

## Effects of spatial resolution on the performance and interpretation of marine ecosystem models

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Received 8 January 2003; received in revised form 2 September 2003; accepted 27 October 2003

### Abstract

Simplifying models by using coarse spatial resolution can be desirable because it reduces structural, computational and data requirements and can make model interpretation easier. However, spatially simplified models may be incapable of reproducing important dynamics observed in nature. To consider this issue the effect of spatial structure on the output of two trophic ecosystem models (Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM)) was considered using a theoretical approach known as ‘deep–shallow model’ comparison. This involved comparing simulation runs of 1-, 3-, and 8-box versions of the ecosystem models (the ‘shallow’ models) with a 59-box version that was used to represent the real world (the ‘deep’ model). The results indicate that simpler spatial configurations (geometries) can result in less short-term variation, changes in predicted spatial patterns and trophic self-simplification (loss of functional groups), as the opportunity for spatial refuges is reduced. More importantly, models with very little spatial resolution (i.e. 1- and 3-box models) do not capture the effects of changes in nutrient loads or fishing pressure as well as more complex models. The results for the 8-box models used here indicate that some simplification is acceptable, as overall model performance is not overwhelmed by the impacts of trophic self-simplification and a loss of spatial heterogeneity. However, using models with very little spatial resolution (i.e. 1- and 3-box models) can be misleading, as the impacts on system dynamics of the reduced heterogeneity increase.

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**Keywords:** Spatial structure; Biogeochemistry; Ecosystems; Models

### 1. Introduction

Spatial structure and scale have been an important focus of ecology for many years (Huffaker, 1958; MacArthur and Wilson, 1967; Levins, 1970; Maynard Smith, 1974; Weins, 1989; Levin, 1992; Rhodes and Chesser, 1996; Keitt, 1997). It has been found that the

scale of observations can have substantial impacts on the processes observed and how they are interpreted. For example, the generality of rocky shore intertidal communities shaped by keystone predators (Paine, 1966) or competitive hierarchies (Connell, 1961) may be reinterpreted when the influence of large-scale hydrodynamics and larval transport are considered (Roughgarden et al., 1988). Model studies have also found that the inclusion of the spatial dimension is important as it can allow for the production of more realistic dynamics (Sharov, 1996) and prevent extinc-

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tion (Nisbet and Gurney, 1976; Gurney and Nisbet, 1978; Keitt, 1997; Johnson and Seinen, 2002) or competitive exclusion (Skellam, 1951; Hassell et al., 1994; Johnson, 1997; Johnson and Seinen, 2002), by providing refugia.

In the application of numerical models, enhanced spatial resolution generally requires more data for model construction, parameterisation, calibration and validation, and can lead to vast increases in computing time. These issues have often led to models being built and applied to natural systems at point locations (e.g. Balsfjord Norway, Bax and Eliassen, 1990), or to the use of geometries that summarise large areas by a small number of boxes (e.g. ERSEM I, Baretta et al., 1995). While there may be clear benefits of this approach, it can be hard to discern any consequences of the use of a restricted geometry if only a single representation is employed. Studies that consider the application of the same model, or similar versions of a model (e.g. ERSEM I versus ERSEM II, Baretta et al., 1995; Baretta-Bekker and Baretta, 1997), to multiple geometries can be quite informative. For example, Murray (2001) found sufficient shared features between models applied on alternative spatial scales that simpler models could be used as a design tool for effective development of larger, more spatially detailed models. However, the same study emphasises that the similarities between predictions made by the two models break down as nutrient loading changes.

The majority of research into the effects of spatial structure on the stability and behaviour of models has concentrated on relatively simple trophic assemblages (Donalson and Nisbet, 1999) or substantial abstractions (Leibold, 1996). Recently, international treaties and national legislation have focused attention on responsible ecosystem management, and as a result ecosystem models have become more popular. It is not clear whether findings for simpler ecological models hold for large ecosystem models, which have reticulated webs, mass conservation and more realistic assumptions. In an attempt to clarify this issue, two ecosystem models (Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM)) were implemented on four different geometries. This allowed the evaluation of logistic (sampling and computational demands) and ecological impacts at the various scales.

## 2. Methods

The output of two trophic ecosystem models, Bay Model 2 (BM2) (Fulton et al., submitted-a) and the IGBEM (Fulton et al., submitted-b), are used to consider the effects of spatial structure on model behaviour and the conclusions that can be drawn from the model output. The approach employed in this study is the ‘deep–shallow model’ comparison, in which a complex 59-box simulation model (IGBEM) that incorporates complex processes thought to occur in nature, acts as an artificial world or deep ‘baseline’ against which the performance of other (simpler ‘shallow’) models are compared. A great advantage of this approach is that it allows the modeller to begin with a detailed, but validated, model and then simplify it to determine the effect of those simplifications on model behaviour, and identify parsimonious models. Importantly, this approach separates those parts of the model complexity issues concerned with model structure from those of the accuracy and precision of sample data, as it deals with perfect knowledge. The research discussed here considers only the effect of model formulation on behaviour and does not attempt to consider effects of data uncertainty. It is also important to note that in the work discussed here the models are not being used as a simulated replica of any one system. For convenience they do utilise the physics of a particular Australian bay (Port Phillip Bay, Melbourne), but they are actually being used to create a hypothetical system that has the general ecological structure and dynamics typical of most temperate bays. As BM2 and IGBEM have been found to realistically reproduce the behaviour of real shallow marine ecosystems (Fulton et al., submitted-a,b) the results for the hypothetical system modelled here should generalise to real marine bays.

BM2 and IGBEM were developed explicitly as a basis for this ‘deep–shallow model’ comparison. They cover many of the same processes and use very similar trophic webs (Fig. 1), but the formulations used in each case differ greatly in the amount of physiological detail incorporated. A brief overview of the models follows, and a summary of the major assumptions of the two models is given in Table 1. More detailed descriptions of the formulation of the models is beyond the scope of this paper and are given in Fulton et al. (submitted-a,b).

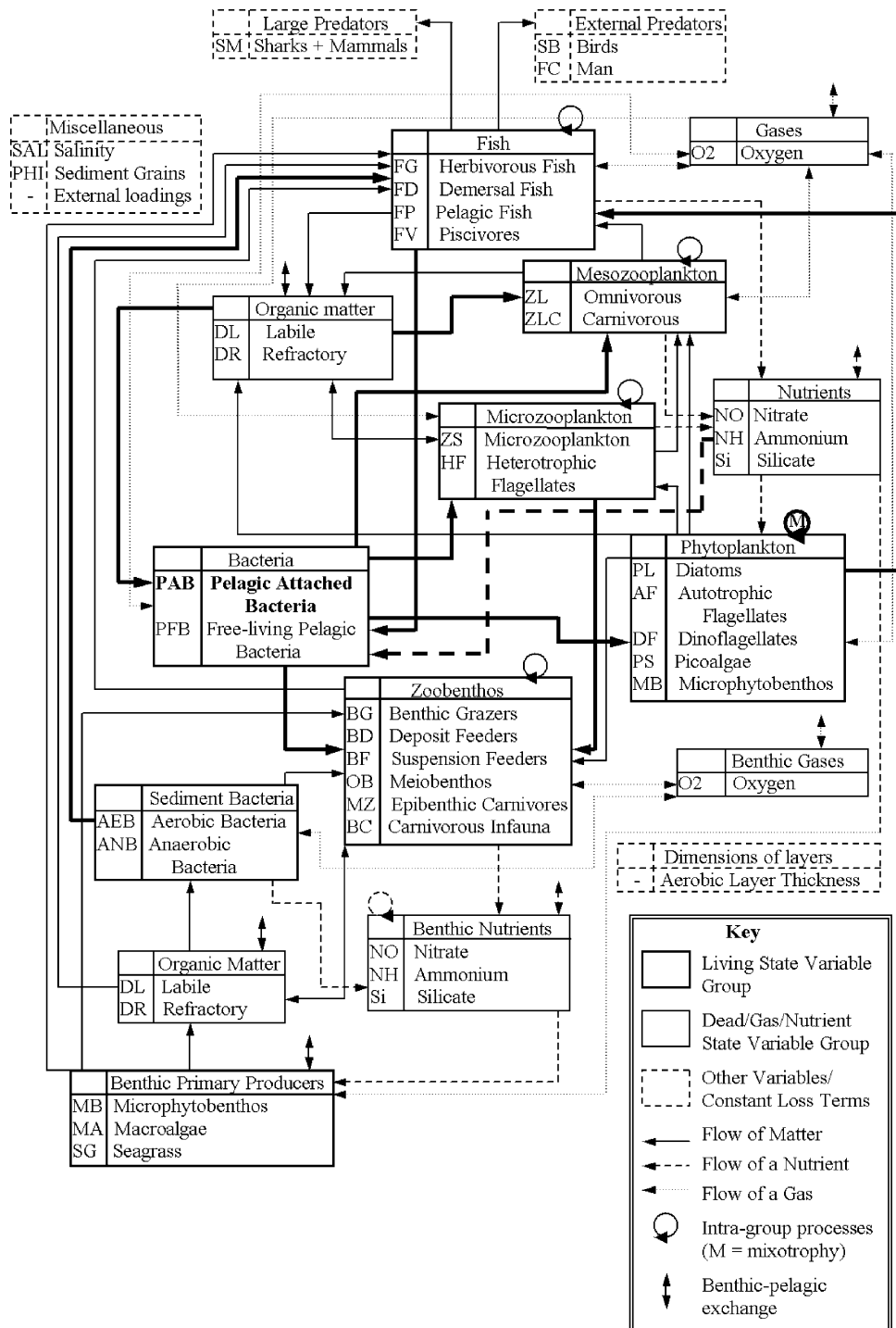


Fig. 1. Trophic webs of Bay Model 2 (BM2) and the IGBEM. Flows marked in bold, and pelagic attached bacteria, are features of the web in BM2 that are not present in IGBEM.

Table 1

Comparison of the underlying assumptions and formulations of the standard implementations of Bay Model 2 (BM2) and the IGBEM

Feature	BM2	IGBEM
<b>General features</b>		
Numerical integration scheme	Simple forward difference method	Simple forward difference method
Biological time step	Adaptive <sup>a</sup>	Adaptive <sup>a</sup>
Overall time step (physics and biology)	Daily <sup>b</sup>	Daily <sup>b</sup>
Vertical structure	Single water column, epibenthic and sediment layer in each box	Single water column, epibenthic and sediment layer in each box
Biomass units	mg N m <sup>-3</sup>	mg m <sup>-3</sup> of C, N, P, Si
Input forcing	Nutrients and physics on interannual, seasonal, and tidal frequencies	Nutrients and physics on interannual, seasonal, and tidal frequencies
Level of biological detail	Functional group (defined based on organism size and feeding guild)	Functional group (defined based on organism size and feeding guild)
<b>Process related</b>		
Bioturbation and bioirrigation	Yes	Yes
Consumption formulation	Logistic (Holling type II)	Mixed: logistic (Holling type II) or sigmoid (Holling type III)
Formulation detail	General equations: only growth, mortality and excretion explicit	Physiologically resolved equations: the processes of assimilation, basal/activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit for each group
Light limitation	Optimal irradiance fixed	Phytoplankton can acclimate to ambient light levels
Mixotrophy	Dinoflagellates	None
Nutrient limitation	External nutrients determine uptake	Internal nutrient ratio determines nutrient uptake and disposal
Nutrient ratio	Redfield	Internal specific nutrient ratio
Oxygen limitation of demersal fauna	Yes	Yes
Sediment burial	No	Yes
Sediment chemistry	Dynamic, with sediment bacteria	Empirical, sediment bacteria are a tracer only
Shading of primary producers	Yes	Yes
Spatial structure	Flexible with the potential for multiple vertical and horizontal cells	Flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	Yes	Yes
Transport model used for hydrodynamics flows <sup>c</sup>	Yes	Yes
<b>Model closure</b>		
Top predators represented by static loss terms	Yes	Yes
Linear mortality terms	Yes	Yes
Quadratic mortality terms	Yes	No
<b>Fish and fisheries related</b>		
Age structured fish	9 age classes	9 age classes
Fishery discards	Target species only	Target species only
Invertebrate fisheries	Yes	No
Stock–recruit relationship	Constant recruitment	Constant recruitment
Stock structure	External: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock	External: reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock

<sup>a</sup> Nominally daily, but it is reduced so that fluxes into and out of the component with the fastest turnover rates remain stable. The size of the adaptive time step is set so that the relative change in any variable does not exceed a specified tolerance.

<sup>b</sup> Smaller adaptive time steps are repeated until a 24-h period has accumulated, then the physical mixing processes are performed as a part of the overall daily model time step.

<sup>c</sup> Flows between boxes represent the effects of advection and diffusion and are calculated from particle tracking performed in a highly spatially resolved, three dimensional, non-linear, variable density hydrodynamic model. The hydrodynamic model gives the concentrations of passive tracers given inputs of water, salt, heat and passive tracers, and forcing by wind, atmospheric pressure gradients and tides.

IGBEM is a physiologically explicit biogeochemical process model, which follows the carbon, nitrogen, phosphorus and silicon pools of 7 primary producer groups (3 benthic, 4 planktonic), 4 zooplankton groups, 3 infaunal groups, 3 epifaunal groups, 3 bacterial groups and 4 fish groups. It was constructed from the biological groups of the European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al., 1995; Baretta-Bekker and Baretta, 1997) and the physical and biogeochemical submodels of the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow, 1997, 1999). This framework was then extended to cover benthic biological groups omitted from ERSEM II (those in the benthic primary producer subweb). This level of process and trophic detail is at the upper bound of what is normally employed in ecosystem models (e.g. SSEM, Sekine et al., 1991 and ERSEM II, Baretta-Bekker and Baretta, 1997) and it makes IGBEM one of the most detailed biogeochemical ecosystem models constructed.

BM2 was developed from IGBEM by replacing the physiologically based process equations used for each of IGBEM's trophic groups with formulations of the form used in PPBIM. Consequently, in BM2 physiological processes are not modelled explicitly, but are represented by generalised equations for assimilation and waste production (Fulton et al., submitted-a). In addition, BM2 models only the nitrogen components and relies on Redfield ratios, rather than internal nutrient ratios, to determine the form of nutrient dependent activities (such as the growth of primary producers). This level of detail is more representative of most existing models of eutrophication and water column trophic dynamics (Fransz et al., 1991).

The focus of this work is the effect of simplifying spatial resolution on model results and so in this context both of the 59-box models (of BM2 and IGBEM) can be considered deep models. In addition, because BM2 and IGBEM include the same trophic groups and physical details (vertical layering, transport, mixing and spatial geometry) but differ in the degree of process detail used in their formulation (Table 1), BM2 may also be treated as a 'shallow' model (in comparison with IGBEM). This means the trade-offs associated with employing less physiological detail in a marine ecosystem model can also be evaluated.

The transport model used as the physical basis of BM2 and IGBEM can be applied on any geometry

(any number of boxes). Fluxes between the boxes represent the effects of advection and diffusion and are derived from particle tracking in a finely resolved three-dimensional non-linear, variable density hydrodynamics model (Walker, 1999). The standard geometry used during the development and validation of BM2 and IGBEM was a 59-box configuration (Fig. 2a). As the basis for the study reported here, the runs performed on this 59-box geometry were taken as a 'baseline' against which runs performed on 8-, 3- and 1-box equivalents (Fig. 2b–d) were compared. These alternative geometries were selected as they reflect the higher order zonation seen in the bay underlying the physical model adopted for this theoretical study. Flows for these geometries were determined by summing over the flows between boxes in the 59-box version. All geometries used in this study had a single water column, epibenthic and sediment layer per box. This level of vertical simplification is typical of marine ecosystem models of this form. Vertical processes that may be affecting flows are, accounted for in the hydrodynamics model, used to derive the flows between boxes. The models also use a daily time step, which is much longer than the processes involved in the turnover of the water column in well mixed coastal systems such as Port Phillip Bay.

The same physical forcing (e.g. light and nutrient inputs), 20-year run time and two-weekly record period were used in all models. The same parameter set was generally used for all model runs. The majority of parameters did not require adjustment as the processes they were associated with (e.g. rates of assimilation) did not alter across the geometries. Explicit migration by the fish groups was adjusted so that it was equivalent across the geometries. Migration of each fish group is represented by prescribed migration matrices, that define the proportion of the population in each box in each quarter, and the migration submodel interpolates between these matrices to allow a smooth transition from one distribution to the next. The matrices employed for the geometries using fewer boxes were constructed by summing across the proportions used in the 59-box model. To check for discrepancies due to applying the interpolation procedure to different geometries, the summation applied to the parameter matrices was applied to the interpolated matrices at each step. In each case, the total proportions in an area matched across all spatial geometries. It is recog-

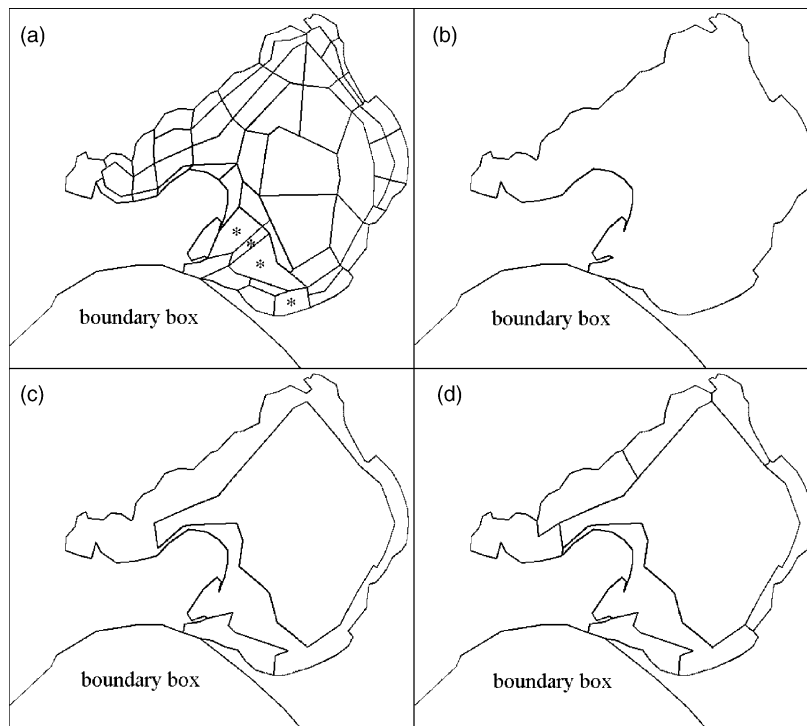


Fig. 2. Maps of the geometries used with the models: (a) 59-boxes, (b) 1-box, (c) 3-boxes, and (d) 8-boxes.

nised that while the use of density- and forage-based fish movement in place of prescribed migration does not alter behaviour of the 59-box versions of IGBEM and BM2 (Fulton, 2001), this may not be the case for the other geometries and consideration of this issue is currently underway.

Apart from the migration matrices, the only retuning of model parameters was to correct for numerical instabilities that arose for some groups in BM2 (which can be sensitive to environmental conditions; Fulton et al., submitted-a). The groups concerned were the metazoan infauna (meiobenthos, deposit feeders and benthic infaunal carnivores), and the planktivorous and demersal herbivorous fish. These groups became unstable as a result of the altered dynamics of their predators or prey on the alternative geometries. The growth and mortality parameters of these groups causing the numerical instability were recalibrated until stability was achieved, with the restriction that the final values for the parameters must remain within the range of empirical estimates reported in the literature. For the fish groups, recalibrating the growth and mortality param-

eters to achieve stability on the 8-box geometry (by lowering the growth parameters by 20–30% of the magnitude of uncertainty and setting the mortality rates to their lowest recorded values) produced a parameter set that did not require further retuning for the 3- and 1-box geometries. In contrast, the metazoan infauna groups had to undergo further calibration with each change in spatial resolution. For each of the metazoan infauna groups the growth rates had to be increased and the mortality rates decreased, as the spatial resolution became coarser. The size of the required changes was also related to the physical size of the animal and its position in the food web. The parameters for the meiobenthos, which are small and at the base of the infauna food web, required the largest changes (changing by 38–60% of the magnitude of uncertainty), while the larger benthic deposit feeders and benthic infaunal carnivores did not require as much recalibration (their values changed by only 1–55% and 9–16.5% of the magnitude of uncertainty, respectively).

Work done during model development had shown that between 10 and 15 years was required for the

models to equilibrate (Fulton, 2001). Hence, only the final 4 years of the full 20-year simulations were used to judge the model performance as this removes the chance of confounding due to transient dynamics produced by initial conditions. Relative production, consumption and biomasses, or the coefficients of variation of these measures, were found to be the most useful way of comparing model behaviour across the different geometries. To check for consistency in the results across varying anthropogenic pressures, the runs were repeated when fishing pressure or nutrient load was increased or decreased fivefold. These levels of change were selected as they reflect the order of change seen in real exploited ecosystems and because they are known to substantially perturb the standard 59-box configuration of the models.

### 3. Results

#### 3.1. Smoothing of local variation

Comparing the coefficient of variation for the time-series of any of the groups or processes with short turnover times (e.g. chlorophyll *a*) across the various model geometries indicates that decreased spatial resolution reduces short-term fluctuations regardless of the model chosen (Fig. 3). This effect is clearest close to point source inputs. There is also a decrease in

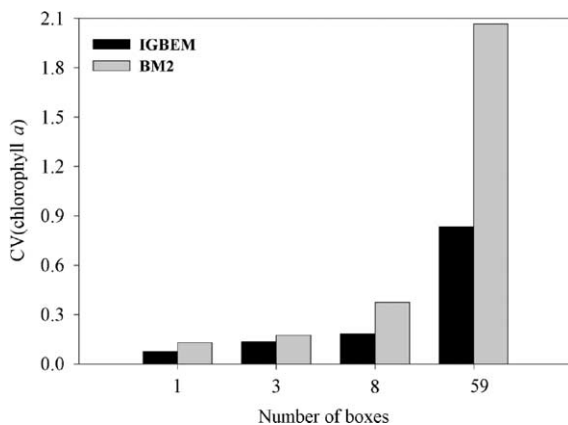


Fig. 3. Variance of chlorophyll *a* in the box receiving strong point source inputs over the final 4 years of the 20-year runs for different levels of spatial resolution in the Bay Model 2 (grey bars) and IGBEM (black bars) models (1–59 boxes).

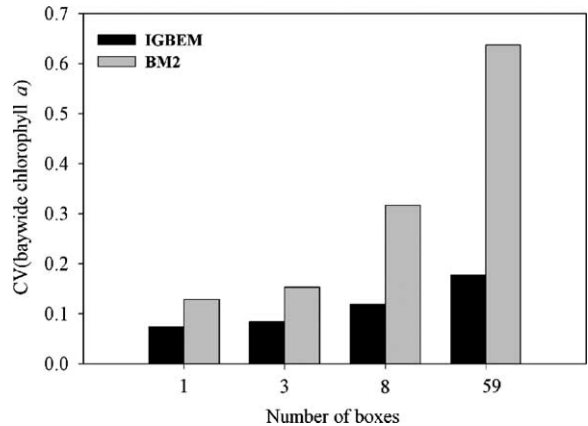


Fig. 4. Variance in the bay-wide average chlorophyll *a* over the final 4 years of the 20-year run for different levels of spatial resolution in the Bay Model 2 (grey bars) and IGBEM (black bars) models (1–59 boxes).

the variation of bay-wide averages with coarser spatial resolution, but three to four times smaller (Fig. 4). The effect of spatial resolution on the variability in the chlorophyll estimates is lower at bay-wide scales as local variations cancel out or are diluted by less variable behaviour in boxes further from input sources. Dilution of inputs is also why variation is lower on the more spatially aggregated geometries. Comparing the response of the two models, it is apparent that the effects of spatial aggregation are stronger for BM2 than IGBEM, particularly at the bay-wide scale.

#### 3.2. Self-simplification

Potentially the most important effect of the use of differing geometries is that the simpler geometries may not support the same food web as the 59-box case. In both models trophic self-simplification (i.e. loss of functional groups) occurs when using the simpler geometries (Table 2). In the water column groups, this simplification is illustrated by the dependence on boundary condition reseeding of the affected groups (they persist only in the southern most boxes and their patterns of change are strongly tied to the tidal forcing across the bay mouth). Within the benthos, simplification results in the effective extinction of several groups (with the biomass dropping to <0.00001% of the value in the 59-box model). In some cases the effect of reduction in spatial structure is obvious even



Table 2

Persistence of the trophic groups in runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM) using 8-, 3- and 1-box geometries

Trophic group	BM2			IGBEM		
	8-box	3-box	1-box	8-box	3-box	1-box
Diatoms	Y	Y	Y	Y	Y	Y
Picophytoplankton	Y	BC	BC	D	D	D
Autotrophic flagellates	Y	Y	Y	BC	BC	BC
Dinoflagellates	BC	BC	BC	Y	Y	Y
Heterotrophic flagellates	BC	BC	BC	BC	BC	BC
Microzooplankton	Y	Y	D	D	D	D
Large omnivorous zooplankton	Y	Y	Y	Y	Y	Y
Large carnivorous zooplankton	Y	Y	Y	Y	Y	Y
Pelagic attached bacteria	Y	Y	D	–	–	–
Pelagic free bacteria	BC	BC	BC	Y	Y	Y
Planktivorous fish	Y	D	D	Y	Y	Y
Piscivorous fish	Y	D	D	Y	D	D
Demersal fish	Y	D	D	D	D	D
Demersal herbivorous fish	Y	Y	D	Y	D	D
Microphytobenthos	BC	BC	BC	BC	BC	BC
Macroalgae	R	NO	NO	R	NO	NO
Seagrass	Y	Y	D	Y	Y	Y
Aerobic bacteria	D	D	D	D	D	D
Anaerobic bacteria	D	D	D	D	D	D
Meiobenthos	D	NO	NO	NO	NO	NO
Benthic deposit feeder	R	Y	NO	Y	Y	Y
Benthic infaunal carnivores	R	Y	NO	Y	Y	Y
Benthic filter feeders	Y	D	Y	R	Y	Y
Benthic herbivorous grazers	Y	Y	D	Y	Y	Y
Macrozoobenthos	Y	Y	Y	Y	Y	Y

The state of a trophic group after 20 simulated years are indicated by: Y: wide spread and as abundant as in the 59-box geometry; R: restricted in distribution compared with the 59-box geometry; BC: persists only because of continual reintroduction from the boundary box (see Fig. 2); D: >75% reduction in abundance; and NO: decline to bay-wide extinction. Note that pelagic attached bacteria are not present in IGBEM.

on the 8-box geometry, while other groups show restricted distribution in the 8-box case and only undergo bay-wide extinction in the 3- and 1-box runs (e.g. macroalgae; Fig. 5).

The self-simplification of the food web is not as strong across both models. IGBEM loses half as many groups as does BM2 for the same reduction in spatial resolution. The groups lost from IGBEM are also lost from BM2 except for autotrophic flagellates, which shows no reduction in abundance in BM2 irrespective of the spatial resolution employed. It is worth noting that the groups that are lost are all from the lower to mid-trophic levels, and are generally either microscopic or infauna (Table 2). The single exception is macroalgae, which is replaced by seagrass on the simpler geometries.

Even those groups that are not totally displaced on the coarser geometries may show significant depletion (Table 2), as they can no longer partition resources with competitors or easily find spatial refuges from predators. The geometries with coarser spatial resolution have more homogeneous physical conditions, as gradients in depth, nutrients and hydrodynamic properties across the bay are reduced or removed. The reduction in the size of these gradients affects the outcome of local interactions and partitioning of resources becomes less likely. In addition, the models use differential equations and so, without lags imposed by spatial structure, groups cannot escape the influence of their predators or competitors. It may be possible to reparameterise the models on the simpler geometries to reduce the impact of preda-



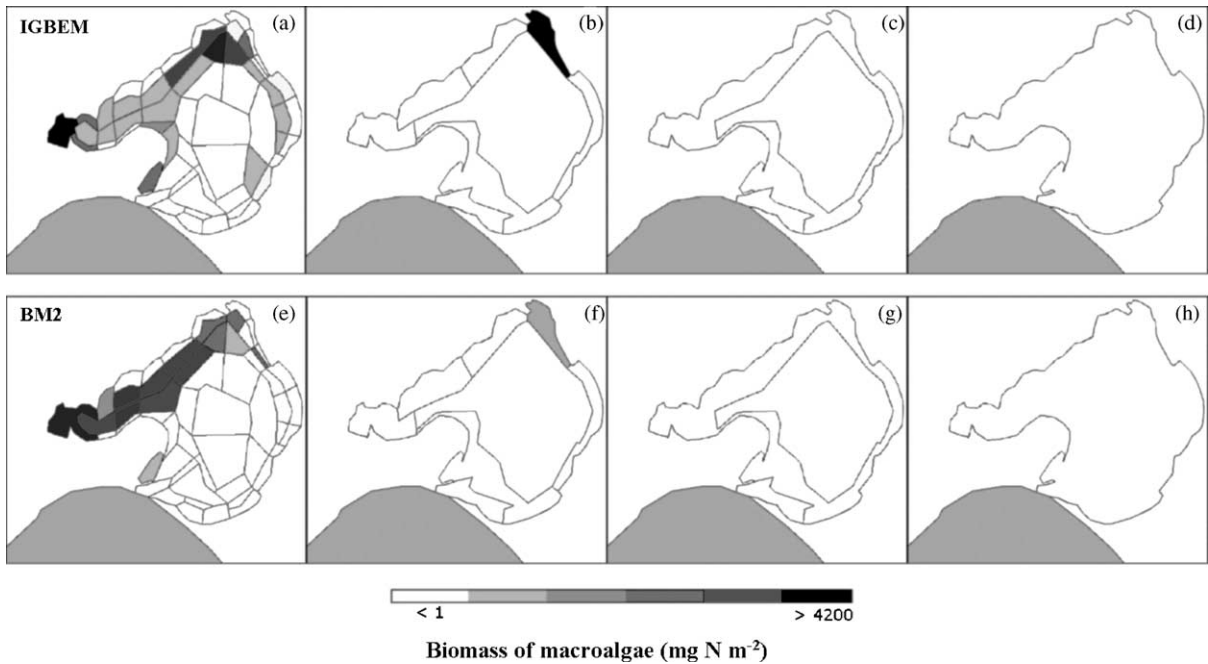


Fig. 5. Effects of spatial resolution on self-simplification. This example shows that the distribution of macroalgae is contracted to the point of extinction with decreasing spatial resolution. The maps show the distribution of macroalgal biomass ( $\text{mg N m}^{-2}$ ) on day 6594 of the run for each geometry of the IGBEM and Bay Model 2 (BM2) models. (a) to (d) are the macroalgal biomass predicted by the different version of IGBEM; (a) 59-boxes, (b) 8-boxes, (c) 3-boxes, and (d) 1-box. (e) to (h) are the macroalgal biomass predicted by the different version of BM2; (a) 59-boxes, (b) 8-boxes, (c) 3-boxes, and (d) 1-box.

tors, but as there are no “competition parameters” per se (rather groups deplete resources that may also be depleted by other groups), competitive exclusion on the coarser geometries cannot always be reasonably prevented in this way. For instance, without allowing parameter values to range far beyond those reported in the literature, no acceptable parameter set for IGBEM could be found that allowed for the co-existence of meiobenthos and benthic deposit feeders on the coarser geometries while maintaining the overall form of the biological system being modelled. This is because the groups do not only interact with each other but with other members of the web too and so any reparameterisation to allow for the presence of meiobenthos and benthic deposit feeders required changes throughout large portions of the food web (all the benthic groups, as well as the pelagic groups that interact with the benthos) to the point that a substantially different biological system is being represented (with different food availabilities and linkage strengths).

### 3.3. Bay-wide estimates

Those groups that are removed or depleted by self-simplification of the food web on coarser geometries obviously do not have similar biomass estimates across all model geometries. Within the groups that do remain, several display a relatively constant average biomass irrespective of the geometry employed. Large carnivorous zooplankton in BM2 is one example, with its mean biomass varying by less than 2% across the geometries. In contrast, others increase substantially. For example, the biomass of autotrophic flagellates in BM2 increases by 145–160% in the run using 1-box compared with the run using a 59-box geometry. While the change in the biomass of the predators and competitors of the autotrophic flagellates does contribute a little to this increase, the majority of the increase is actually a result of an increase in influence of the boundary condition box (shown in Fig. 2) on the large central areas of the bay in the less spatially resolved geometries. In the 59-box model there are a

set of shallow boxes across the bay mouth (marked with \* in Fig. 2a) that prevent large scale transfers between the bay centre and the boundary condition box. With the loss of spatial resolution this blockage is removed and the effects of the boundary box penetrate further into the bay. Modifying the values given in the boundary box so that their effect on the dynamics of the model are decreased does mitigate the problem, but does not completely solve it. This problem is exemplified by the autotrophic flagellates in the 1-box version of BM2, where there is a strong bifurcation in behaviour. Either a non-zero boundary condition is employed and the group is present at elevated levels, or the boundary condition is set to zero and the group is eventually lost from the system.

The effect of changes in biomass on higher level aggregated measures (such as those in the lower half of Table 3) can vary from minor to substantial. Generally, the performance of IGBEM was relatively consistent across all geometries, with most estimates for the 1-, 3- and 8-box models being within a twofold range of those for the 59-box model. In contrast, the performance of BM2 shows progressive deterioration when using the 1-, 3- and 8-box models, with the per-

centage of estimates outside a twofold range of the 59-box model values rising from 31% for the 8-box model to 63% for the 1-box model (Table 3). Notably, total benthic primary production (BPP), sediment bacteria and denitrification are too low when using fewer boxes in either model. These failures are pronounced as they are closely linked: low levels of BPP result in lower levels of detritus, which in turn means that there is less bacterial activity and lower rates of denitrification. The decline in BPP is due to a number of factors. The shape of the BPP-light availability function across the model geometries is such that a reduction is inevitable (due to Jensen's Inequality (Chesson, 2000)). However, by itself it does not account for the full drop observed, which is also partly due to the change in community structure (the macroalgae is lost), flushing rate (and the impact that has on nutrient levels) and trophic interactions between the groups that feed on the benthic primary producers and the other groups in those food webs. This complicated mix of processes and interactions is why the pattern of decline is not straight forward (e.g. the value given for BPP in the 1-box version of IGBEM is closer to the value in the 59-box model than the values in the 3- and 8-box

Table 3

Relative (value from the lower geometry run/value from the 59-box run) biomass, production and consumption for the runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM) on the smaller geometries

	BM2			IGBEM		
	1-box	3-box	8-box	1-box	3-box	8-box
Bay-wide average biomass						
Chlorophyll a	1.26	1.69	1.59	1.11	1.34	1.05
Zooplankton	0.76	1.18	0.93	0.92	0.93	0.92
Fish	<b>0.27</b>	<b>0.44</b>	0.64	0.76	1.20	1.73
Benthic primary producers	<b>0.42</b>	1.29	1.04	0.77	<b>0.23</b>	0.64
Benthos	<b>0.02</b>	<b>2.84</b>	<b>3.56</b>	1.09	0.83	1.03
Infauna	<b>0.00</b>	<b>2.96</b>	<b>3.73</b>	1.09	0.83	1.03
Epifauna	<b>0.40</b>	0.69	0.55	1.02	0.80	0.78
Pelagic bacteria	1.57	0.98	1.04	0.56	0.63	0.72
Sediment bacteria	<b>0.09</b>	<b>0.09</b>	<b>0.33</b>	<b>0.19</b>	<b>0.23</b>	<b>0.26</b>
Bay-wide annual totals						
Denitrification	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	<b>0.02</b>	<b>0.06</b>	<b>0.13</b>
Water column primary production	1.03	1.30	1.01	2.87	1.97	0.74
Benthic primary production	<b>0.03</b>	<b>0.27</b>	<b>0.14</b>	<b>0.54</b>	<b>0.26</b>	<b>0.34</b>
Water column secondary production	1.56	1.53	1.08	1.22	0.90	0.81
Benthic secondary production	<b>0.02</b>	1.11	0.80	1.06	0.97	0.61
Water column consumption	1.45	1.47	1.08	1.10	0.88	0.79
Benthic consumption	<b>0.09</b>	0.79	0.94	1.11	1.08	0.64

Any entries in bold signify a difference of more than twofold between the simpler geometry and the 59-box case.

models). This combination of factors also means that changes in the aggregate measures due to reductions in spatial structure are not consistently larger or smaller than those due to parameter uncertainty. Some measures (e.g. denitrification, BPP in BM2) are much more heavily impacted by spatial structure than parameter uncertainty, while the reverse is true for other groups (e.g. zooplankton), and others see a similar magnitude of change in both cases (e.g. BPP in IGBEM).

### 3.4. Spatial zonation

The physical characteristics of each cell are increasingly ‘smeared’ as spatial resolution is decreased.

As a consequence, there is less gradient in community structure and processes from the edge to the centre, and from the north to the south of the modelled bay. As a result, the biological assemblages that demarcate distinctive ‘edge’ and ‘central’ assemblages in the 59-box case are less clear in the 3- and 8-box geometries. On the coarser geometries, the microfauna (planktonic groups, meiobenthos and microphytobenthos) either become ubiquitous or are lost entirely. Only the epifauna and larger infauna retain any semblance of the ‘edge’ versus ‘central’ zonation, but even their distribution is over-stated on the coarser geometries due to the low level of spatial resolution.

Table 4

Groups demonstrating different responses to spatial structure under alternative amounts of fishing and nutrient loads in Bay Model 2

Conditions	Change in response to spatial structure	Groups
Increased fishing pressure	Macrophyte barren cycle → constant D → BC Y → BC	Seagrass (8, 3) Microzooplankton (1) Microzooplankton (8, 3)
Decreased fishing pressure	BC → D D → Y More widespread Y → BC Y → D Y → D Y → D Y → D Y → D Y → NO	Picoalgae (3, 1) Planktivorous fish (3) Seagrass (8, 3) Diatoms (3) Picoalgae (8) Piscivorous fish (8) Demersal herbivorous fish (3) Benthic infaunal carnivore (3) Benthic filter feeder (8, 1) Benthic deposit feeder (3)
Increased nutrient loading	BC → Y D → Y D → Y More widespread R → Y R → Y R → Y Y → BC Y → R	Dinoflagellates (8, 3, 1) Meiobenthos (8) Anaerobic bacteria (8, 3) Seagrass (8, 3) Macroalgae (8) Benthic deposit feeder (8) Benthic infaunal carnivore (8) Picoalgae (8) Benthic filter feeder (8)
Decreased nutrient loading	D → Y R → Y Y → D Y → NO	Meiobenthos (8) Benthic deposit feeder (8) Herbivorous demersal fish (3) Benthic infaunal carnivore (3)

The number(s) in brackets after the group name indicates the geometries (in terms of the number of boxes used) where the effect of spatial resolution differed from runs using the baseline forcing. The meaning of the codes for the state of a trophic group after 20 simulated years are: macrophyte barren cycle: long-term boom-bust cycling of macrophytes; constant: only small scale interannual variation present; more widespread: wider spatial distribution even accounting for larger cell sizes on coarser geometries; Y: wide spread and as abundant as in the 59-box geometry under the same forcing conditions; R: restricted in distribution compared with the 59-box geometry under the same forcing conditions; BC: persists only because of continual reintroduction from the Bass Strait boundary box; D: >75% reduction in abundance; and NO: decline to bay-wide extinction.

Table 5

Groups demonstrating different responses to spatial structure under alternative amounts of fishing and nutrient loads in the IGBEM

Conditions	Change in response to spatial structure	Groups
Increased fishing pressure	D → Y	Microzooplankton (8, 3, 1)
	More widespread	Diatoms (8, 3)
	More widespread	Large omnivorous zooplankton (8, 3)
	More widespread	Seagrass (8, 3)
	More widespread	Benthic deposit feeder (8, 3)
	More widespread	Benthic infaunal carnivore (8, 3)
	R → D	Benthic filter feeders (8)
	Y → D	Planktivorous fish (3, 1)
	Y → D	Piscivorous fish (8)
	Y → D	Demersal herbivorous fish (8)
Decreased fishing pressure	More widespread	Benthic deposit feeder (8, 3)
	More widespread	Benthic infaunal carnivore (8, 3)
	R → D	Benthic filter feeders (8)
	R → NO	Macroalgae (8)
	Y → D	Piscivorous fish (8)
	Y → D	Demersal herbivorous fish (8)
Increased nutrient loading	D → Y	Picoalgae (8)
	D → Y	Microzooplankton (8)
	D → Y	Demersal fish (8)
	R → NO	Macroalgae (8)
	R → Y	Benthic filter feeders (8)
	Y → D	Dinoflagellates (1)
	Y → D	Large omnivorous zooplankton (3, 1)
	Y → D	Macrozoobenthos (8, 3, 1)
Decreased nutrient loading	D → Y	Picoalgae (8, 3, 1)
	D → Y	Microzooplankton (1)
	D → Y	Demersal fish (8)
	D → Y	Demersal herbivorous fish (1)
	D → Y	Anaerobic bacteria (8, 3, 1)
	D → Y	Microzooplankton (8, 3)
	More widespread	Benthic deposit feeder (8, 3)
	More widespread	Benthic infaunal carnivore (8, 3)
	More widespread	Macrozoobenthos (8, 3)
	More widespread	Macroalgae (8)
	R → NO	

The number(s) in brackets after the group name indicates the geometries (in terms of the number of boxes used) where the effect of spatial resolution differed from runs using the baseline forcing. The meaning of the codes for the state of a trophic group after 20 simulated years are: more widespread: wider spatial distribution even accounting for larger cell sizes on coarser geometries; Y: wide spread and as abundant as in the 59-box geometry under the same forcing conditions; R: restricted in distribution compared with the 59-box geometry under the same forcing conditions; BC: persists only because of continual reintroduction from the Bass Strait boundary box; D: >75% reduction in abundance; and NO: decline to bay-wide extinction.

### 3.5. Model divergence with changing pressures

Self-simplification of the model food web (i.e. the loss of functional groups) and inconsistencies in predicted estimates of biomass, production and consumption are often exacerbated with decreasing spatial resolution when nutrient loading and fishing pressures

are also altered (increased or decreased). However, the nature of the effect of changing spatial resolution does not always match those of the runs under baseline conditions (Tables 4 and 5). Generally, changes in nutrient loading produces corresponding changes in the resource base, particularly for the benthic groups, and this underpins effects of spatial resolution on simpli-

fication. The impacts of a reduction in spatial resolution observed under baseline conditions are expressed at a different level of spatial resolution when nutrient loads or fishing pressure is changed. If nutrients increase, the effects of self-simplification largely disappear from the 8-box case, while decreasing nutrients usually intensifies the effects of self-simplification. A reduction in nutrient load intensifies the effects of simplification for all but two groups in the 8-box version of BM2 (Table 4), but in IGBEM some groups show fewer effects of a reduction in spatial resolution. This may indicate that IGBEM has some sensitivity to the forcing conditions used, but that they are at a different nutrient level to, and not as strong as, that in BM2. The effects of changing fishing pressure are not so easily characterised, beyond the observation that trophic cascades are stronger on simpler geometries. Cascades caused by the release or depletion of fish are more pronounced and extend further through the web on the simpler geometries because the lack of heterogeneity allows predators and prey to overlap for longer periods and over larger areas.

## 4. Discussion

### 4.1. Spatial resolution and temporal variability

The ecosystem models BM2 and IGBEM display more short-term fluctuation when applied on more spatially resolved geometries. The mechanisms identified by Harris et al. (1996) for corresponding behaviour of PPBIM also explains the behaviour of BM2 and IGBEM. More finely resolved spatial resolution results in a higher degree of local variation in environmental conditions because (1) changes in advection and mixing along broadscale gradients can be influenced by local point source inputs, (2) point source inputs are not immediately diluted by mixing with sizeable proportions of the total capacity of the bay, and (3) advection on the more detailed geometries continually brings local communities into contact with new levels of nutrients, keeping these groups in a perpetual state of flux. As a result of these mechanisms, the less spatially resolved geometries underestimate local variation as they homogenise the many influences of environmental heterogeneity and allow the planktonic groups to inappropriately attain steady state.

### 4.2. Spatial resolution and the scale of habitat variability

The homogenisation of across bay depth profiles and nutrient, chemical and hydrodynamic properties means that effectively different systems are modelled when using alternative spatial resolutions. Coarser geometries do not have the steep depth gradients across the bay seen in the 59-box model and so, for example, sediment light levels are more conducive to widespread seagrass populations rather than the restricted populations seen in the 59-box model. More importantly, the flushing time of the bay for coarser geometries is much shorter than in the 59-box model. With a drop in resolution over the southern boxes around the bay mouth, flushing time drops from more than 270 days for the 59-box geometry to less than 93 days for the 3-box model (Walker and Sherwood, 1997) and less than 25 days for the 1-box model. Flushing time and other environmental conditions have direct habitability effects on at least some of the biological components of the system and this alone could produce differing dynamics (including extinction) depending on the geometry used. One drawback of the method used here, to calculate the flows between boxes (Walker, 1999), is that it did not account for effectively enhanced diffusion within cells in the model. The homogeneous nature of the cells means that anything transported into the cell is instantaneously available to the entire cell. Alternative methods of calculating flows are being developed to avoid this problem in the future.

It may be argued that the inclusion of explicit vertical structure within the water column in these model geometries may affect the results reported here. Given that the three-dimensional nature of the hydrodynamics model used to derive the transport flows used in BM2 and IGBEM included vertical structure and processes, and also given the shallow well mixed nature of the ecosystem being modelled and the observation that many of the most heavily impacted groups (the groups that decline or effectively disappear from the model) are benthic it is unlikely that the general effects of reduced spatial resolution would have changed with an increased number of explicit vertical layers. This may not be the case in other more intensively stratified ecosystems.

#### 4.3. Spatial resolution and persistence stability

The most pronounced impact of removing heterogeneity when applying models on the coarser geometries is the tendency for self-simplification of the food webs. Collapse of the web in this way is produced by two interacting consequences of the smearing of environmental conditions with coarser spatial resolution. The first is that the removal of boxes and the general homogenisation of conditions removes spatial refugia that otherwise facilitated the persistence of some groups. For example, deposit feeders and meiobenthos, which are competitors but also predator and prey, are spatially disjunct in the 59-box case in that the deposit feeders line the edge of the bay while the meiobenthos inhabit the deeper areas of the bay. With coarser geometries this spatial partitioning is not possible and the meiobenthos are completely excluded. This is a direct result of the use of differential equations in the model. Within each box, competitors and predators are effective ‘everywhere’ and encounter rates are not related to abundance as they are in nature. The functional response used for grazing does include an ‘availability’ parameter, but as this is a fixed proportion of the prey biomass the equations do not inherently include many refuges or lags.

One way these refuges may be added is by using a spatially resolved system, as differential abundance across the boxes creates lags and refugia. As a result, the full trophic web is supported when the models are run on spatially resolved geometries, but the web collapses when coarser geometries are used. Notably, this important effect of spatial resolution on trophic stability was not considered in many of the traditional models addressing the effects of system complexity on stability (May, 1974; Pimm, 1982; Cohen and Newman, 1988). These earlier models predicted that larger food webs were unstable, whereas the models considered here, which include more realistic conditions (e.g. nutrient conservation, omnivory, detrital infusion, ontogenetic diet shifts and mixotrophy), suggest that a large number of trophic groups do not destabilise the system when environmental heterogeneity is present. Johnson and Seinen (2002) and reach similar conclusions for competition systems, and modelling work by Keitt (1997) and Donalson and Nisbet (1999) also indicate that species persis-

tence increases with system size and heterogeneity. This implies that spatial heterogeneity is one form of complexity that is a required part of the theoretical consideration of realistic food web dynamics and community structure.

It may be argued that the stabilising effects of spatial structure can occur at scales much finer than the boxes represented here, and that our results are an artefact of the assumption that mass-action interactions can be used regardless of the size of the pools being considered (Walters, personal communication). However, it is noteworthy that models using alternative functional responses derived explicitly from the assumption that trophic interactions on small scales can limit interaction rates (e.g. ECOSIM) do not escape the problem of food web self-simplification due to insufficient spatial structure and associated refugia (Christensen et al., 2000). This suggests that the findings here are not invalidated by the use of mass-action interactions, and that while the fine-scale processes may be important, large-scale gradients and habitat structure may also act to stabilise systems by providing refugia at a larger scale.

#### 4.4. Spatial resolution and the impact of changing conditions

Trends in the effect of spatial structure noted under baseline conditions of BM2 and IGBEM do not hold as nutrient loads and fishing pressure changes. For example, under an increase in nutrients, the standard 59-box run of BM2 predicts that seagrass will effectively become extinct throughout the bay. This is not the case when using simpler geometries, where it persists despite the change in nutrient levels. Murray (2001) also found that under increasing nutrient loads the 1-box PPBIM model no longer reflects the dynamics of its 59-box counterpart, as different processes emerge as important in the two cases. Spatial variation proves to be a crucial determinant of bay dynamics as the PPBIM model system moves from a mesotrophic to a eutrophic state (Murray, 2001). Thus, these studies show that complex system behaviour introduced by spatial heterogeneity cannot be ignored if the models are to be used to evaluate the impact of changing conditions.



#### 4.5. Spatial resolution and model structural complexity

While there has been some previous work addressing spatial refugia and model dynamics, there has been little consideration of the interaction of spatial resolution and model structural complexity. BM2 and IGBEM use very different levels of model formulation detail and by comparing their results some general conclusions on this topic may be drawn. While some spatial resolution may always be necessary, it was clear that IGBEM was less affected by a reduction in spatial resolution. This suggests that there may be a form of trade-off in model complexity occurring.

Fulton et al. (submitted-a) found that for the purposes of understanding ecosystem dynamics physiological detail is not always required and that simpler formulations, such as those employed in BM2, are generally adequate for learning and general predictive purposes. It was also found that BM2 was generally sensitive to physical conditions (e.g. it performed poorly in oligotrophic conditions) and this apparently extends to the spatial resolution used. It appears that models that employ simpler formulations may need to be more spatially resolved in order to maintain their ability to reproduce ecosystem dynamics. The implications of this is that if spatially resolved information is not available then extra effort will be required in determining the value of physiological parameters. Given (1) the computational advantages associated with using simpler models (e.g. compared with IGBEM, BM2 requires less than one tenth of the time to validate, verify and calibrate), (2) how difficult it is to measure physiological parameters, and (3) the current improvements in sampling technology, designing spatially resolved sampling might be the easier route to take.

## 5. Conclusions

Spatial resolution is a critical issue when considering the dynamics of ecosystems. The complex and emergent features of ecosystem behaviour mean that there are strong limitations on minimum sampling effort in time and space. Removing complexity by using coarse spatial dimensions relative to the dynamics of the system is a two edged sword. By simplifying model systems and increasing the scale at which variation is

considered, storage requirements are reduced drastically, calibration time falls sharply and some trends are easier to discern. However, this comes at the cost of losing crucial emergent properties, the ability to capture the full web structure and changing importance of mechanisms that appear to characterise natural systems. Models need not be highly resolved, but to be informative the spatial resolution employed must allow for expression of the dominant gradients and dynamics in the system (Nihoul and Djenidi, 1998). It is clear that spatial phenomena play a crucial role in influencing ecosystem behaviour. As pointed out by Polis and Strong (1996), complexity and variation may be inconvenient to a theoretical understanding of ecosystems, but they may also be two of the most important driving forces of those systems. Without their inclusion it may be impossible to use models to understand systems and how they respond to change.

## Acknowledgements

The authors are grateful for the many discussions with John Parslow and Sandy Murray about Port Phillip Bay and its dynamics and to Christine Crawford, Jemery Day and two anonymous reviewers, who commented on an early draft of this paper. The CSIRO Division of Marine Research and the University of Tasmania (funds awarded to C.R.J.) provided financial support for this work.

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