web is either negligible or unresponsive (does not change with the size of the modelled

group in question). Whereas a quadratic term assumes that the biomass (and resulting predation pressure) of the groups not explicitly covered by the model changes with the biomass of the modelled group. Beyond their ecological implications the two forms of model closure can lead to differing model behaviour (Steele and Henderson 1992, Murray and Parslow 1999b). The issue of trophic closure in Nutrient-Phytoplankton-Zooplankton models has received a good deal of attention (Steele and Henderson 1992, Edwards and Brindley 1996 and 1999, Murray and Parslow 1999b, Edwards and Yool 2000). However, the same level of consideration does not seem to have been given to higher trophic levels and by and large the different forms of mortality used are either constants or they are assumed to be linear and additive.

Experience with IGBEM indicates that more thought about model closure is necessary. It would be hoped that an ecosystem model could provide some insight into the pristine state of systems that have been impacted by human actions. To this end runs where there is no fishing were undertaken. Under the standard parameterisation there is some shift seen in community composition and biomasses, but the model is still stable. However, during an exploration of the parameter space it is found that if the system was set more in line with the levels of fish biomass and community composition found in places such as the North Sea then the linear closure terms are insufficient to ensure model stability. This may simply reflect the magnitude of human impact on systems such as the North Sea, and that models with fixed parameters cannot cope with the level of change such systems manifest as they return to more pristine states. Nonetheless, it can also be argued that failure to cope with the removal of fishing pressure in this case suggests that there may be potential problems with the closure of the model and that the issue of how models are closed, regardless of the number of trophic levels included, needs wider consideration. In a study comparing three ecosystem models across a range of eutrophication and fishing scenarios (chapter 7), it was found that using linear closure

terms for the predation effects caused by highest order predators may not be a suitable model of system dynamics. This is because populations of the higher predators do not change linearly with fluctuations in their major prey groups. Extension of the individual-based handling of the fish groups to include seabirds, mammals and sharks may be beneficial if only to check whether they can then be omitted. Similarly, consideration of the impact of quadratic rather than linear closure of ecosystem models may prove instructive, with regard to whether the extra parameters are justified in terms of improved model stability, more realistic model behaviour and, potentially, more realistic underlying assumptions.

Constant recruitment

It was found (chapter 7) that the constant recruitment term employed in IGBEM could have a substantial influence on the predicted impacts of eutrophication and fishing pressure. The fish groups in IGBEM are buffered against the impacts of large-scale changes in system productivity due to their constant recruitment. Further assumptions about the form of the linkages between the lower and upper ends of the trophic spectrum could have profound consequences for model behaviour. To check this, alternative recruitment formulations were trialed in IGBEM. Of the alternative recruitment relationships, the use of the Beverton-Holt recruitment relationship gives the most satisfactory result, as it displays the increases and declines with stock size and productivity that have been observed in other models (chapter 7) and in the field. Recruitment based on primary productivity requires further refinement as it does not show decline in fish stocks with eutrophication (the biomasses actually rise by a factor of 4.6 - 7.3). If this form of relationship is to be used then the relationship must be tied to specific parts of the planktonic community if realistic dynamics are to be produced. The final, lognormally distributed, recruitment relationship does not have the freedom

to respond to changes in productivity any more than does the constant recruitment term (as the parameters used in the distribution do not change). Nevertheless, it may be useful in the future for the evaluation of the effects of varying cohort strength at the system level.

Prescribed movement

The prescription of fish movement does not have a large impact on the dynamics of the model. However, the prediction of artificially high predation rates in some boxes with low productivity (and vice versa) when using prescribed movement (Bryant et al. 1995), in conjunction with theories regarding optimal foraging, led to the creation of a forage- and density-dependent based fish movement module. It was found that under this movement scheme only the planktivorous fish show movement that is a close approximation of that observed in PPB. These fish move north in the spring to take advantage of the blooms in the northern boxes, but are more generally spread during winter when they return to the southern boxes. This is largely in agreement with what is observed for the anchovies in PPB (the pilchards do not remain in the bay all year round, leaving in winter) (Gunthorpe et al. 1997). The demersal herbivorous fish show some features that resemble the seasonal movements of mullet (entering the mouth of the estuaries and bays in late summer). This resemblance is probably superficial, since mullet migrate to these locations to spawn and then return to their more standard habitats (Gunthorpe et al. 1997), whereas the demersal herbivorous fish were switching from a winter (detritus based) to higher quality summer (macrophyte) based diet and redistributing accordingly. The other two fish groups show little, if any, resemblance to reported patterns (the demersal fish are consistently homogeneously spread across the bay and the piscivores track the distribution of their major prey items). While an

intriguing beginning, this module requires more work before it shows any real advantage over the use of prescribed movement.

1.5 Conclusions

All facets of society are becoming increasingly concerned with whole systems rather than those directly affected by harvesting or pollution. As a consequence dynamic models that try to concisely capture the important aspects of ecosystems are receiving more attention (Bax and Eliassen 1990, Sekine et al. 1991, Riegman and Kuipers 1993, Baretta et al. 1995, Baretta-Bekker and Baretta 1997, Walters et al. 1997, Murray and Parslow 1999a, Walters et al. 1999, Walters et al. 2000). One specific area that is proving to be crucial is the question of model complexity (O'Neill and Rust 1979, Silvert 1981, Ludwig and Walters 1985, Costanza and Sklar 1985, Silvert 1996, Yool 1998). IGBEM was built as the foundation of a study of model complexity, to provide the "baseline" against which other models of simpler form and detail could be compared. For there to be confidence in the results of such a study it would be advantageous if the output of IGBEM resembles real temperate coastal systems. Consideration of the biomasses, productivity, temporal and spatial dynamics and the response of the model's behaviour to changes in nutrient loading indicates that, despite some weaknesses, the behaviour of IGBEM does resemble that of real temperate marine systems. The ability to reproduce real world dynamics across a range of conditions suggests IGBEM provides a sound reference for the study of complexity and the effects of formulation.

Like all models, IGBEM has its weaknesses. While it does a good job of addressing several issues that plague the models it was developed from (such as resuspension and a web-like rather than a parallel chain structure) and considerably extends the trophic coverage of its predecessors, it falls short in other areas. The

problems encountered with the sediment bacteria and nitrification-denitrification submodel indicate that it may be advantageous to develop ways of making empirical relationships more flexible with a minimum of additional formulation, rather than replacing them with equations that need an order of magnitude more parameters, interpretation and effort to validate.

Model validation and parameterisation is one of the largest constraints on the widespread use of dynamic models of substantial complexity. IGBEM requires in excess of 750 parameters, some of which are difficult to measure. While the set of standard parameters is sufficient for the representation of a generic system or the gross consideration of particular systems, it is obvious that use of IGBEM in a detailed evaluation of a specific system requires tuning it to the local conditions and taxa. Unfortunately, with such a large parameter set only the most intensively studied systems (such as PPB, Chesapeake Bay and the North Sea) can provide appropriate levels of information. Varela et al. (1995) expressed a similar concern with regard to the validation of ERSEM. While more information on marine systems is required across the board (Baretta et al. 1998), models of this level of physiological and process detail may be approaching the upper bound of what can be usefully employed. Nevertheless, the richness of the behaviour of these models may prove to be more than enough, at least for learning purposes. For example, without explicitly building them into the model, IGBEM can produce many of the behaviours observed in nature - competitive exclusion, keystone groups, spatial self-organisation, stable state changes (with and without human induced triggers) and adaptation to changes in ambient conditions. The prognostic usefulness of such large models may still be under debate, but the learning potential they provide cannot be denied.

Whether dynamic ecosystem models are used solely for learning or become an integral part of the management of marine resources, it is clear that no single set of

assumptions will suffice (Harris et al. 1996). Sensitivity analysis has become an accepted part of model construction (Jørgensen 1994), though it is commonly applied only to the parameters and not the assumptions or structures used in a model. Sampling schemes for the efficient use of computational experiments to assist in the analysis of model sensitivity have received some attention (Morris 1991). Moreover, ecosystem modelling packages such as ECOPATH explicitly acknowledge the need for sensitivity analysis through the inclusion of modules such as ECORANGER, which allows for the consideration of the implications of the levels of uncertainty associated with the ECOPATH input parameters (Christensen et al. 2000). Unfortunately, it is still largely impractical to attempt an inclusive and systematic sensitivity analysis of most models with even modest numbers of parameters. This does not mean that model sensitivity can be neglected. The judicious use of factor screening appears to be an expeditious means of identifying the most sensitive parts of the model and the exploration of the effects of the resulting restricted set of parameters is a much simpler task (Morris 1991). While not as thorough as a formal and systematic sensitivity analysis it is a necessary first step if the utility of any results are to be trusted with any significant measure of confidence. Further, in these large scale and detailed system-level models it is not only the parameter values that must be explored in this way, but the fundamental assumptions used to build parts of the models. Building a number of modules in parallel and then judging the performance and change in output that results when the different modules are employed is a sound way of identifying structural sensitivity in the model as well as identifying scenarios and options that are robust across a wide range of assumptions. This can be taken a step further if multiple models of differing types rather than just multiple modules are employed. For instance, biogeochemical models (e.g. IGBEM) and dynamic aggregate models (e.g. ECOSIM) are based on very different modelling philosophies but can be applied to the same questions (chapter 7). Nevertheless,

regardless of how it is done and whether the models are to be used as a learning or management tool, the form and structure of the models must be given careful consideration if preventable and unexpected events are to be avoided. This approach has worked well with IGBEM. The model reproduces real world dynamics quite well across a range of parameter settings and those areas where it does show some weaknesses have been identified and can be monitored, or improved.