

Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems

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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 (PP-BIM). Additional functional groups (such as benthic herbivorous invertebrates) and modules (dealing with sediment chemistry and mixing) have been incorporated or modified to ensure a more complete representation of temperate bay ecosystems and their processes, and a seamless amalgam of ERSEM II and PPBIM. The standard form of the entire model compares well with real ecosystems, such as Port Phillip Bay in Australia, and conforms to general ecological checkpoints such as the expected Sheldon Spectrum and Monbet's relationship between chlorophyll *a* and dissolved inorganic nitrogen. The model also produces spatial zonation and long-term cycles characteristic of natural systems. Despite the model taking a generalised biomass per functional group form, it captures well the system dynamics and allows for exploration of the effects of ecological driving forces such as predation and competition.

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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 modules 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

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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 (Olson and Hood, 1994). 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) use a variety of biological formulations based on trophic identity to capture the critical performance of the different components.

There was a bloom of highly detailed deterministic ecosystem models during the 1970s (Young et al., 1996), but it became apparent that complicated models did not necessarily capture system dynamics well and there was a widespread 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 un-

certain) parameter values, they are useful as a system of knowledge management. That is, 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 one particular system, but a generic representation of a temperate embayment. For convenience IGBEM utilises the physics of a particular Australian bay (Port Phillip Bay, Melbourne; Fig. 1), but it has the general biology and functional groups typical of most temperate bays.

IGBEM was based on two existing ecosystem models. The Port Phillip Bay Integrated Model (PPBIM) provided the spatial layout and most of the physical processes, while the ERSEM was the source of the majority of the biological processes included in IGBEM. 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

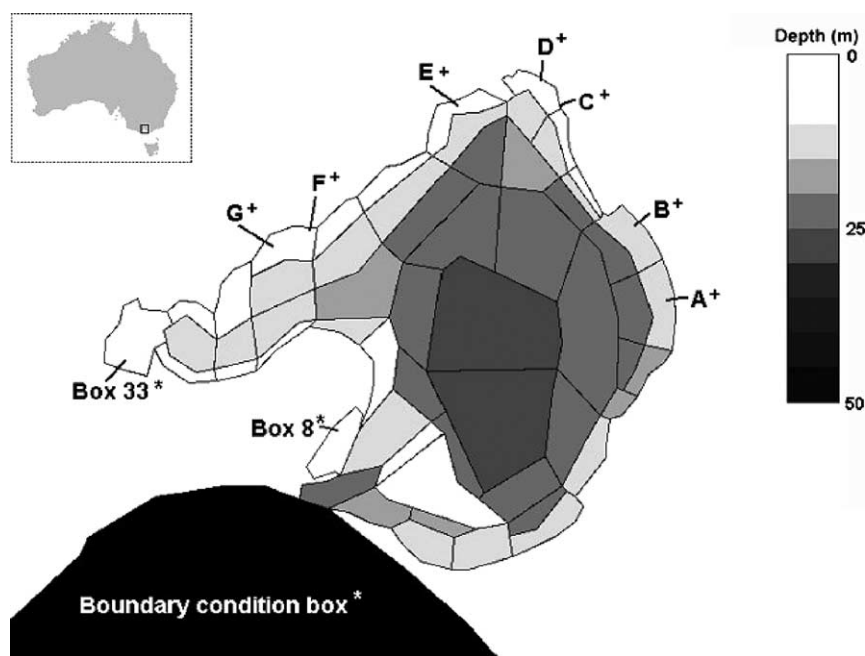


Fig. 1. Map of box geometry used for the standard runs of the Integrated Generic Bay Ecosystem Model. It represents Port Phillip Bay, Melbourne, Australia (location marked on map inset). Specific boxes referred to in the text (marked with *) and the location of point source-sinks used in the model (marked by +) are indicated.

benefit from being built upon a reference model that resembled reality as much as possible. To judge the ability of the model to reproduce realistic ecosystem dynamics over a range of conditions, the nutrient inputs were scaled to match those seen in a range of bays from around the world. The model outputs, and indicators derived from it, were then compared with literature values. Here we outline the construction of IGBEM and the exploration of its capacity to reflect real world behaviours.

2. Building IGBEM

Port Phillip Bay (PPB) has a number of features that make it an attractive site for study. It is a large marine embayment, approximately 1930 km², that has over half its volume in waters less than 8 m (it is 24 m at its deepest point). Only eight 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 subject to several 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 PPBIM is a biogeochemical model created as part of the most recent PPB study. It is both detailed and successful (Murray and Parslow, 1999). 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. As a result, it was necessary to extend the model's capabilities. The European Regional Seas Ecosystem Model II (ERSEM II) (Baretta-Bekker and Baretta, 1997) is well suited to being grafted to PPBIM, as it is a marine biogeochemical box-model 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 functional groups and processes thought to be important in coastal marine systems and state-of-the-art biogeochemical models.

IGBEM was created by integrating the biological and physical modules of PPBIM (Murray and Parslow, 1997, 1999) and the biological modules from ERSEM II (Baretta et al., 1995; Baretta-Bekker and Baretta, 1997). The PPBIM modules adopted by IGBEM were the three biological modules (representing water column, epibenthic and sediment biota) and a physical module. The biological process from ERSEM II were added directly to the appropriate IGBEM module (Fig. 2). For those functional groups that are covered by both ERSEM II and PPBIM, both formulations are included for optional use in IGBEM. Only the ERSEM II formulations were employed in the runs presented here. A summary of the source and modifications made to each part of IGBEM are given in Table 1.

The final form of IGBEM provides a spatially and temporally resolved model of nutrient cycles and population biomasses in an enclosed temperate bay. The model has 24 living components (groups), two dead, five nutrient, six physical and two gaseous components (Table 1). These components are linked through both biological and physical interactions and the resultant network (Fig. 3) is reminiscent of flow diagrams for real systems. The model is replicated spatially using the three layer (water column, epibenthic, sediment), 59 box geometry (Fig. 1) developed for PPBIM. Overall, a daily time-step is utilised for the standard runs of IGBEM as this best matches the transport model that underlies its physical module, and is very similar to that of PPBIM. Within the biological modules however, a daily time-step may make the variables with fast dynamics become unstable. Therefore, within each overall model time-step an adaptive time-step is used for the biological modules and when one 24-h period has been completed using this adaptive time-step then the transport model steps are performed. 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 regarding PPBIM can be found in Walker (1999) and Murray and Parslow

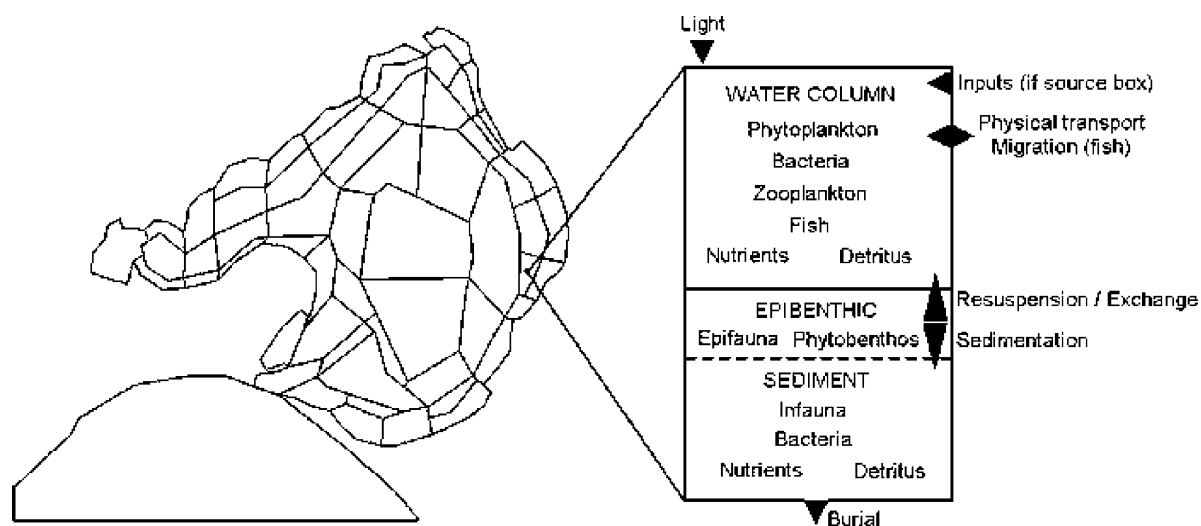


Fig. 2. Schematic diagram of the main modules in the Integrated Generic Bay Ecosystem Model. Details of the biological interactions are given in Fig. 3.

(1999). The level of process detail and the diet matrix used in the IGBEM are outlined in Tables 2 and 3, respectively.

Two biological groups were modified during the integration of PPBIM and ERSEM II. The microphytobenthos from PPBIM was modified after Blackford (1999), so that it more closely resembled the phytoplankton groups of ERSEM II. In addition, the ERSEM II benthic suspension feeders had their diets and behaviour adapted to better match those of PPBIM. This involved changing one of their dietary components from refractory to labile detritus, and the inclusion of an incidental transfer of refractory detritus from the water column to the sediment via suspension feeding. In addition to these modifications, the additional functional groups of epibenthic herbivorous scavengers and herbivorous fish were developed explicitly for IGBEM. These were added to take advantage of the macrophyte food sources represented in PPBIM. These groups were written by duplicating the general form of appropriate existing groups (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 3) based on diet data from the literature (Shepherd and Thomas, 1982; Heymans and

Baird, 1995; Levinton, 1995; Kuiter, 1996; Gunthorpe et al., 1997).

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 than 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) (Fig. 4). The only components

Table 1

A summary of the source and any modifications made to each of the components of the Integrated Generic Ecosystem Model (IGBEM)

IGBEM component or process	Code	Source	Modifications
Component			
Diatoms ^a	PL	ERSEM II, PPBIM	Light adaptation added to PPBIM version
Autotrophic flagellates	AF	ERSEM II	
Picoalgae	PS	ERSEM II, PPBIM	Light adaptation added to PPBIM version
Dinoflagellates	DF	ERSEM II, PPBIM	Light adaptation added to PPBIM version
Pelagic bacteria	PB	ERSEM II	
Heterotrophic flagellates	HF	ERSEM II	
Microzooplankton	ZS	ERSEM II, PPBIM	
Large omnivorous zooplankton	ZL	ERSEM II	
Large carnivorous zooplankton	ZLC	ERSEM II, PPBIM	
Planktivorous fish	FP	ERSEM II	
Piscivorous fish	FV	ERSEM II	
Demersal fish	FD	ERSEM II	
Demersal herbivorous fish	FG	New group	Based on ERSEM II standard organism; all associated trophic links added
Macroalgae	MA	PPBIM	
Seagrass	SG	PPBIM	
Microphytobenthos ^a	MB	PPBIM	Expanded to include ERSEM II-like process detail (after Blackford, 1999)
Macrozoobenthos (Epifaunal carnivores)	MZ	ERSEM II	
Benthic (Epifaunal) grazers	BG	New group	Based on ERSEM II standard organism; all associated trophic links added
Benthic suspension feeders	BF	ERSEM II, PPBIM	Refractory detritus replaced by labile detritus in the diet; incidental transfer of refractory detritus via suspension feeding added to ERSEM II version
Infaunal carnivores	BC	ERSEM II	
Benthic deposit feeders	BD	ERSEM II	
Meiobenthos	OB	ERSEM II	
Aerobic bacteria	AEB	ERSEM II	
Anaerobic bacteria	ANB	ERSEM II	
Labile detritus	DL	ERSEM II, PPBIM	
Refractory detritus ^a	DR	ERSEM II, PPBIM	
DON	DON	ERSEM II, PPBIM	
DIP	DIP	ERSEM II, PPBIM ^b	
Ammonia	NH	ERSEM II, PPBIM	
Nitrate	NO	ERSEM II, PPBIM	
Dissolved silicate	Si	ERSEM II, PPBIM	
Dissolved oxygen	O ₂	ERSEM II, PPBIM ^b	
Carbon dioxide	CO ₂	ERSEM II	
Light	IRR	ERSEM II, PPBIM	
Salinity	SAL	PPBIM	
Sediment grain types	PHI	PPBIM	
Bottom stress	STRESS	PPBIM	
Porosity	PORE	PPBIM	
Volume	VOL	PPBIM	
Process			
Bioirrigation		PPBIM	Linked to dynamic sediment fauna using an ERSEM II-like ‘enhancement’ term
Bioturbation		Based on proposals for PPBIM (Walker, 1997) that had not been implemented	Linked to dynamic sediment fauna using an ERSEM II-like ‘enhancement’ term
Sediment chemistry		PPBIM	Links to dynamic bacteria were trialed but failed (further work in this area is necessary)

PPBIM stands for Port Phillip Bay Integrated Model (PPBIM) and ERSEM II is the European Regional Seas Ecosystem Model II (ERSEM II). Note that all living and dead components have carbon (C), nitrogen (N) and phosphorous (P) pools.

^a Also these have an internal silicon (Si) pool.

^b Handled in PPBIM 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).

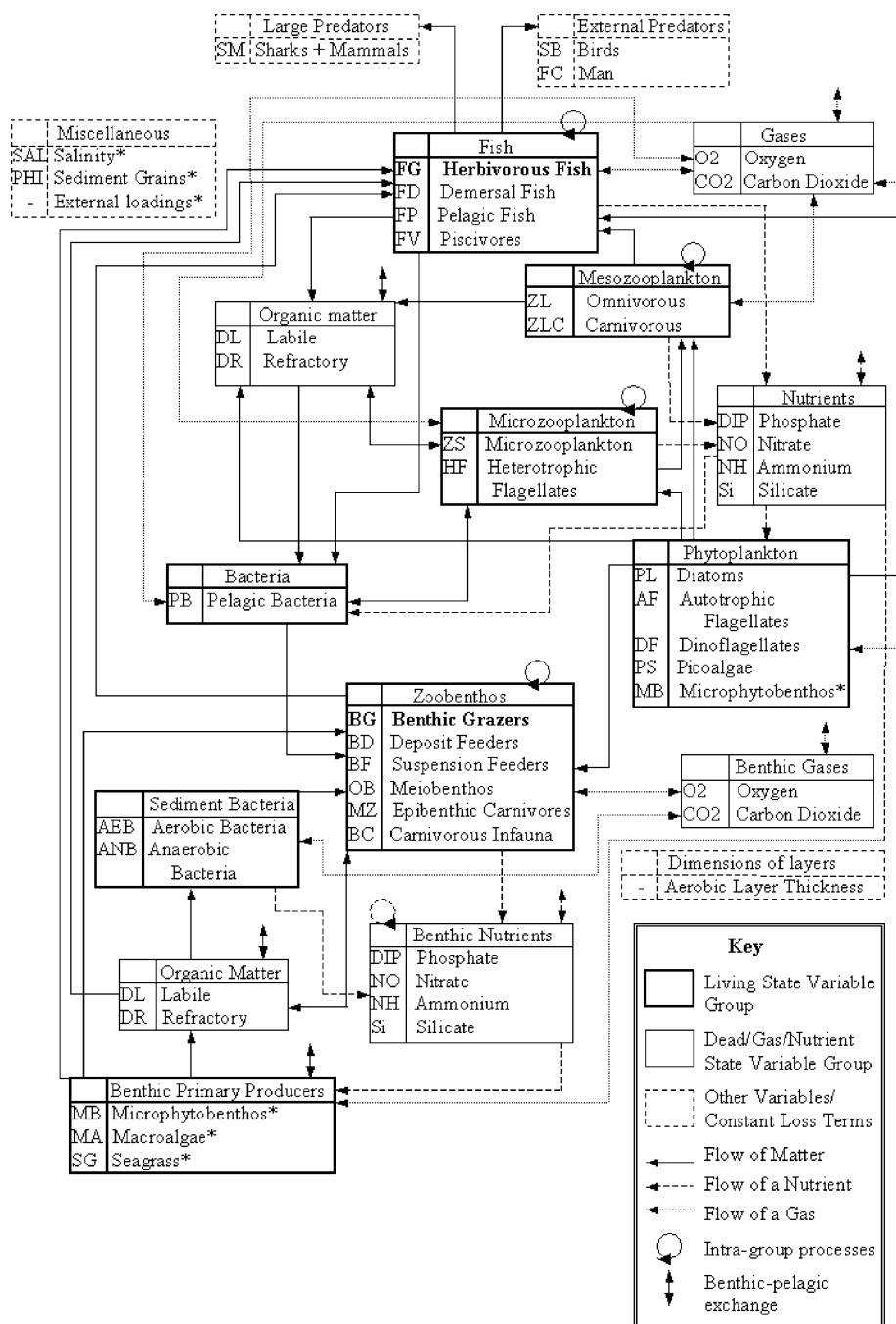


Fig. 3. Biological and physical interactions between the components used in the Integrated Generic Bay Ecosystem Model (IGBEM). A (*) indicates those components from the Port Phillip Bay Integrated Model, and those in bold are components built specifically for IGBEM, while the remainder are from European Regional Seas Ecosystem Model II (Blackford and Radford, 1995). The code for each component is given by its name.

Table 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

Process	Component																		
	C	N	P	Si	PL	DF	AF	PS	PB	ZS	HF	ZL	ZLC	FP	FV	MB	DR	DL	
(a) Water column components and processes																			
Used by phytoplankton	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Used by bacteria	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+
Flux from excretion	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+
Mineralisation	–	–	–	–	–	–	–	–	p	–	–	–	–	–	–	–	–	+	+
Nitrification	–	+	–	–	–	–	–	–	p	–	–	–	–	–	–	–	–	–	–
Oxygen production	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–	+	–	–	–
Growth	–	–	–	–	Int	Int	Int	Int	ra	+	+	+	+	+	+	Int	–	–	–
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 ^a	**	+	+	–	–	–	–	–	+	–	–	–	–	–	–	–	+	+	+
(b) Sediment components and processes																			
Sediment	C	N	P	Si	BD	BC	OB	AEB	ANB	PL	DF	PS	AF	MB	DR	DL			
Used by microphytobenthos	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–			
Used by bacteria	+	+	+	–	–	–	–	–	–	–	–	–	–	–	ontm	ontm			
Flux from excretion	+	+	+	+	–	–	–	–	–	–	–	–	–	–	+	+			
Mineralisation	–	–	–	–	–	–	–	p	p	–	–	–	–	–	+	+			
Nitrification	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Denitrification	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Oxygen production ^b	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–			
Growth	–	–	–	–	ot	ot	ot	ra	ra	–	–	–	–	Int ^b	–	–			
Respiration	–	–	–	–	ra	ra	ra	otra ^b	otra ^b	–	–	–	–	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	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–			
(c) Epibenthic components and processes																			
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	Intw	Intw	+	+	–	–						
Lysis (nutrient stress)	–	–	–	–	ra	ra	ra	x	x	ra	ra	–	–						
Nutrient uptake	–	–	–	–	–	–	–	+	+	–	–	–	–						
Predation losses	–	–	–	–	+	+	+	+	+	cd	cd	+	+						
Cannibalism	–	–	–	–	+	–	–	–	–	+	–	–	–						

Table 2 (Continued)

Process	Component																	
	C	N	P	Si	PL	DF	AF	PS	PB	ZS	HF	ZL	ZLC	FP	FV	MB	DR	DL
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 ^c	–	–	–	–	–	–	–	–	–	–	–	+	+					
Impact upon bioirrigation and bioturbation	–	–	–	–	+	+	+	–	–	–	–	–	–					

Component codes are as stated in Table 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; **D**IN (epiphytic growth) effect; search and **h**andling times included; **i**nternal pool controls; **l**ight limitation; depth effect (**m**); **n**utrient effect; **o**xxygen effect; **p**erforms this physical activity; **r**est; **s**tarvation; **t**emperature effect; **c**rowding; assumed in formulation but not **e**xplicit ; **p**hysical bottom stress effect; present (+); absent (–). ** indicates that there is a flux of C from the static returns, but in the form of carbon dioxide.

^a A percentage of the losses to fishing/seabirds/large predators.

^b It is used to determine the oxygen horizon.

^c A percentage of the losses to fishing/seabirds/large predators.

Table 3

Diet matrix for the living components in a standard run of the Integrated Generic Bay Ecosystem Model

Prey	Grazer																
	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	−	−	−	−	−	−	−	+	+	+	+	+	−	+	−	+	

Component codes are as for Table 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.).

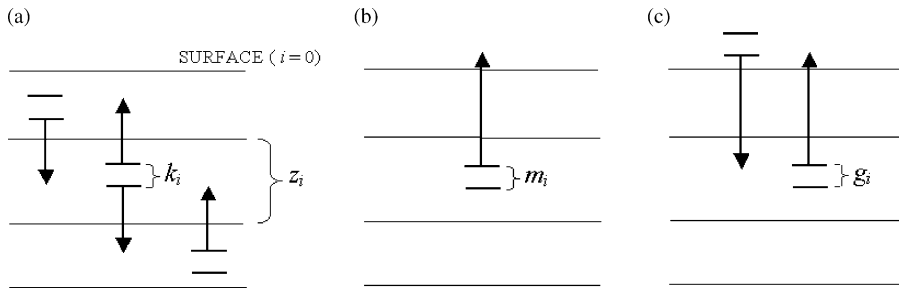


Fig. 4. Bioturbation related sediment mixing processes included in the Integrated Generic Bay Ecosystem Model (IGBEM): (a) particulate diffusion, (b) expulsion, and (c) exchange.

(tracers) acted upon by bioturbation were those particulate tracers that were allowed in the sediments and were not macrobenthos, i.e. 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 ($C_i(t)$) at the end of a time-step as:

$$C_i(t + \Delta t) = (C_{i+1}(t)k_{i+1} + C_{i-1}(t)k_{i-1} + C_i(t)z_i - 2C_i(t)k_i - C_i(t)m_i - C_i(t)g_i + C_0(t)g_0)(k_{i+1} + k_{i-1} + z_i - 2k_i - m_i - g_i + g_0)^{-1} \quad (1)$$

$$k_i = \psi \delta \tau \theta_i (z_i)^{-1} \quad (2)$$

$$m_i = \gamma \delta \tau \theta_i \quad (3)$$

$$g_i = \eta \delta \tau \theta_i \quad (4)$$

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 layer and z_i is the thickness of layer i . Baseline density of biological activity is represented by δ ; τ represents the modification made to the baseline to reflect dynamic sediment fauna activity in the ecological submodel (calculated in much the same way as that of ERSEM (see Ebenhöh et al., 1995)); 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)); 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 (meter per Δt per unit biomass of bioturbative benthos per m^2); and η is the rate of exchange between the surface and deeper layers (meter 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, 1999) more dynamic by incorporating more of the processes included in the calculation of ERSEM II'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 is 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 (1999) 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.

Space precludes detailing the many other alternative settings that were built into the model. These alternatives included forage- and density-dependent move-

ment 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 °C 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 of all parameter space is not currently possible (potential solutions to this are addressed in Section 4.4). Thus, growth and mortality parameters and those associated with processes pro-

ducing 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.

3. Model runs

All functional groups are active in the standard run of IGBEM. Runs usually simulated a 20-year period (beginning after a 10-year ‘burn-in’ period), but 100-year simulations were also run to allow consideration of long-term cycles and to check whether the model reached a representative state by the end of the usual 20-year run. The files containing the forcing

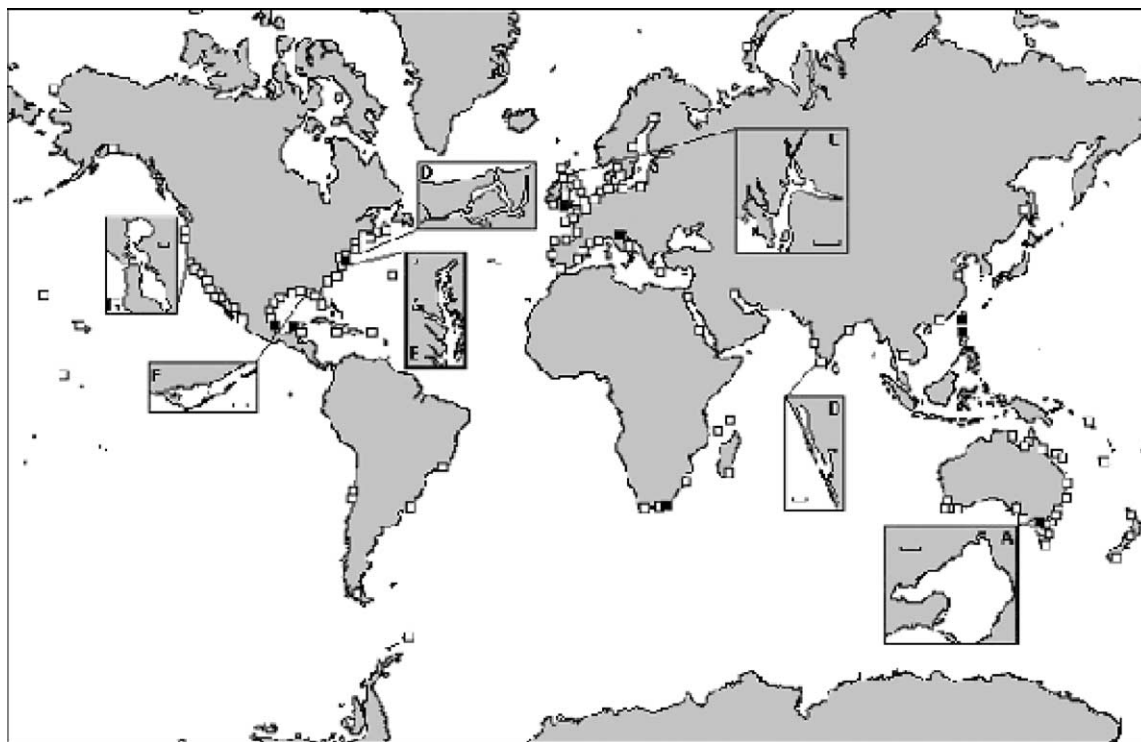


Fig. 5. Map of the world showing the bays used to evaluate the performance of the Integrated Generic Bay Ecosystem Model (IGBEM). Boxes mark the locations of all the systems for which marine biomass or production estimates are available for comparison with the output of IGBEM. The solid black boxes indicate 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.

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, although the exact date of recruitment varies stochastically by up to a few weeks. Alternative forms of fish movement (forage- and density-dependent) and recruitment (lognormal, Beverton-Holt, and a function of primary productivity) have been tried in IGBEM. As these alternative schemes make little difference to the results presented here they will not be discussed.

To evaluate how well the model replicates existing systems and changes in system state which accompany eutrophication, a number of other bays around the world that have similar physical conditions (tidal range and relative size of opening to the sea) (Fig. 5) were identified. The inputs to these bays (from Monbet, 1992) were then scaled based on the area of the bay relative to Port Phillip Bay (PPB) and the nutrient forcing files were adjusted to match. Thus, while the exact geography of the bay was not changed, nutrient conditions were altered to capture the state of several well-studied bays. Since the biological parameters for the run under baseline conditions are based on species from temperate marine bays in many parts of the world, the biological parameters were not retuned to represent a particular bay. The ability to achieve a plausible representation of these other bays was based on the model's output values for chlorophyll a (chl a), dissolved inorganic nutrients (DIN), biomasses and other measures identified from the literature.

Despite being under anthropogenic pressure, PPB has not become eutrophic. Therefore, when evaluating the model's ability to capture changes in a system as it becomes eutrophic, it was necessary to use values from another bay to represent the (expected) eutrophic values of PPB. Of all the bays where there is enough available biological information to give a relatively complete assessment of model performance, Chesapeake Bay is closest to the expected form of PPB were it to become eutrophic. Thus, to judge how well the model replicates state changes due to eutrophication, the values from the runs using nutrient loadings from

Port Phillip Bay (PM run) and Chesapeake Bay (CM run) were compared to empirical values from these two bays.

4. Results and discussion

4.1. IGBEM versus real bays

Spatially, temporally and taxonomically explicit information on each of the individual components present in the model is not generally available for real bays. Consequently output has to be aggregated so that it matches the most common resolution of the data available in the literature. To differentiate between the highly resolved output of IGBEM and the aggregated forms, the latter are referred to as trophic sets. The list of trophic sets is made up of chlorophyll a (also referred to as chl a, this was used 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).

4.1.1. Biomasses

Empirical estimates of average biomasses for the trophic sets covered in IGBEM were obtained from the literature for 261 coastal marine systems (Fig. 5; 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 Fig. 5) 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 Fig. 5). Thus, the published values allow a 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 is high and the values for the sediment bacteria are low, which are attributes that the model has inherited from ERSEM (Baretta-Bekker et al., 1995).

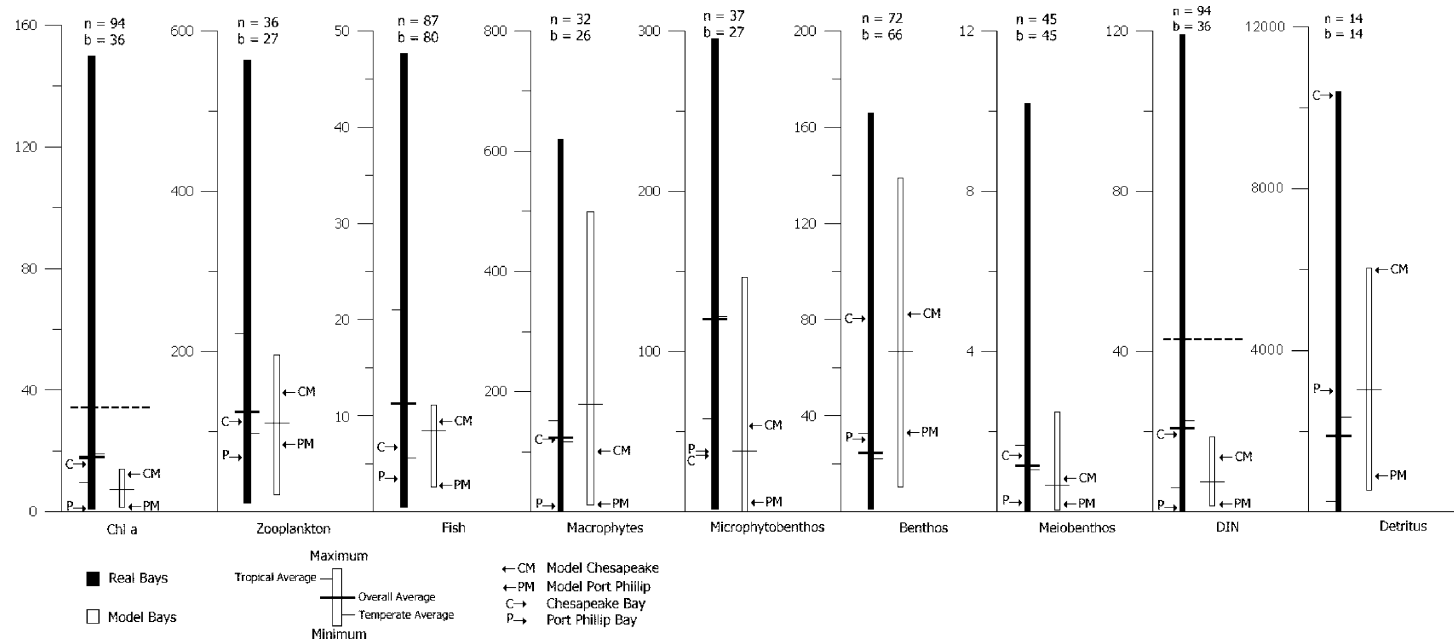


Fig. 6. Ranges and average values for the main sets of the model in comparison with field values worldwide. The systems giving the maximum and minimum for the field data for each trophic set are marked beside the reference in [Appendix A](#). The number of field data points (n) and the number of bays (b) the data came from are marked on the figure. The model values come from the runs under different nutrient inputs based on inputs for real bays (A–G in [Fig. 4](#)). The y-axis for zooplankton is biomass in mg AFDW/m³; for fish, macrophytes, benthos, meiobenthos and detritus the y-axis is biomass in g AFDW m⁻²; the y-axis for chl a is mg chl a m⁻³; for DIN it is mmol DIN m⁻³; and for microphytobenthos it is mg chl a m⁻². The dashed line cutting the black bar in chl a and DIN marks the maximum value of chl a and DIN recorded for those bays with the same nutrient loads as used to run IGBEM.

Table 4

Absolute values of Student's *t*-statistic calculated using the empirical values and model values for each trophic set

Trophic set	<i>t</i>	d.f.
Chlorophyll a (chl a)	1.35	99
Zooplankton	0.32	44
Fish	0.71	82
Macrophytes	1.08	40
Microphytobenthos	2.58*	44
Benthos	3.81*	80
Meiobenthos	0.73	51
Dissolved inorganic nitrogen (DIN)	1.16	21
Detritus	1.45	99

* Significant with $\alpha = 0.05$.

4.1.2. Average biomass

The average biomasses indicate a mixed, but still satisfactory, performance. Given the magnitude of the range in field values, the average model values are not far from the average empirical values of temperate bays in most cases (Fig. 6). Only two of the trophic sets (benthos and microphytobenthos) have an average model value that is significantly different (Table 4) to the average empirical value.

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

When the specific empirical values for the trophic sets in PPB and Chesapeake Bay (CB) are compared with the respective model values (Fig. 6), the estimates for trophic sets from the model are usually within the bounds of empirical interannual variation, with the exception of the microphytobenthos and detritus. The model consistently yields detrital biomasses that are too low. Similarly, 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. In the model, the average biomass of microphytobenthos rose while the field values dropped marginally, if at all, given interannual variation in field values.

IGBEM does not include extremely refractory detritus, whereas the field data may, and this may account, in part, for the low detrital biomasses predicted by the model. However, it is also likely that estimates of the atmospheric component of detrital inputs to PPB were 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.

The low levels of microphytobenthos in the PM run are, at least in part, the result of two things. Firstly, this group competes with the large macrophytes, 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, where light limitation for microphytobenthos is not as pronounced as for the other benthic primary producers (the microphytobenthos light saturation is set at 3 W/m² compared to 5 W/m² for macroalgae and 60 W/m² for seagrass). Secondly, as a result of very little available information on benthic interactions, the availability of the microphytobenthos to the deposit feeders and meiobenthos may 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, but more importantly, all aspects of the infauna and benthic microfauna in IGBEM and other biogeochemical models (Silvert, 1991) would benefit from an increased understanding of benthic interactions and ecology.

4.1.4. Community composition

Another biomass related comparison that can be made for the PM run is the relative composition of the fish and benthic communities (Table 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. Despite this, there is room for improvement when the predicted communities are compared to those from PPB.

The relative values for the fish community indicate that the IGBEM run over-emphasises the pelagic component of the fish community. This may be because the currently available estimate of the relative contribution of the planktivores to the PPB community may be an underestimate as it is based primarily on trawls (which catch few of the pelagic species). In addition, the fish groups in IGBEM do not represent the entire fish pop-

Table 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

Functional group	PM (model) (percentage of total biomass)	PPB (empirical) (percentage 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

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.

ulation, but only part of it with the rest of the fish fauna (sharks and other large demersals) represented by static closure terms imposed on the dynamic fish groups. 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, then IGBEM does compare reasonably well with those observed in PPB (values in parenthesis in Table 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.

In contrast to the fish community, the relative composition of the benthic community in IGBEM is close to that observed in PPB (Table 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. Secondly, there may be a mechanism in nature that influences the population dynamics that is not present in IGBEM. For example, a burrow effect may be appropriate (as it would lessen the impact

of anoxic conditions in the sediment). Alternatively, an index of habitat type (such as the percentage 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.

4.1.5. Standard relationships

While a good fit to biomasses across most 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 chlorophyll a and dissolved inorganic nitrogen (DIN) in the water column, and the model shows a similar relationship (Fig. 7) (references for the real bays are in Appendix A). Note that only microtidal estuaries and bays (tidal range < 2 m) 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

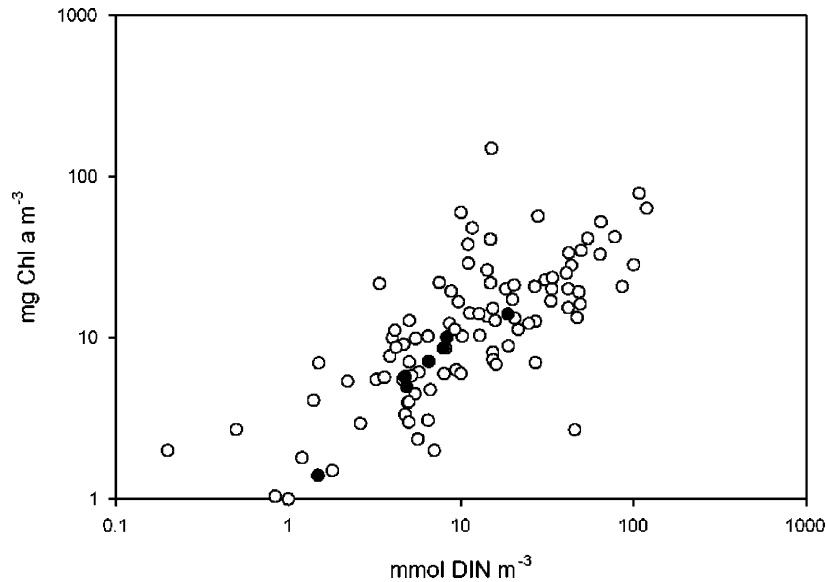


Fig. 7. The relationship between the mean annual concentration of dissolved inorganic nitrogen (DIN) and chlorophyll a (chl a) for microtidal marine systems. See Appendix A for references used to give values for real bays.

observed by Monbet (1992) and there is no significant difference between regression lines fitted to the empirical and model values ($F_{2,97} = 0.86$, $P > 0.25$).

There are also established 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, i.e. the 'Sheldon spectrum' is almost flat. In contrast, benthic communities have a spectrum that is W-shaped (Schwinghamer, 1981). We compared the Sheldon spectra for the benthic and pelagic components of the model to empirical spectra. The spectrum for the pelagic components of IGBEM (Table 6) indicates that the model output is in accord with Sheldon et al.'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/Meiofauna, Macrofauna) given by Schwinghamer rather than the specific values per size

interval (converting the form of the spectrum from a 'W' into a 'U'). In this case the model does not conform well with field observations (Table 7). While the two larger classes (meiofauna/microalgae and macrofauna) are within, or close to, the bounds given by Schwinghamer (Table 7), the bacteria are <2% of the field average.

4.1.6. System indices

Given the holistic nature of ecosystem studies, simple reductionist comparisons of biomasses, productivity and other ecosystem attributes are insufficient to summarise 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

Table 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 7

Summary of the Sheldon spectra for the benthic classes in the baseline (PM) and nutrient load 10× (CM) runs of IGBEM

Class	PM (cm ³ /m ²)	CM (cm ³ /m ²)	Average Schwinghamer (cm ³ /m ²)	Minimum Schwinghamer (cm ³ /m ²)	Maximum Schwinghamer (cm ³ /m ²)
Bacteria	0.2	1.4	80.1	8.1	168.2
Meiobenthos and microphytobenthos	0.7	4.3	6.1	0.9	37.0
Macrofauna	149.5	373.2	473.0	1.6	1817.0

As a guide, the ranges and total mean biomass for each class after Schwinghamer (1981) are also provided.

calculated for the baseline (PM) and nutrients 10× (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 nine real marine systems (Table 8). A correlation coefficient was also calculated between the average values for each index (except total throughput, which overwhelmed the contributions from the other indices if included) for the real bays and the model runs. The comparison indicates that the model conforms well with the real systems ($r = 0.91$). The value for the total throughput for the CM run is the only model value 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 other real systems considered.

The correlation between PPB and the PM run indicates a strong concordance in the values of their indices ($r = 0.90$ with total throughput omitted). Despite this, only four of the 11 indices show a close match (i.e. where the PM value is within a factor 2 of the PPB value). The ‘System Omnivory Index’, ‘Dominance of Detritus’, ‘Path length’ and ‘Relative Ascendancy’ all suggest that the real and modelled systems are similar, while the remaining indices suggest some 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 modelled 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 8 is based on parameters determined from species resident in PPB and the

correlation coefficient (omitting total throughput) between this run and PPB ($r = 0.95$) is higher than that between PM and PPB ($r = 0.90$). In addition, the model values are within a factor of two of the real values for all but one of the eleven indices. Thus, the standard parameter set does a sound job of reproducing a generic coastal system while tuning can produce a close fit to the holistic form of a specific system.

4.2. 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.

4.2.1. 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 fourth root transform of the average biomasses of all groups in each box were compared on a two-dimensional non-metric multi-dimensional scaling (MDS) plot derived from a Bray Curtis similarity matrix to identify groups of boxes of similar community structure. The fourth root transform was used as the Bray-Curtis as it is sensitive to large values (Field et al., 1982). The average values of the physical variables and the biomass per group were examined (using the SIMPER routine of the PRIMER software package (Clarke and Warwick, 1994)) to ascertain which groups most influenced the separation of clusters. This analysis identified approximately homogeneous areas in the model, i.e. sets of contiguous boxes in the model

Table 8

System level indices for a range of real coastal areas (values for the first eight 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 10×)	50702	18.7	0.019	0.04	0.15	0.47	0.0418	3.36	0.06	4.59	29.8

sharing similar biological and/or physical characteristics. Only the PM and CM runs were analysed in this way since they were considered representative of the ‘mesotrophic’ and ‘eutrophic’ states of the model output.

Based on the analysis, fourteen biological areas (Fig. 8a) and twelve geophysical areas (Fig. 8b) 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 example, certain functional groups consistently occur together with high biomasses in the same cells, and we group these as ‘communities’ (Table 9). A comparison of the communities and attributes per biological area (Table 10) shows that box 8 (area 4) and box 33 (area 9) are distinct from the main bay. This is due to their shallow depth, large macrophyte communities and restricted connection with the main bay. Within the

main bay, the ‘biological areas’ reveal 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 area communities persist over time in the model output.

When the CM run is analysed only ten distinct biological areas and nine physical areas can be identified (Fig. 9). The decline in the number of the physical areas, from twelve to nine, 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 show some overlap, but it is still clear that abiotic factors alone are not the only cause of the biological areas. As before, the mix of biotic and abiotic agents appears 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 11). However, in the CM run 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 margin of the northern parts of the bay. Moreover, the distinction between ‘edge’ and ‘central’ planktonic communities is less clear. Boxes 8 and 33 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. This suggests that the model is replicating the simplification of habitat and the reduction in diversity that is typically seen with eutrophication.

Table 9

Definitions for the various communities found in the output of the Integrated Generic Bay Ecosystem Model runs

Community	Functional groups present
Planktonic	Diatoms and autotrophic flagellates Picoalgae and microzooplankton Picoalgae, autotrophic flagellates, dinoflagellates, heterotrophic flagellates, large omnivorous zooplankton and large carnivorous zooplankton Heterotrophic flagellates
Epibenthic	Benthic suspension feeders Macrozoobenthos (epifaunal carnivores)
Macrophyte	Seagrass Macroalgae and benthic (epifaunal) grazers
Fish	Planktivores Piscivores Demersal herbivorous fish and demersal fish Piscivores and demersal fish
Benthic	Benthic deposit feeders and infaunal carnivores Meiobenthos and microphytobenthos
Remineralisation	Pelagic bacteria, aerobic bacteria, anaerobic bacteria, labile and refractory detritus Pelagic bacteria Aerobic bacteria Labile and refractory detritus

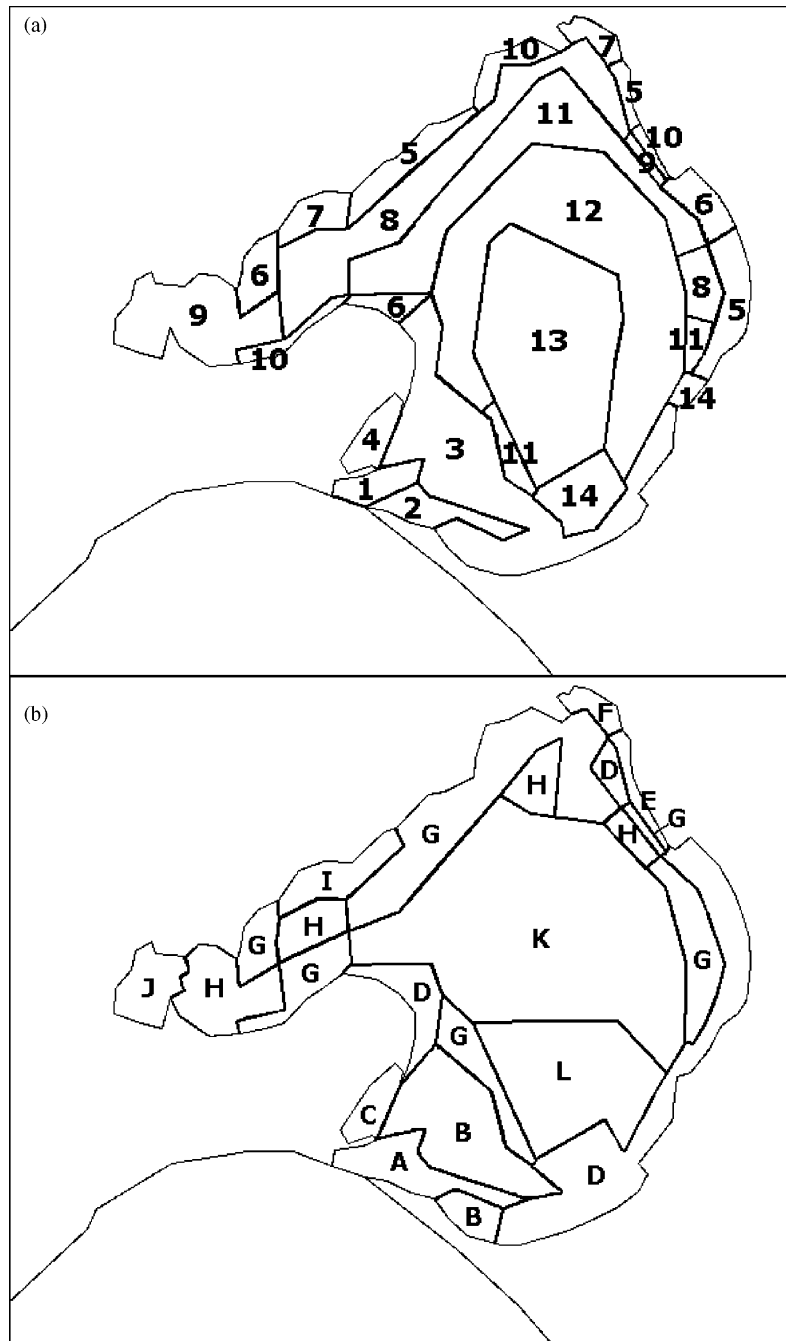


Fig. 8. Maps of the location of the physical and biological areas identified in the output of the PM: (a) the biological areas (sections of the bay that are in the same 'biological area' are marked with the same number), and (b) the physical areas (sections of the bay that are in the same 'physical area' are marked with the same letter).

Table 10
Dominant communities and physical attributes characterising each biological area identified in the PM run

Area	Biological communities							Physical attribute			
	Planktonic	Fish	Epibenthic	Benthic	Macrophyte	Remineralisation	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	

Codes for the functional communities are as of Table 9. 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.

Table 11
Dominant communities and physical attributes characterising each biological area identified in the CM run

Area	Biological communities							Physical attribute			
	Planktonic	Fish	Epibenthic	Benthic	Macrophyte	Remineralisation	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

Codes for the functional communities are as of Table 9. 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 contribute significantly to the definition of the area. A blank entry for a physical attribute signifies low to negligible levels for that attribute.

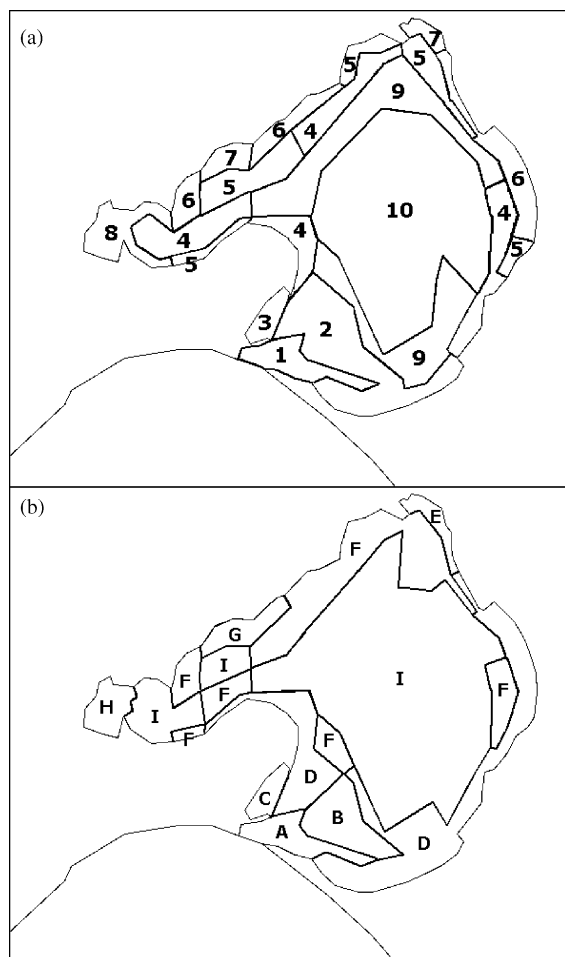


Fig. 9. Maps of the location of the physical and biological areas identified in the output of the CM: (a) the biological areas (sections of the bay that are in the same 'biological area' are marked with the same number), and (b) the physical areas (sections of the bay that are in the same 'physical area' are marked with the same letter).

4.2.2. Temporal structure

Distinct temporal patterns are evident in the long-term output of the PM run, including seasonal, inter-annual and decadal cycles (Fig. 10a–c). The cycles seen in fish biomass will not be discussed here as they are largely prescribed by the movement and fishing regime employed, with only minor amounts of variation occurring due to interannual variation in their growth as it tracks food supply.

While there are high levels of short-term fluctuation in the phytoplankton groups, seasonal cycles within

the planktonic groups are nonetheless clear (Fig. 10a). 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 (D and G, Fig. 1), lead to bloom events in spring when light levels begin to rise. The form of the blooms is least stable in these boxes, where local flows cause a lot of variation. Further away from the point sources, the cycles are much more stable. Similar seasonal cycles can be seen in the benthic primary producers (e.g. macroalgae, Fig. 10b) and the detritus based web fed by them (Fig. 10c). 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 (Fig. 10c) 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, which 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 behaviour of PPBIM (Murray and Parslow, 1997) and ERSEM (Ebenhöh et al., 1995).

The interaction of physical forcing and biotic interactions 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 Fig. 10b) where the macrophytes are at high levels (equivalent to temperate kelp forests) for between 2 and 7 years before dropping to very low levels ($<1 \text{ mg N/m}^3$ 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

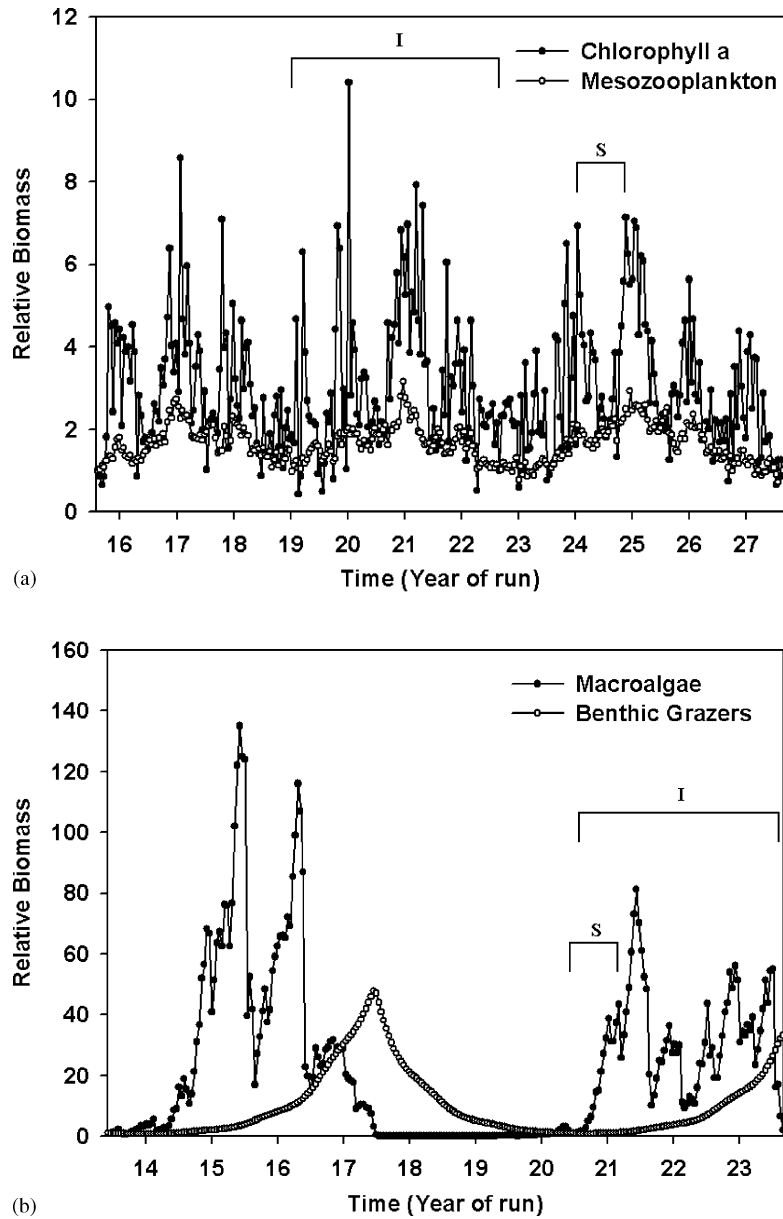


Fig. 10. Relative biomass (biomass/biomass on first day of period shown) (y-axis) through time (x-axis) showing temporal patterns for representative groups in the PM run of the Integrated Generic Bay Ecosystem Model. The tick mark given for the year of the run coincides with January 1 of that year. The 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) is an example of decadal scale cycles. Plots (a) and (b) are from edge boxes, while (c) is from the large central box.

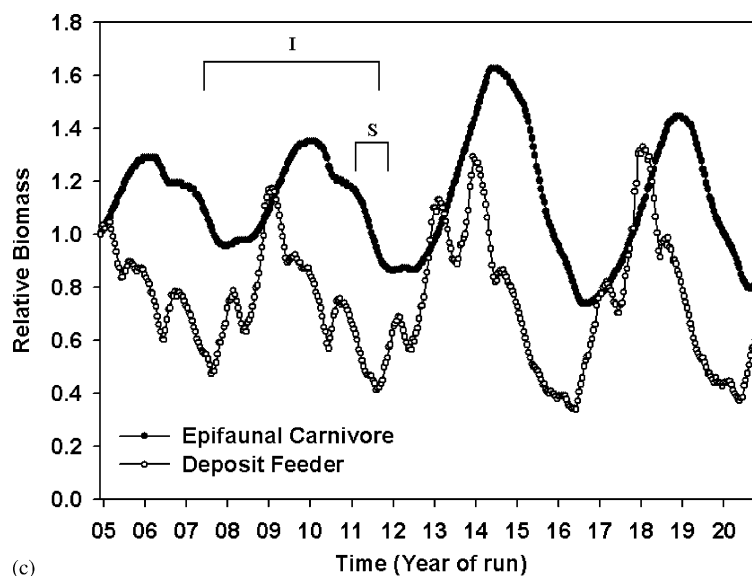


Fig. 10. (Continued).

the 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 and no such cycle has been recorded for PPB. 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 (Fig. 10c) depending on the food web from which they receive most prey. 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 'macrophyte-barrens' cycle begins its decline later in the year), then the cycle switches to one with larger amplitudes. This cycle gradually slips back into the previous state in which the benthic grazers make up a smaller proportion of the diet. 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.

Human actions do have the potential to cause widespread changes in system behaviour, however, 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 (e.g. the microzooplankton in box 33), 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 (as a result of eutrophication, see below) means that the coincidence of events required to cause the change in the cycle of interannual variation in the epifaunal carnivores no longer arises. This supports the view that anthropogenically induced changes can cause large alterations in system behaviour beyond simple reductions in diversity and shifts in biomass.

4.2.3. *Effect 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 small, rapidly growing forms. 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. As ERSEM I and II consistently give ratios of small to large phytoplankton that are high, despite field observations indicating the reverse is true for the North Sea (Varela et al., 1995; Ebenhöh et al., 1997), it is probable that IGBEM has inherited this characteristic from ERSEM II. A potential explanation for the behaviour 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 increases, 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 Marshal, 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.

Within the fish groups there is some increase in production and biomass (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 (reduced 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). However, as nutrients rise to 30× 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 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 off 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 this is not as strong as it should be. 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.

The model does show a simplification of the overall system with eutrophication similar to that observed in the field (Harris et al., 1996). This is evidenced by: a shift in relative compositions in all of the communities to smaller, faster growing more opportunistic groups; simplification of habitat; and a substantial expansion of those communities tolerant to low light, high nutrients and detritus. 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 de-

spite possible shortcomings of its current parameterisation.

4.3. Overall model performance

It is clear from the summary of all of the results (Table 12) that IGBEM does have some weaknesses, most of which have to do with poorly known benthic groups and processes. In particular, the sediment chemistry could be improved by making it dynamic, but this will only improve model performance once the behaviour of the microscopic benthic fauna and flora (e.g. microphytobenthos and bacteria) has also been improved. Despite these problems, overall IGBEM is capable of producing levels of biomass and

Table 12
Overview of all results

Measure	Results
Average biomass	Only benthos and microphytobenthos have average model values that are significantly different from the average empirical value
Biomass—PM vs. PPB	Model biomass for microphytobenthos is too low, as is the predicted biomass of detritus. All other biomasses are within the bounds of empirical interannual variation
Biomass—CM vs. CB	Model biomass for detritus is too low, but all other biomasses are within the bounds of empirical interannual variation
Community composition (PM vs. PPB)	IGBEM over represents pelagic fish groups. Relative community composition of the benthos in the model is close to that of PPB, though there is some suggestion that the model underplays the detritus based web
Monbet's relationship (chl a vs. DIN)	No difference between the regression lines through the empirical and model points ($F = 0.86$ with d.f. = 2.97 for the general relationship and $F = 0.78$ with d.f. = 2.29 for the comparison of the model points with the specific bays used to set the nutrient scenarios)
Size spectra	Size spectra of pelagos holds with Sheldon et al.'s (1972) observations for real ecosystems. Benthos does not hold with Schwinghammer's (1981) relationship, as the bacteria in the model are <2% of the field average (from Schwinghammer 1981)
System indices—range	Only total throughput for the CM run is beyond the range of values given by real ecosystems
System indices—average	Model values conform well with empirical values ($r = 0.91$)
System indices—PM vs. PPB	Overall a strong relationship exists between the model and empirical values ($r = 0.90$), but only four of the eleven indices have model values that are within a factor of two of the empirical estimates
System indices—BASE vs. PPB	Relationship between the model and empirical values is strengthened ($r = 0.95$) and 10 of the 11 indices have model values that are within a factor of two of the empirical estimates
Spatial structure	Fourteen biological areas and twelve geophysical areas exist in the PM run, and ten biological areas and nine physical areas in the CM run. Biological interactions and physical factors produce the biological areas. 'Central communities' and 'edge communities' exist
Temporal structure	Seasonal, interannual and long-term (5–20 years) cycles are evident
Effects of eutrophication	No groups are lost from the model as nutrients increase, but it does predict changes in habitat structure, increase in production and biomass of pelagic groups, a peak and then decline in benthic groups, shifts in community composition to more opportunistic (smaller, faster growing) groups and an expansion of communities tolerant to low light and high levels of nutrients and detritus. This matches general characteristics of the observed changes in real systems with eutrophication (Harris et al., 1996). However, the shift in the phytoplankton community composition is not consistent with that observed in real systems (the model predicts rise in small phytoplankton rather than the diatoms). IGBEM also fails to predict any fish stock collapses, as seen in severely eutrophied ecosystems

ecosystem dynamics that are close to those from real ecosystems.

4.4. Model sensitivity

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). In addition to the methods proposed by Morris (1991), other methods such as the stochastic response surface method (Isukapalli et al., 2000) and the various forms of Latin hypercube sampling (Iman and Conover, 1980; Huntington and Lyrantzis, 1998; Helton and Davis, 2003) show significant potential. Unfortunately, due to the dimensionality and non-linearity of ecosystem models, it is still largely impractical to attempt an inclusive, thorough and systematic sensitivity analysis of the entire parameter space for most of these kind of models. 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. Moreover, with the continuing increases in computing power it may also be simpler in the near future to implement Latin hypercube sampling or the factor-designs advocated by Morris (1991) for ecosystem models and so address the problems regarding the logistical requirements of thorough and systematic sensitivity analyses of models with large parameter sets.

In these large scale and detailed system-level models it is not only the parameter values that must be explored with regard to model sensitivity, but the fundamental assumptions used to build parts of the models must also be considered. 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 approach was used with IGBEM, particularly for the fish recruitment and movement schemes, and although space precludes presenting the results here it is worth noting that the approach was found to be informative (Fulton, 2001).

5. Conclusions

All facets of society are becoming increasingly concerned with whole systems rather than those portions 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, 1999, 2000; Murray and Parslow, 1999). One specific area that is proving to be crucial is the question of model complexity (O'Neill and Rust, 1979; Silvert, 1981, 1996; Ludwig and Walters, 1985; Costanza and Sklar, 1985; Yool, 1998). IGBEM was built as the foundation for a study of model complexity, to provide a '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 behaviour of IGBEM resembles real temperate coastal systems. Consideration of the biological, ecological, 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 resembles 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 is successful in addressing several issues that afflict the models it was developed from (such as resuspension and using 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 Port Phillip Bay, 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—such as competitive exclusion, keystone groups, spatial self-organisation, shifts in stable state (with and without human induced triggers) and adaptation to changes in ambient conditions. In addition to increasing understanding of system behaviour, developing these models and deciphering their dynamics is extremely useful for locating gaps in understanding of real ecosystems. The prognostic usefulness of such large models may still be under debate, but the learning potential they provide cannot be denied.

Acknowledgements

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Appendix A. Biomass, production and consumption per set for real bays

Values marked with the superscript U or L indicate bays that mark the bounds (upper and lower) of the range for that set in Fig. 5. See Tables A.1–A.7.

Table A.1

Dissolved inorganic nitrogen (DIN), chlorophyll a (chl a) and primary production for real bays

Country	Bay	DIN (mmol DIN m ⁻³)	Chl a (mg chl a m ⁻³)	References
Australia	Albatross Bay	1.8	1.5	Burford et al. (1995)
	Port Phillip Bay	0.8	1.0	Harris et al. (1996); Murray and Parslow (1997)
Brazil	Baia de Guanabara	28.0	57.0	Kjerfve et al. (1997)
	Patos Lagoon	5.6–9.2	2.3–11.3	Abreu et al. (1995)
Canada	Bedford Basin	3.6–21.5	5.7–11.3	Monbet (1992)
India	Cochin Backwater	5.7	6.1	Monbet (1992)
Italy	Palude della Rosa			Carrar and Opitz (1999)
Mexico	Bahia de Los Angeles	1.0–1.5	1.0 ^L –7.0	Delgadillo-Hinojosa et al. (1997)
The Netherlands	Wadden Sea	3.9	7.7	Monbet (1992)
New Zealand	Beatrix Bay	0.2 ^L –1.4	2.0–4.1	Gibbs and Vant (1997)
UK	Firth of Clyde	7.0–9.4	2.0–6.3	Monbet (1992); Bock et al. (1999)

Table A.1 (Continued)

Country	Bay	DIN (mmol DIN m ⁻³)	Chl a (mg chl a m ⁻³)	References
USA	Apalachicola Bay	2.2–5.0	5.4–7.1	Monbet (1992); Mortazavi et al. (2000)
	Buzzards Bay	4.2	8.7	Borkman and Turner (1993)
	Charlotte Harbour	6.6–15.3	4.8–15.2	Monbet (1992)
	Chesapeake Bay	5.5–42.2	9.9–33.7	Monbet (1992)
	Chincoteague Bay	7.5	22.0	Boynton et al. (1996)
	Columbia River	15.3	7.3	Monbet (1992)
	Flax Pond	4.6–5.2	5.5–5.8	Monbet (1992)
	Galveston Bay	16.0	6.9	Santschi (1995)
	Hilsborough	47.1–48.1	13.4–19.3	Monbet (1992)
	Hudson River	33.6–45.6	2.7–23.7	Monbet (1992)
	Isle of Wight Bay	11.0	38.0	Boynton et al. (1996)
	James River	54.3	41.4	Monbet (1992)
	Long Island Sound	8.2	8.6	Borkman and Turner (1993)
	Massachusetts Bay	6.5	3.1	Borkman and Turner (1993)
	Monterey Bay	5.0–10.0	3.0–6.0	Pennington and Chavez (2000)
	Narragansett Bay	4.7–10.2	9.1–10.3	Monbet (1992); Smayda (1983)
	Neuse River	5.0	12.8	Monbet (1992)
	North Inlet	27.0	7.0	Monbet (1992)
	Patuxent River	8.6–63.9	12.3–48.1	Monbet (1992)
	Peconic Bay	2.6	2.9	Turner et al. (1983)
	Potomac River	8.8–119.2 ^U	12.7–78.9	Monbet (1992)
	Rappahanock River	3.4–24.7	4.5–21.7	Monbet (1992)
	Rhode River	10.0–15.3	8.1–150.0 ^U	Monbet (1992); Gallegos et al. (1997)
	San Francisco Bay	4.0–40.9	8.9–25.2	Monbet (1992)
	South River	9.7	16.8	Monbet (1992)
	York River	4.8–4.9	3.3–4.0	Monbet (1992)

Table A.2

Zooplankton biomass, production and consumption for real bays

Country	Bay	Zooplankton (mg AFDW/m ³)	References
Australia	Port Phillip Bay	68.4–68.5	Holloway and Jenkins (1993); Beattie et al. (1996); Murray and Parslow (1997); Fulton and Smith (in press)
Chile	Tongoy Bay	20.0	Wolff (1994)
Denmark	Kattegatt	106.0	Kjørboe and Nielsen (1994a,b)
France	Arcachon Bay	150.0	Poulet et al. (1996)
	Cantabrian Coast	82.4–102.0	Poulet et al. (1996)
	Gironde	43.8	Plounevez and Champalbert (1999)
	Ushant	50.0	Poulet et al. (1996)
	West English Channel	150.0	Poulet et al. (1996)
France/UK	Celtic Sea	200.0	Poulet et al. (1996)
India	Bay of Bengal	36.3	Kumari and Goswami (1993)
Ireland	West Irish Sea	26.9	Dickey-Collas et al. (1996)
Italy	Palude della Rosa	72.7	Carrer and Opitz (1999)
Jamaica	Kingston Harbour	331.0	Hopcroft et al. (1998)
Mexico	Chetumal Bay	10.7 ^L	Gasca and Castellanos (1993)
	Tampamachoo Lagoon	79.2	Rosado-Solorzano and Guzmán del Prío (1998)
	Terminos Lagoon	322.0	Manickchand-Heileman et al. (1998)
The Netherlands	Westerschelde	60.0	Soetaert and Herman (1994)
Philippines	Laguna de Bay	400.0–563.0 ^U	Delos Reyes and Martens (1994)

Table A.2. (Continued)

Country	Bay	Zooplankton (mg AFDW/m ³)	References
Russia	Barents Sea	60.0	Sakshaug et al. (1994)
South Africa	Kromme Estuary	30.0	Heymans and Baird (1995)
Spain	Galicia	125.0	Poulet et al. (1996)
	La Coruna	170.8	Poulet et al. (1996)
Taiwan	Chiku Lagoon	40.8	Lin et al. (1999)
UK	Plymouth	30.0	Harvey (1950)
USA	Chesapeake Bay	71.4–148.0	Park and Marshal (2000)
	Corpus Christi Bay	144.8	Buskey (1994)
	Monterey Bay	28.0	Olivieri and Chavez (2000)
	Narragansett Bay	201.8	Durbin and Durbin (1998)

Table A.3

Fish biomass, production and consumption for real bays

Country	Bay	Total fish (g AFDW m ⁻²)	References
Australia	Albatross Bay	5.5	Blaber et al. (1994)
	Alligator Creek	2.4	Robertson and Duke (1990)
	Botany Bay	1.4	Bell et al. (1984)
	Embley Estuary	15.8	Blaber et al. (1989)
	Groote Eylandt	5.5	Blaber et al. (1994)
	Great Barrier Reef	35.6	Williams and Hatcher (1983)
	Gulf of Carpentaria	2.7	Blaber et al. (1994)
	Moreton Bay	3.1	Morton (1990)
	North West Shelf	>0.47	Sainsbury (1987)
	One Tree	47.6 ^U	Russell (1977)
	Peel-Harvey Estuary	0.5 ^L	Loneragan et al. (1986)
	Port Phillip Bay	3.3	Hall (1992); Parry et al. (1995)
	South East Gulf	2.8	Blaber et al. (1994)
	Western Port Bay	1.2	Robertson (1980)
Bermuda	Bermuda	10.8	Bardach (1959)
Chile	Tongoy Bay	4.6	Wolff (1994)
China	Western Yellow Sea	>0.1	Rhodes (1998)
Crete	Heraklion Bay	9.5	Kallianiotis et al. (2000)
Egypt	Gulf of Aqaba	21.2	Whitfield (1993)
Eritrea	Dahlak Archipelago	7.7	Russell (1977)
France	Port Cros	1.7	Francour (1997)
Hawaii	French Frigate Shoals	29.7	Freidlander and Parrish (1997)
	Hanalei Bay	16.6	Freidlander and Parrish (1997)
	Hawaii	20.4	Russell (1977)
	Hulopoe-Manele	44.6	Freidlander and Parrish (1997)
	Kaneohe Bay	23.8	Freidlander and Parrish (1997)
	Midway Atoll	28.6	Freidlander and Parrish (1997)
	Oahu	20.5–21.0	Freidlander and Parrish (1997)
	Waikiki	5.8	Freidlander and Parrish (1997)
India	Marmugao Bay	1.5	Ansari et al. (1995)
	Aguada Bay	1.1	Ansari et al. (1995)
Indian Ocean	Mayotte	30.9	Letourneur et al. (2000)
	Réunion	21.45	Letourneur (1998)
Italy	Palude della Rosa	2.5	Carrer and Opitz (1999)

Table A.3. (Continued)

Country	Bay	Total fish (g AFDW m ⁻²)	References
Mexico	Huizache-Caimanero Lagoon	2.3	Warburton (1979)
	Tampamachoo Lagoon	1.2	Rosado-Solorzano and Guzmán del Prío (1998)
	Teacapan-Agua Brava Lagoon	2.2	Flores-Verdugo et al. (1990)
	Terminos Lagoon	1.4–2.5	Manickchand-Heileman et al. (1998)
New Caledonia	Barrier reefs	>5.07	Letourneur et al. (2000), Kulbicki et al. (2000)
	Belep Island	23.1	Letourneur et al. (2000)
	Chesterfield Islands	30.8	Letourneur et al. (2000)
	Cooks Reef	39.0	Letourneur et al. (2000)
	East Reefs	15.8	Letourneur et al. (2000), Kulbicki et al. (2000)
	Francais Reef	44.7	Letourneur et al. (2000)
	Fringing reefs	>4.99	Letourneur et al. (2000), Kulbicki et al. (2000)
	Intermediate reefs	>5.87	Letourneur et al. (2000), Kulbicki et al. (2000)
	Lagoon bottoms	>8.41	Kulbicki et al. (2000)
	North Lagoon	2.0	Wantiez (1998)
	Ouvéa	49.2	Letourneur et al. (2000)
	South Reefs	25.9	Letourneur et al. (2000)
New Zealand	Goat Island	11.4	Russell (1977)
	Eniwetok Atoll	10.6	Odum and Odum (1955)
	Laguna de Bay	3.2–4.2	Delos Reyes and Martens (1994)
	Barents Sea	7.9	Sakshaug et al. (1994)
Solomon Islands	Solomon Islands	2.6	Blaber and Milton (1990)
South Africa	Cape of Good Hope	10.9	Whitfield (1993)
	Kromme Estuary	12.4	Heymans and Baird (1995)
	Durban	15.1	Berry et al. (1982)
	Swartvlei Lake	2.7	Whitfield (1993)
Spain/France	Northwest Mediterranean	15.0	McClanahan and Sala (1997)
Taiwan	Chiku Lagoon	47.6	Lin et al. (1999)
Thailand	Sichang Islands	18.3	Menasveta et al. (1986)
	South China Sea	>1.0	Wantiez et al. (1996)
UK	Ardmucknish Bay	>0.88	Gibson et al. (1993)
	Plymouth	2.9	Harvey (1950)
USA	Bathtub Rock	15.1	Quast (1968)
	Biscayne Bay	0.7	Brock (1977)
	Bogue Sound	1.3	Adams (1976)
	Chesapeake Bay	1.2–12.0	Lubbers et al. (1990)
	Corpus Christi	4.9	Whitfield (1993)
	Del Mar	8.3	Quast (1968)
	Horn Island	1.6	Ross et al. (1987)
	Laguna Madre	2.6	Whitfield (1993)
	Monterey Bay	12.4	Russell (1977)
	Mustang Island	1.6–1.65	Russell (1977)
	Papalote Bay	7.6	Quast (1968)
	Santa Barbara Channel	25.5	Love et al. (2000)
	St Andrew Bay	0.6	Whitfield (1993)
	Sth New England	2.0	Russell (1977)
	Whitewater Bay	2.5	Thayer et al. (1987)
USA (Alaska)	Prince William Sound	1.5	Dean et al. (2000)
Virgin Islands	Virgin Islands	35.2	Russell (1977)

Table A.4

Biomass of benthos and meiobenthos, maximum water depth, and total benthic production and consumption for real bays

Country	Bay	Total benthos >1 mm (g AFDW m ⁻²)	Meiobenthos (g AFDW m ⁻²)	References
Australia	Bagot Point	11.4		Edgar and Shaw (1995)
	Barker Inlet	58.0		Edgar and Shaw (1995)
	Cararma Inlet	6.3		Edgar and Shaw (1995)
	Cloudy Lagoon	7.9		Edgar and Shaw (1995)
	Crib Point	7.3		Edgar and Shaw (1995)
	French Island	8.0		Edgar and Shaw (1995)
	Frenchmans Bay	6.0		Edgar and Shaw (1995)
	Lake King	40.0		Edgar and Shaw (1995)
	Parker Point	1.0 ^L		Edgar and Shaw (1995)
	Porpoise Bay	10.3		Edgar and Shaw (1995)
	Port Gawler	76.0		Edgar and Shaw (1995)
	Port Phillip Bay	26.4–33.5	0.2	Poore (1992); Wilson et al. (1993); Wilson et al. (1998); Harris et al. (1996)
	Princess Royal Bay	17.3		Edgar and Shaw (1995)
	Rockingham	14.5		Edgar and Shaw (1995)
	Thomsons Bay	5.4		Edgar and Shaw (1995)
	Western Port Bay	17.3		Robertson (1984); Edgar et al. (1994)
Bermuda	Woodmans Point	2.4		Edgar and Shaw (1995)
	Castle Harbour		1.0	Rudnik et al. (1985)
Canada	Flemish Cap	2.5		Steimle (1985)
	Georges Bank	27.4		Steimle (1985)
	Grand Banks	4.6		Steimle (1985)
	Labrador	2.2		Steimle (1985)
	Nain Bay	45.8		Mills (1975)
	Newfoundland	6.5		Steimle (1985)
	North Nova Scotia	17.5		Steimle (1985)
	Scotian Shelf	2.3		Steimle (1985)
Chile	Tongoy Bay	16.3	1.8	Wolff (1994)
Denmark	Kysing Fjord		0.2	Rudnik et al. (1985)
	Oresund		2.5	Rudnik et al. (1985)
France	Arcachon Bay	5.4		Bachelet et al. (1996)
	Bay of Banyuls-sur-mer	3.3–4.3	87.0	Rudnik et al. (1985); Grémare et al., 1998
	Bay of Brest	19.2		Jean and Thouzeau (1995)
	Bay of Lyon		0.4	Rudnik et al. (1985)
	Etang de Thau Lagoon	43.0		Palomares et al. (1993)
	Gironde Estuary		0.4	Santos et al. (1996)
France/Spain	North West Mediterranean	70.7		McClanahan and Sala (1997)
Finland	Tvarminne		1.5	Rudnik et al. (1985)
Germany	Helgoland Bight		0.4	Rudnik et al. (1985)
	Kiel Bight		0.2	Rudnik et al. (1985)
India	Bay of Bengal		<0.1 ^L	Rudnik et al. (1985)
	Goa		0.2	Rudnik et al. (1985)
Ireland	Irish Sea		0.5	Rudnik et al. (1985)
Iran/Iraq	Tigris and Euphrates Estuary		0.2	Rudnik et al. (1985)
Italy	Adriatic Sea		0.2	Rudnik et al. (1985)
	Palude della Rosa	96.7	10.2 ^U	Carrer and Opitz (1999)
Mexico	Celestun Lagoon	2.6	3.3	Chavez et al. (1993)
	Gulf of Mexico	115.0		Talley et al. (2000)

Table A.4 (Continued)

Country	Bay	Total benthos >1 mm (g AFDW m ⁻²)	Meiobenthos (g AFDW m ⁻²)	References
	Tampamachoo Lagoon	2.0	1.2	Rosado-Solorzano and Guzmán del Prío (1998)
	Terminos Lagoon	14.6	5.2	Manickchand-Heileman et al. (1998)
The Netherlands	Dutch Wadden Sea	16.5		Möller et al. (1985)
	Westerschelde		0.3	Soetaert et al. (1994)
North Sea	Fladen		0.5	Rudnik et al. (1985)
Pacific	Eniwetok Atoll	92.0		Odum and Odum (1955)
Philippines	Laguna de Bay	5.6		Delos Reyes and Martens (1994)
Poland	Gulf of Gdansk	33.3		Drgas et al. (1998)
South Africa	Kromme Estuary	30.5	0.4	Heymans and Baird (1995)
South Orkney	Signy Island		4.5	Vanhove et al. (1998)
Spain	Bay of Cadiz	18.4		Arias and Drake (1994)
	Ria de Arosa		0.2	Rudnik et al. (1985)
	Ria de Muros		<0.1	Rudnik et al. (1985)
Sweden	Baltic Sea	21.0		Möller et al. (1985)
	Bassholm	5.6		Möller and Rosenberg (1982)
	Bothnian Bay		0.3	Rudnik et al. (1985)
	Bothnian Sea	12.8	0.7	Möller et al. (1985); Rudnik et al. (1985)
	Central Baltic		1.2	Rudnik et al. (1985)
	Gota Estuary		0.2	Rudnik et al. (1985)
	Gullmarsvik	2.4		Möller and Rosenberg (1982)
	Kungsbacka		0.1	Rudnik et al. (1985)
	Sandvik	1.6		Möller and Rosenberg (1982)
	Skagerrak	38.0		Möller et al. (1985)
	Swedish Sound	5.2		Möller et al. (1985)
	Sweden	25.4		Pihl-Baden and Pihl (1984)
	West Central Baltic		0.1	Rudnik et al. (1985)
Taiwan	Chiku Lagoon	59.0		Lin et al. (1999)
UK	Clyde Sea		0.2	Rudnik et al. (1985)
	English Channel		0.2	Rudnik et al. (1985)
	Liverpool Bay		0.5	Rudnik et al. (1985)
	Loch Nevis		0.7	Rudnik et al. (1985)
	Lynher Estuary	13.3		Warwick and Price (1975)
	Northumberland Coast		0.3	Rudnik et al. (1985)
	Plymouth	17.0		Harvey (1950)
	Scotland	11.2		Hibbert (1976)
	Southampton	166.0 ^U		Hibbert (1976)
USA	Biscayne Bay	6.4		Brock (1977)
	Block Island Sound	15.8		Steimle (1982)
	Buzzards Bay		0.3	Rudnik et al. (1985)
	Cape Cod Bay		1.0	Rudnik et al. (1985)
	Chesapeake Bay	5.0–50.0		Fredette et al. (1990); Dauer and Alden (1995)
	Chesapeake Bight	10.1		Steimle (1985)
	Christiansem Basin	19.1–23.6		Steimle (1985)
	Long Island Sound		0.6	Rudnik et al. (1985); Vanhove et al. (1998)
	Martha's Vineyard Sound		0.2	Rudnik et al. (1985)
	Massachusetts	24.6		Steimle (1985)
	Narragansett Bay		2.9	Rudnik et al. (1985)
	Nauset Marsh	47.7		Heck et al. (1995)

Table A.4 (Continued)

Country	Bay	Total benthos >1 mm (g AFDW m ⁻²)	Meiobenthos (g AFDW m ⁻²)	References
	New Jersey Shelf	28.0		Steimle (1985)
	New York Bight	7.3–25.1	0.4	Steimle (1985); Rudnik et al. (1985)
	Niantic River		4.5	Rudnik et al. (1985)
	San Francisco Bay	13.3		Heck et al. (1995)
	South Carolina		1.3	Rudnik et al. (1985)
	St Joseph Bay	67.5		Valentine and Heck (1993)

Table A.5

Macrophyte biomass and primary production for real bays

Country	Bay	Total macrophytes (g AFDW m ⁻²)	References
Australia	Port Phillip Bay	1.4–15.1	Chidgey and Edmunds (1997); Murray and Parslow (1997)
	Western Port Bay	167.0	Robertson (1980)
Chile	Tongoy Bay	5.5	Wolff (1994)
France	Etang de Thau Lagoon	94.2	Gerbai and Verlaque (1995)
France/Spain	North West Mediterranean	199.5	McClanahan and Sala (1997)
Italy	Palude della Rosa	168.0	Carrer and Opitz (1999)
Mexico	Celestun Lagoon	35.0	Chavez et al. (1993)
	Tampamachoo Lagoon	10.5	Rosado-Solorzano and Guzmán del Próo (1998)
	Terminos Lagoon	239.0	Manickchand-Heileman et al. (1998)
New Zealand	Otago Harbour	141.2	Grove and Probert (1999)
Pacific Ocean	Eniwetok Atoll	618.2 ^U	Odum and Odum (1955)
Philippines	Laguna de Bay	1.1 ^L	Delos Reyes and Martens (1994)
South Africa	Kromme Estuary	147.9	Heymans and Baird (1995)
Sweden	Gota River Bays	591.3	Pihl et al. (1994)
USA	Chesapeake Bay	33.1–46.6	Murray and Wetzel (1987); Madden and Kemp (1996); Buzzelli et al. (1998)
	Childs River	193.6	Valiela et al. (1992)
	Bass Harbour Marsh	64.6–183.5	Kinney and Roman (1998)
	Branford River	81.4	Welsh (1980)
	Green Hill Pond	164.4	Kinney and Roman (1998)
	Mumford Cove	204.2	Kinney and Roman (1998)
	Ninigret Pond	141.2	Kinney and Roman (1998)
	Quashnet River	74.8	Valiela et al. (1992)
	Sage Lot Pond	31.7	Valiela et al. (1992)
	Waquoit Bay	71.6	Valiela et al. (1995)

Table A.6

Total detritus for real bays

Country	Bay	Total detritus (g AFDW m ⁻²)	References
Australia	Bagot Point	3.2 ^L	Edgar and Shaw (1995)
	Carama Inlet	10.6	Edgar and Shaw (1995)
	Lake King	101.0	Edgar and Shaw (1995)
	Porpoise Bay	4519.0	Edgar and Shaw (1995)
	Port Gawler	331.0	Edgar and Shaw (1995)
	Port Phillip Bay	1731.0–2953.4	Nicholson et al. (1996)
	Rockingham	1659.0	Edgar and Shaw (1995)
	Woodmans Point	1940.0	Edgar and Shaw (1995)

Table A.6. (Continued)

Country	Bay	Total detritus (g AFDW m ⁻²)	References
French Polynesia	Tiahura	677.5	Ariasgonzalez et al. (1998)
Italy	Palude della Rosa	750.4	Carrer and Opitz (1999)
Mexico	Terminos Lagoon	12.7	Manickchand-Heileman et al. (1998)
South Africa	Kromme Estuary	3000.0	Heymans and Baird (1995)
Taiwan	Chiku Lagoon	48.6	Lin et al. (1999)
USA	Chesapeake Bay	10417.0 ^U	Roden and Tuttle (1996)

Table A.7

Biomass and primary production of microphytobenthos for real bays

Country	Bay	Microphytobenthos (mg chl a/m ²)	References
Australia	Peel-Harvey Estuary	295.0 ^U	MacIntyre et al. (1996)
	Port Phillip Bay	25.0–51.7	Murray and Parslow (1997)
Canada	Bay of Fundy	255.0	Hargrave et al. (1983)
France	Golfe de Fos	38.0	MacIntyre et al. (1996)
	Mediterranean Coast	44.0	Schreiber and Pennock (1995)
Madagascar	Madagascar	58.0	Schreiber and Pennock (1995)
The Netherlands	Dutch Wadden Sea	220.0–225.0	Cadée and Hegeman (1977); MacIntyre et al. (1996)
	Ems-Dollard Estuary	65.0–282.5	Colijn and de Jonge (1984); MacIntyre et al. (1996)
	Lake Grevelingen	215.0	MacIntyre et al. (1996)
Russia	Vostok Bay	135.0	MacIntyre et al. (1996)
South Africa	Kromme Estuary	1.6 ^L	Heymans and Baird (1995)
Spain	Ria de Arosa	66.5	MacIntyre et al. (1996)
Sweden	Laholm Bay	24.5	MacIntyre et al. (1996)
	Oresund	75.5	Schreiber and Pennock (1995)
USA	Bolsa Bay	285.0	Schreiber and Pennock (1995)
	Boston Harbour	190.0	MacIntyre et al. (1996)
	Buzzards Bay	52.5	MacIntyre et al. (1996)
	Chesapeake Bay	35.0	MacIntyre et al. (1996)
	Chukchi Sea	73.5–180.0	Matheke and Horner (1974); MacIntyre et al. (1996)
	Delaware Estuary	122.5	MacIntyre et al. (1996)
	Graveline Bay	215.0	MacIntyre et al. (1996)
	Long Island Sound	113.5	MacIntyre et al. (1996)
	Netarts Bay	162.5	MacIntyre et al. (1996)
	North Inlet	65.0–70.0	MacIntyre et al. (1996)
	Potter Pond Lagoon	235.0	MacIntyre et al. (1996)
	San Antonio Bay	8.0–29.5	MacIntyre et al. (1996)
	Weeks Bay	15.6	Schreiber and Pennock (1995)

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