

Chapter 4 The large and the small of it: The effect of spatial resolution and sampling frequency on the performance of ecosystem models

Abstract

The effects of spatial scale on the dynamics and performance of ecosystem models is an important issue. Simplifying models by using coarser spatial resolution can be desirable, as it cuts down on computational requirements and can make model interpretation easier. Models built on simple geometries may also require relatively few data to parameterise and validate, but they may be incapable of reproducing important dynamics observed in nature. To address this issue the effect of spatial structure on the output of two trophic ecosystem models (Bay Model 2 and the Integrated Generic Bay Ecosystem Model) was considered by performing simulation runs on 1-box, 3-box, 8-box and 59-box spatial configurations. The results indicate that simpler 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 eutrophication as well as do 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 model 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 of the reduced heterogeneity increase.

Sampling frequency is another important issue for both empirical and model studies. Output simulating the state of the system on a daily basis was sub-sampled on weekly, fortnightly, monthly, bimonthly, half-yearly and yearly scales to evaluate the

impacts of different sampling frequencies. It is clear that sampling infrequently (> monthly) may miss important dynamics and variation, while sampling too often (< weekly) does not provide any additional benefit as useful trends are swamped by noise. An intermediate sampling frequency of between 1 – 4 weeks was sufficient to adequately represent system-level processes considered in the model.

Keywords: spatial structure, sampling frequency, biogeochemical, ecosystem, model, BM2, IGBEM

4.1 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) on rocky shores may be reinterpreted when the influence of large-scale hydrodynamics and larval transport are considered (Roughgarden et al. 1988). Modelling 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 extinction (Nisbet and Gurney 1976, Gurney and Nisbet 1978, Keitt 1997) or competitive exclusion (Skellam 1951, Hassell et al. 1994, Johnson 1997), by providing refugia.

Regarding application of models, additional spatial resolution can require much more data for model construction, parameterisation, calibration and validation, and 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 the use of geometries that summarise large areas by a small number of boxes (e.g. ERSEM I, Baretta et al. 1995). While this is not necessarily a bad choice, it can be hard to discern any consequences of the use of a restricted geometry if only a single representation is employed. Studies that have included the application of the same model, or similar versions of a model (e.g. ERSEM I vs ERSEM II, Baretta et al. 1995, Baretta-Bekker and Baretta 1997), to multiple geometries can be informative. For example, Murray (2001) found that there are enough shared features between models applied on alternative spatial scales that simpler models can be used as a design tool for effective development of larger, more spatially detailed models. However, the same study emphasizes 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 unclear whether findings for simpler ecological models hold for the larger 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 and the Integrated Generic Bay Ecosystem Model) were implemented on four different geometries. This allowed for the evaluation of logistic (sampling and computational demands) and ecological impacts at the various scales.

Space is not the only dimension that causes problems in ecology and modelling. Time, and in particular how often sampling occurs, is another important topic. Sampling frequency can have a significant impact on our ability to reliably detect events and

variation over a wide range of time scales, from days to decades (Rantajärvi et al. 1998). Models can provide important insights into this issue as they present a case of perfect knowledge and can clearly demonstrate what benefits or losses are associated with particular sampling frequencies. As a complement to the consideration of spatial scale and ecosystem models, we also investigated the effect of sampling frequency on the conclusions drawn from Bay Model 2 and the Integrated Generic Bay Ecosystem Model.

4.2 Methods

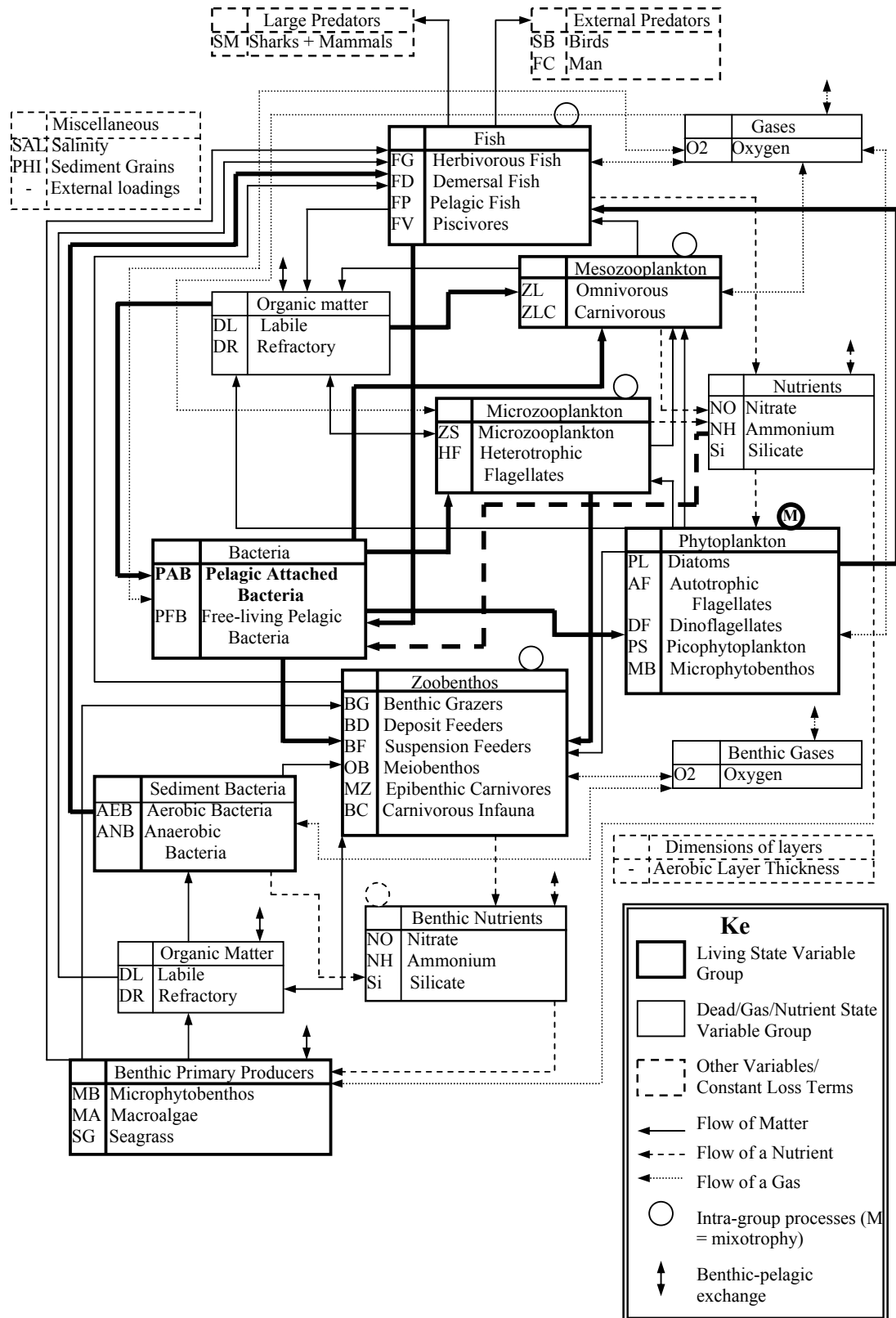
The output of two trophic ecosystem models, Bay Model 2 (BM2) and the Integrated Generic Bay ecosystem Model (IGBEM), are used to consider the effects of spatial structure and sampling frequency on model behavior and the conclusions that can be drawn from the model output. The two models were developed as a part of a wider study of the effects of model structure on performance. They cover many of the same processes and use very similar trophic webs (Figure 4.1), but the formulations used in each case differ greatly in the amount of physiological detail incorporated. A brief overview of the models follows, but a summary of the major similarities and differences between the two models is given in Table 4.1. More detailed descriptions of the formulation of the models is given in chapters 1 and 2.

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 and 4 fish groups (chapter 1). 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, 1999a).

Table 4.1: Comparison of the underlying assumptions and formulations of the standard implementations of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

| Feature | BM2 | IGBEM |
|--|---|--|
| General features | | |
| Biomass units | mg N/m ³ | mg/m ³ of C, N, P, Si |
| Input forcing | nutrients and physics on interannual, seasonal, tidal frequencies | nutrients and physics on interannual, seasonal, tidal frequencies |
| Level of group detail | functional group | functional group |
| Process related | | |
| Bioturbation and bioirrigation | yes | yes |
| Consumption formulation | type II | mixed (type II, type III) |
| Formulation detail | general: only growth, mortality and excretion explicit | physiological: the processes of assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit |
| Light limitation | optimal irradiance fixed | phytoplankton can acclimate to ambient light levels |
| Mixotrophy | dinoflagellates | none |
| Nutrient limitation | external nutrients determine uptake | internal nutrient ratio determines nutrient uptake and disposal |
| Nutrient ratio | Redfield | internal specific nutrient ratio |
| Oxygen limitation | yes | yes |
| Sediment burial | 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 | yes | yes |
| Model closure | | |
| Top predators represented by static loss terms | yes | yes |
| Linear mortality terms | yes | yes |
| Quadratic mortality terms | yes | no |
| Fish and fisheries related | | |
| Age 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 |

Figure 4.1: Trophic webs of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Flows marked in bold, and pelagic attached bacteria, are features of the web in BM2 that are not present in IGBEM.



This framework was then extended to cover benthic biological groups omitted from ERSEM II (those in the benthic primary producer subweb) (chapter 1). This level of process and trophic detail is at the upper bound of what is normally employed in ecosystem models currently in use (e.g SSEM (Sekine et al. 1991) and ERSEM II (Baretta-Bekker and Baretta 1997)) and it makes IGBEM one of the most highly detailed ecosystem models published.

BM2 was developed from PPBIM by extending the framework of that model to cover all of the groups in IGBEM. Consequently, BM2 includes the same trophic groups and physical details (vertical layering, transport, mixing and spatial geometry) as IGBEM, but there are important differences. The two models differ in the formulation of the attached bacteria (chapter 2) and dinoflagellates, but the greatest difference lies in the degree of process detail used in their formulation (Table 4.1). In BM2 physiological processes are not modelled explicitly, but are dealt with as a whole by generalised equations for assimilation and waste production (chapter 2). 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. This general level of detail is more representative of most existing models of eutrophication and water column trophic dynamics (Fransz et al. 1991).

4.2.A Spatial structure

The transport model used as the physical basis of BM2 and IGBEM can be applied on any geometry (any number of boxes). The standard geometry used during development was 59 boxes (Figure 4.2a), but we also ran both ecosystem models on 8, 3 and 1-box equivalents (Figure 4.2b-d), constructed by summing over the flows between boxes. The standard configuration was used in each case (standard parameter set, 2-weekly record period, 20 year run with physical forcing files repeated every 4 years).

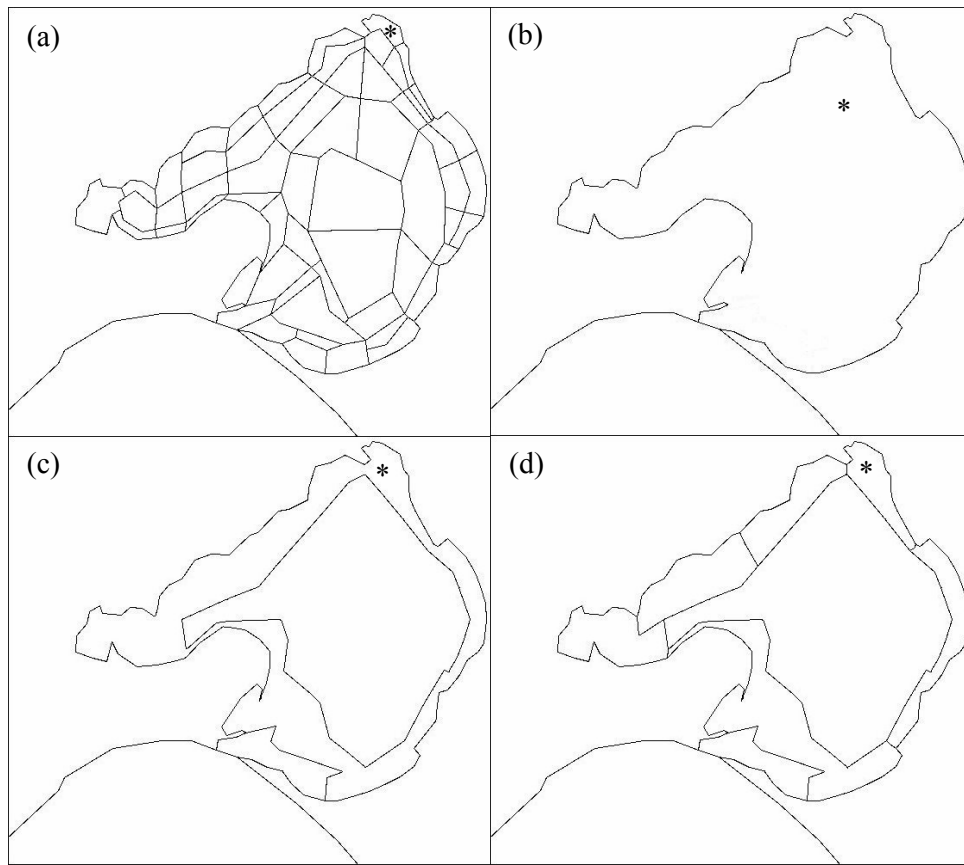


Figure 4.2: Maps of the geometries used with the models: (a) 59-boxes, (b) 1-box, (c) 3-boxes, and (d) 8-boxes. The “*” marks the box receiving inputs from the Yarra River (reference site for later figures)

However, for numerical stability, it was necessary to retune some of the groups in BM2. This is because the coarser model geometries average out the physical conditions and BM2 is sensitive to environmental conditions (chapters 2 and 3). The groups that required retuning were the metazoan infauna (meiobenthos, deposit feeders and benthic infaunal carnivores), and the planktivorous and demersal herbivorous fish.

Only the final four years of the full twenty-year simulations are 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 variance of these measures, were found to be the most useful way of

comparing model behaviour across several geometries. To check for consistency in the results across varying environmental conditions, the runs were repeated when fishing pressure or nutrient load was increased or decreased fivefold.

4.2.B Sampling frequency

The start date, end date and sampling frequency of the output of BM2 and IGBEM is flexible. Daily output is possible, but the standard runs use fortnightly records due to storage requirements and our desire to mimic achievable intensive monitoring of natural systems. This feature was used to consider the implications of differing sampling frequencies. IGBEM and BM2 were run for 20 years under a standard configuration, except that model output was stored daily for the final 2 years of the run (storage of a longer time-series was not possible due to the immense storage requirements). This output was sub-sampled weekly, 2-weekly, monthly, 2-monthly, quarterly, half-yearly and yearly. The summary statistics of model behaviour used include the variance of production, consumption, biomass and denitrification estimates. Effects of shifting nutrient loads and fishing rates away from their baseline values were also considered by repeating the sub-sampling on runs where these forcing conditions were increased or decreased fivefold.

4.3 Results

4.3.A Spatial structure

Smoothing of local variation

Comparing the variance in the time-series for any of the groups or processes with rapid dynamics (such as chlorophyll a, zooplankton or denitrification) across the various model geometries indicates that decreased spatial resolution reduces short-term fluctuations. This effect is clearest close to point source inputs such as the Yarra River,

which flows into the northern most point of the bay (Figure 4.2). Comparing the variance in chlorophyll a (chl a), over the final 4 years of each run, in the box fed by the Yarra River there is a strong decrease in variance with increasingly aggregated geometries, regardless of the model chosen (Figure 4.3). There is also a decrease in the variance of bay-wide averages with coarser spatial resolution, but it is an order of magnitude smaller (Figure 4.4). The variance observed at the bay-wide scale is much smaller than in the box fed by the Yarra river inputs because at the bay-wide scale fluctuations across the bay cancel each other out or are subsumed by the more stable behaviour of boxes further from input sources.

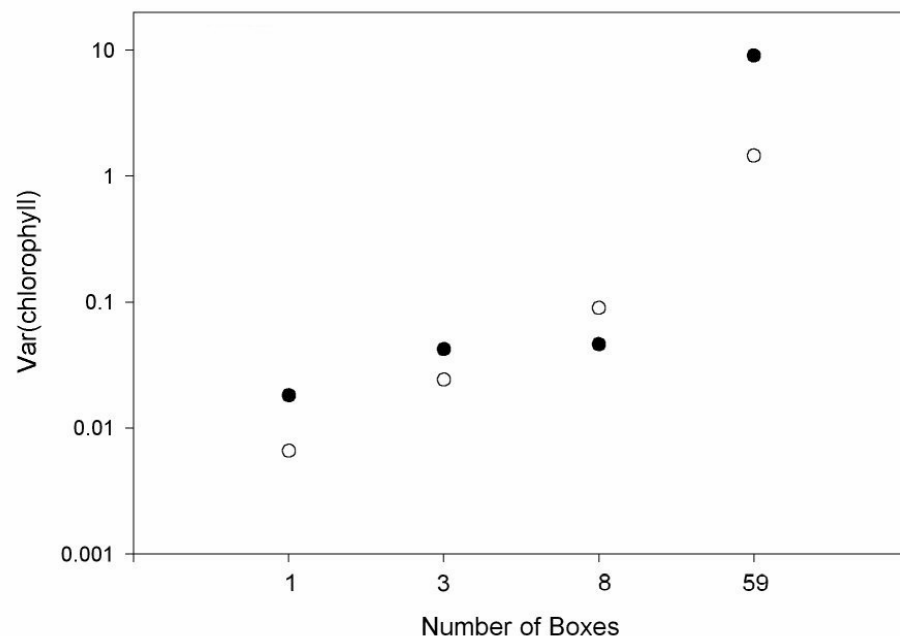


Figure 4.3: Variance of chlorophyll a in the “Yarra River” box (marked by a * in Figure 4.2) over the final 4 years of the 20 year runs for different levels of spatial resolution in the Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) models (1 – 59 boxes).

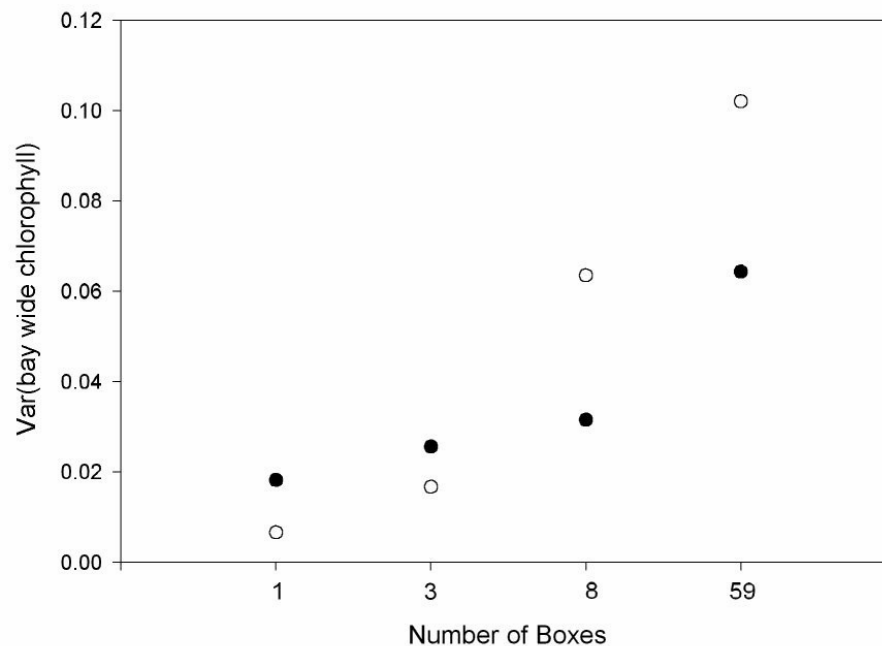


Figure 4.4: Variance in the bay-wide average chlorophyll a over the final 4 years of the 20 year run for different levels of spatial resolution in the Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) models (1 – 59 boxes).

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 4.2). In the water column groups, this simplification is illustrated by the dependence on boundary conditions 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

Table 4.2: Persistence of the trophic groups in runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM) using 8-box, 3-box and 1-box geometries.

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 Bass Strait boundary box; D = >75% reduction in abundance; and NO = decline to baywide extinction. Note that pelagic attached bacteria are not present in IGBEM.

| 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 |

structure is obvious even for the 8-box geometry, while other groups show restricted distribution in the 8-box case and only undergo bay-wide extinction in the 3-box and 1-box runs (e.g. macroalgae (Figure 4.5)).

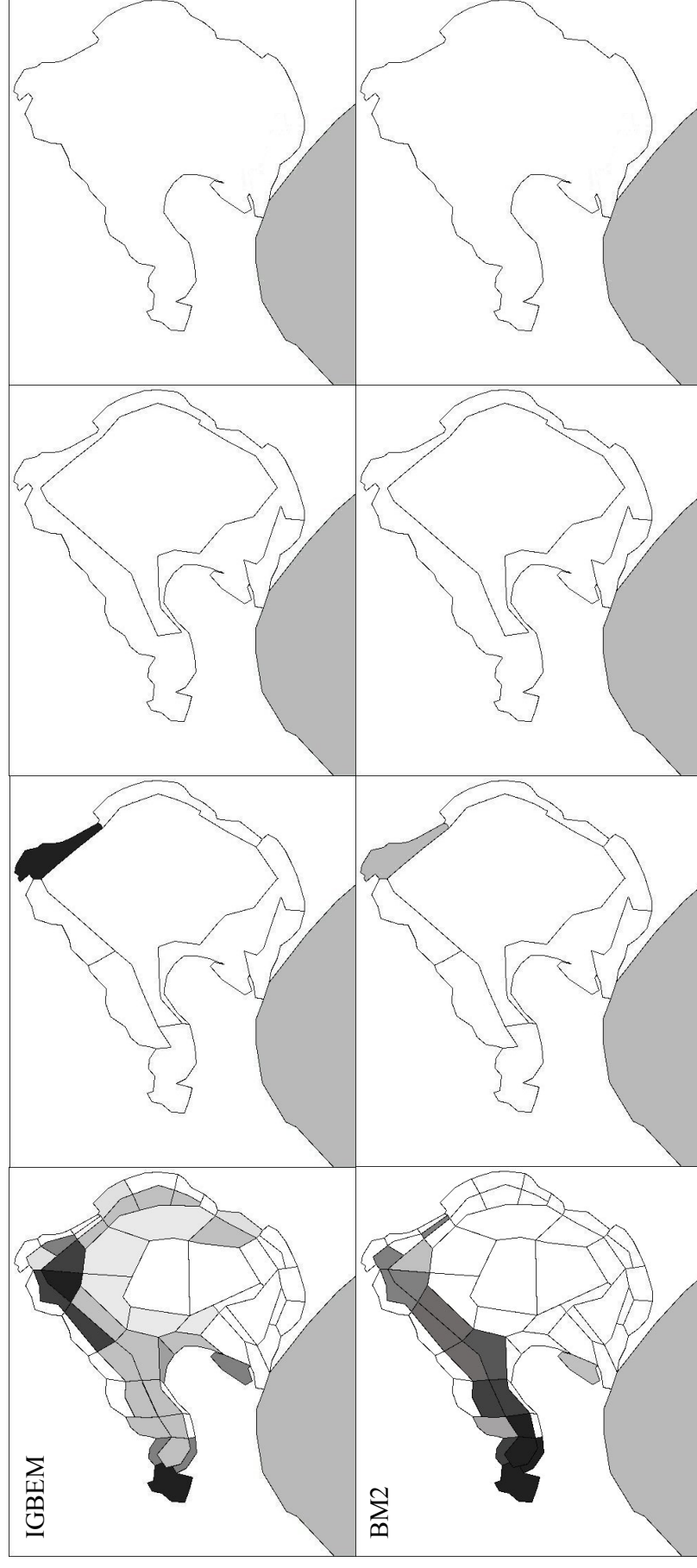
The self-simplification of the food web is not as strong across both models. IGBEM loses half as many groups as does BM2 for the same reduction in spatial resolution. The groups lost from IGBEM are also lost from BM2 except for autotrophic flagellates, which shows no reduction in abundance in BM2 irrespective 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 infaunal (Table 4.2). The single exception is macroalgae, which is replaced by seagrass on the simpler geometries.

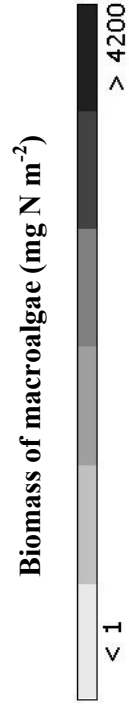
Even those groups that are not totally displaced on the coarser geometries may show depletion (Table 4.2). This is because they can no longer partition resources with competitors or escape predator coverage as easily. The geometries with coarser spatial resolution have more homogeneous physical conditions, as gradients in depth, nutrients and hydrodynamic properties 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.

Overall 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 across all the geometries. Large carnivorous zooplankton in

Figure 4.5: 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 (mg N m^{-2}) on day 6594 of the run for each geometry of the Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) models.





BM2 is one example, with its mean biomass varying by less than 2% across the geometries. In contrast, others increase either as a result or cause of the depletion of other groups. 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. This increase is largely as a result of an increase in influence of the boundary conditions in the less spatially resolved geometries.

The effect of changes in biomass on higher level aggregated measures can vary from minor to substantial. For example, the bay-wide average oxygen concentrations within the sediments is almost identical regardless of the geometry used, while the average bay-wide biomass of pooled biological groups is between 1000x too low to 4x too high depending on the group of interest and which of the simpler geometries is used (Table 4.3). Notably, total benthic primary production, sediment bacteria and denitrification are too low when using fewer boxes in either model. This triplet failure is pronounced as these things are all closely linked; low levels of benthic primary production result in lower levels of detritus, which in turn means that there is less bacterial activity and lower rates of denitrification. Aside from this triplet, the performance of IGBEM was relatively consistent across all geometries, with most estimates for the coarser resolution being within a twofold range of those for the 59-box model. In contrast, the performance of BM2 shows widespread deterioration on the lower geometries, with 40% of the estimates for the coarser geometries falling outside a twofold range of the estimates from the 59-box model.

Spatial zonation

The physical characteristics of each cell are increasingly “smeared” as spatial resolution is decreased. As a consequence, there is less of a gradient in community structure and processes from the edge to the centre, and from the north to the south of

Table 4.3: 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. Any entries in bold signify a difference of more than twofold between the simpler geometry and the 59-box case.

| | 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 | 0.27 | 0.44 | 0.64 | 0.76 | 1.20 | 1.73 |
| Benthic primary producers | 0.42 | 1.29 | 1.04 | 0.77 | 0.23 | 0.64 |
| Benthos | 0.02 | 2.84 | 3.56 | 1.09 | 0.83 | 1.03 |
| Infauna | 0.00 | 2.96 | 3.73 | 1.09 | 0.83 | 1.03 |
| Epifauna | 0.40 | 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 | 0.09 | 0.09 | 0.33 | 0.19 | 0.23 | 0.26 |
| Oxygen | 0.99 | 0.99 | 1.00 | 1.00 | 1.00 | 1.00 |
| Bay-wide Annual Totals | | | | | | |
| Denitrification | 0.00 | 0.00 | 0.01 | 0.02 | 0.06 | 0.13 |
| Water column primary production | 1.03 | 1.30 | 1.01 | 2.87 | 1.97 | 0.74 |
| Benthic primary production | 0.03 | 0.27 | 0.14 | 0.54 | 0.26 | 0.34 |
| Water column secondary production | 1.56 | 1.53 | 1.08 | 1.22 | 0.90 | 0.81 |
| Benthic secondary production | 0.02 | 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 | 0.09 | 0.79 | 0.94 | 1.11 | 1.08 | 0.64 |

the modelled bay. Moreover, because the cells cover larger areas as spatial resolution declines, any group that is present in cells on the smaller geometries will cover a larger part of the bay. It follows that the spatial distribution of groups that do persist on the smaller geometries can be much more widespread than in the 59-box case. The best examples of this are in the benthic groups, especially in IGBEM (Figure 4.6). As a result of wider distributions, areas of the bay are less clearly demarcated on the smaller geometries. The distinctive “edge” and “central” assemblages in the 59-box case are less clear on the 3- and 8-box geometries, as more microfaunal groups are ubiquitous, and of course any spatial zonation is impossible in the 1-box case (Table 4.4).

Figure 4.6: Effects of spatial resolution on the spatial distribution of functional groups. This example shows that the distribution of benthic deposit feeders expands with loss of spatial resolution. The maps show the distribution of the biomass (mg N m^{-3}) of benthic deposit feeders on day 7280 of the run for each geometry of the Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) models.

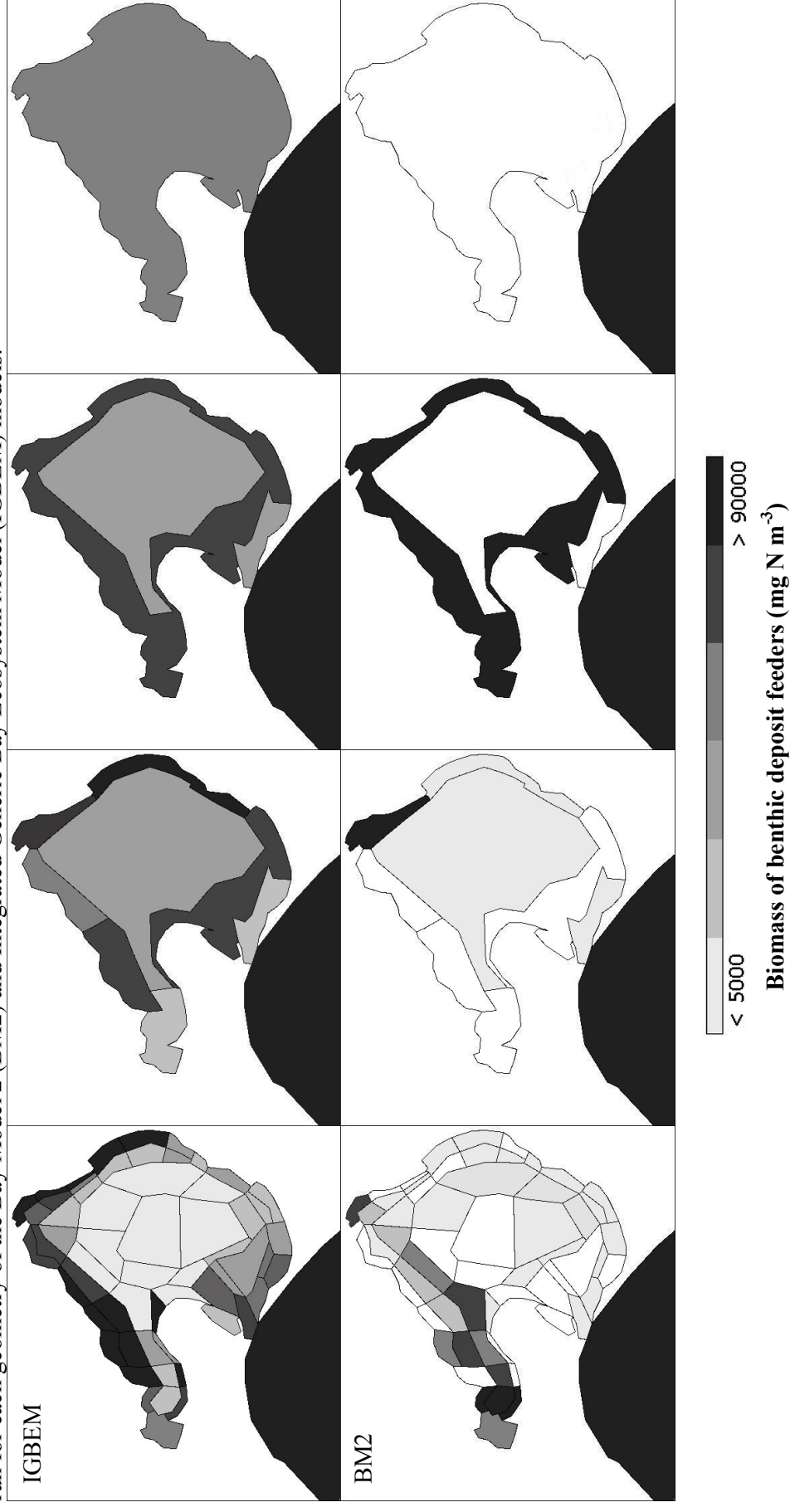
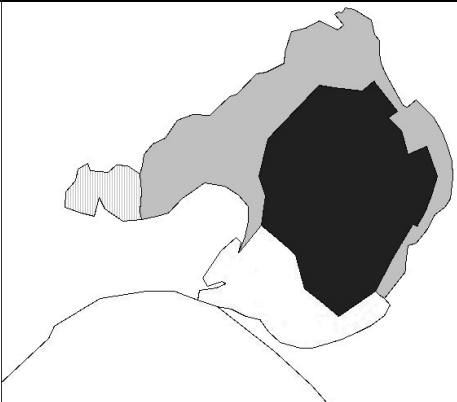
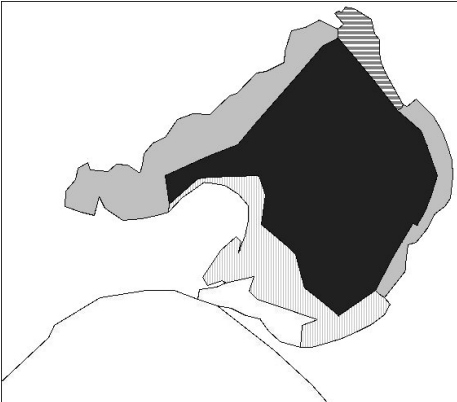
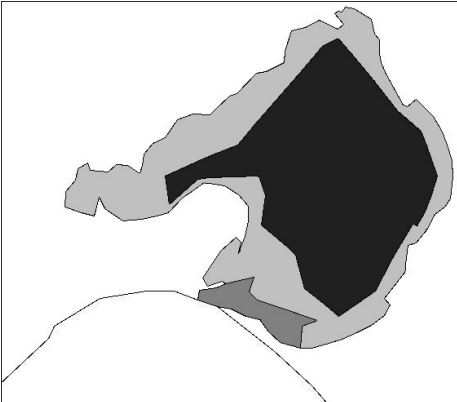


Table 4.4: Spatial distribution of assemblages predicted using Bay Model 2 (BM2) on 59-, 8- and 3-box geometries (the distributions predicted by the Integrated Generic Bay Ecosystem Model are very similar). Boxes containing the same assemblage have been grouped together and shaded in the same colour. Groups marked in bold differ from the 59-box composition.

| Distribution of the assemblages | Edge Assemblage | Central Assemblage |
|---|--|---|
|  | Diatoms and Autotrophic flagellates or Picoalgae and Microzooplankton Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores Macroalgae Seagrass Pelagic Bacteria | Picoalgae Autotrophic flagellates Dinoflagellates Heterotrophic flagellates Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos Meiobenthos Microphytobenthos Aerobic bacteria Anaerobic bacteria Detritus |
|  | Picoalgae, Dinoflagellates and Heterotrophic flagellates or Diatoms and Autotrophic flagellates Large carnivorous zooplankton Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores Meiobenthos Microphytobenthos Macroalgae Seagrass Pelagic Bacteria Aerobic bacteria | Diatoms Picoalgae Autotrophic flagellates Dinoflagellates Heterotrophic flagellates Microzooplankton Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos Meiobenthos Pelagic Bacteria Aerobic bacteria Anaerobic bacteria Detritus |
|  | Diatoms Autotrophic flagellates Picoalgae Dinoflagellates Microzooplankton Large omnivorous zooplankton Large carnivorous zooplankton Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores Microphytobenthos Seagrass Pelagic Bacteria Detritus | Diatoms Picoalgae Autotrophic flagellates Dinoflagellates Microzooplankton Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos Pelagic Bacteria Aerobic bacteria Anaerobic bacteria Detritus |

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 also occurred with decreasing spatial resolution when nutrient loading and fishing pressures are 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 4.5 and 4.6). 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 simplification. 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 increased, 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 4.5), 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 point to, and not as strong as, those identified in BM2 (chapters 2 and 3). The effects of changing fishing pressure are not so easily characterised, beyond the observation that trophic cascades are stronger on simpler geometries. The lack of heterogeneity with coarser spatial resolution allows predators and prey to overlap for longer periods and over larger areas. Thus, cascades caused by the release or depletion of fish are more pronounced and extend further through the web on the simpler geometries.

Table 4.5: Groups demonstrating different responses to spatial structure under alternative amounts of fishing and nutrient loads in Bay Model 2. 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” = longterm 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 baywide extinction.

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

Table 4.6: As for Table 4.5, but for the Integrated Generic Bay Ecosystem Model.

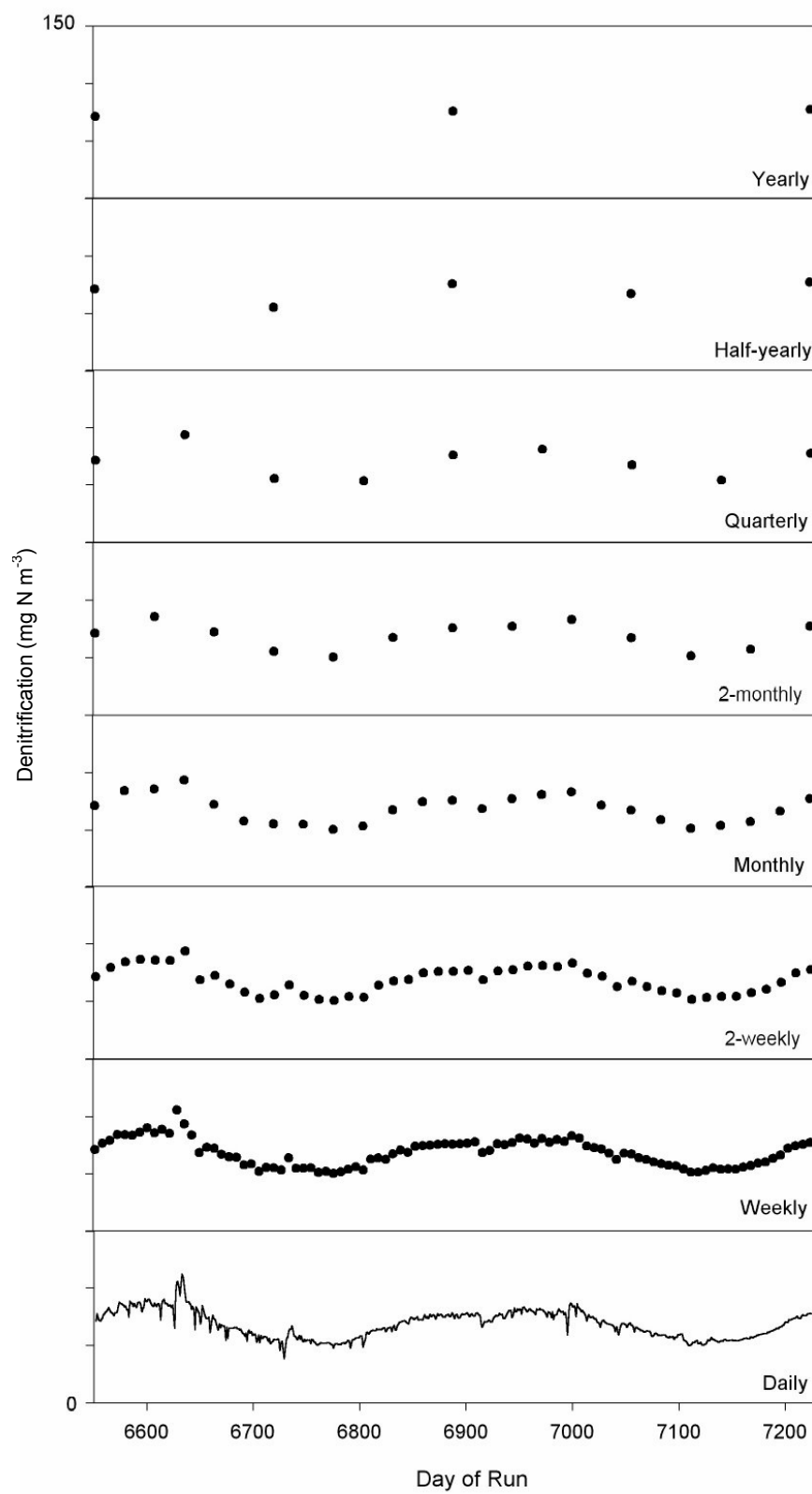
| Conditions | Change in response to spatial structure | Groups |
|----------------------------|---|------------------------------------|
| Increased fishing pressure | D → Y More widespread | Microzooplankton (8,3,1) |
| | | Diatoms (8,3) |
| | | Large omnivorous zooplankton (8,3) |
| | | Seagrass (8,3)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

4.3.B Sampling frequency

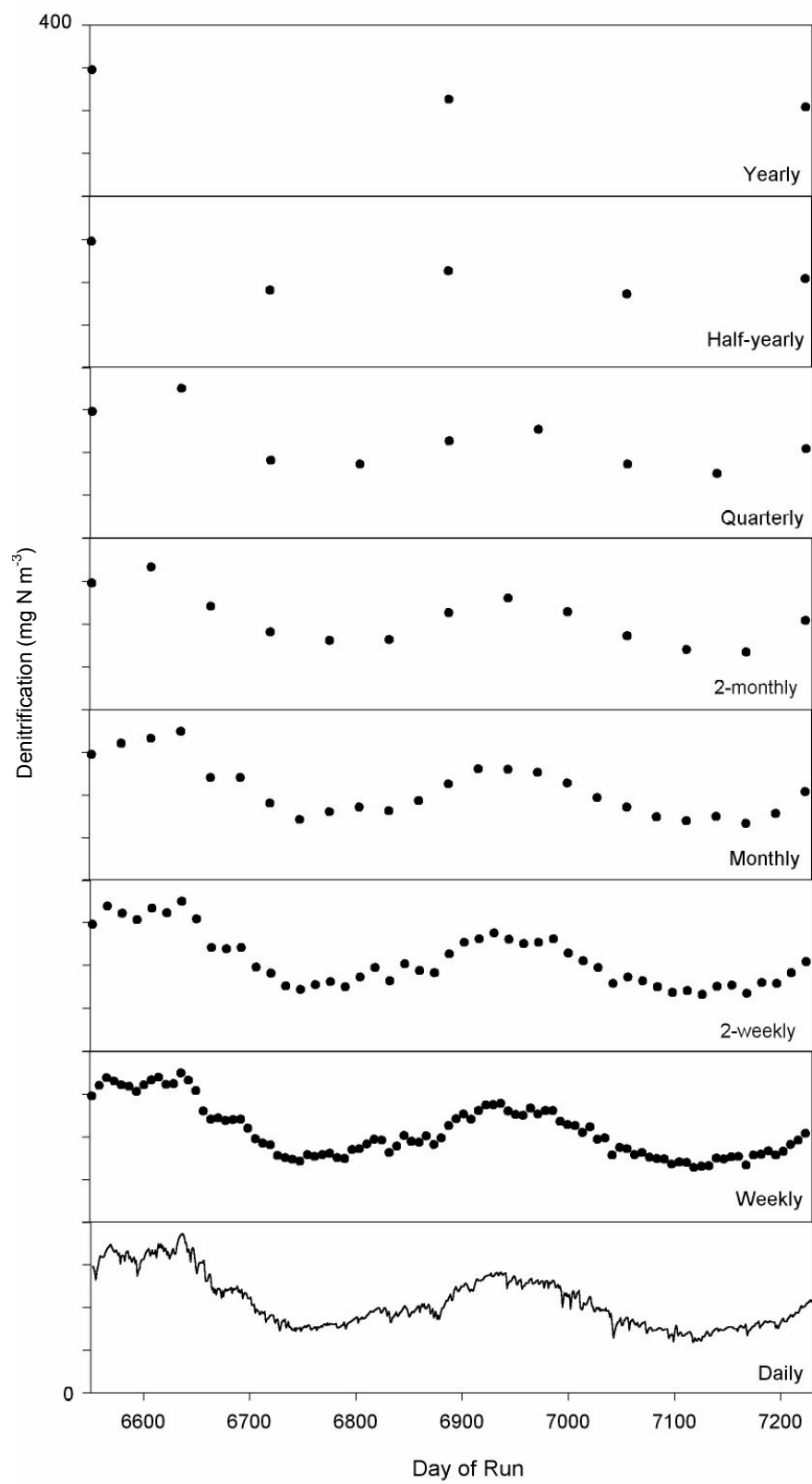
As would be expected, reducing the frequency of sampling reduces the amount of variation observed in the system (e.g. consider the time-series for bay-wide denitrification in BM2 and IGBEM in Figure 4.7). Two-weekly or even monthly sampling removes much of the noise present in the daily samples, but still reveals the underlying trend. Decreasing the frequency further to half-yearly or annual sampling leads to a substantial loss of useful information.

Figure 4.7: Time-series of denitrification as defined by each of the sampling frequencies for

(a) Bay Model 2



(b) the Integrated Generic Bay Ecosystem Model



The effect of apparently reducing variance can have a marked effect on estimates of system-level measures. For example, using sampling frequencies of one or two months cause time-averaged primary production to be overestimated, while longer sampling frequencies often yield substantial underestimates (Figure 4.8). The problem is exacerbated if the sub-samples coincide with extreme peaks or troughs in the series.

The issue of the effects of sub-sampling is much stronger for groups or processes with fast dynamics (many events or generations per year) while estimates involving slower growing groups are not as heavily affected. For example, the estimate for mean production of benthic filter feeders is only marginally affected by sampling frequency (Figure 4.9).

Changing the external forcing of the system (i.e. nutrient loads and fishing rates) does not have a consistent effect across all groups, and different changes to forcings yielded dissimilar results (Table 4.7). Reducing the nutrient load weakens the effects of sampling frequency as much of the variation in the system is removed; i.e. there are fewer, short-term, high-magnitude fluctuations in denitrification, biomass and productivity. When the nutrient load is increased the inaccuracy introduced by using longer sampling frequencies is substantially increased for measures associated with the primary producer and planktonic groups, particularly in IGBEM (e.g. water column primary productivity (Figure 4.10)). The inaccuracy of measures (e.g. productivity) for the other groups, such as the fish and sediment fauna, shows no real change with increasing nutrient load. The ratio of the true value to estimates based on longer sampling frequencies changes by less than 1% for these measures. In contrast, a reduction in fishing pressure and the resulting shifts to higher biomasses and stronger interactions between groups causes an amplification of the effects of using longer sampling frequencies, particularly for the fast-lived groups and associated processes (e.g. water column secondary productivity (Figure 4.11)), but it has little effect on

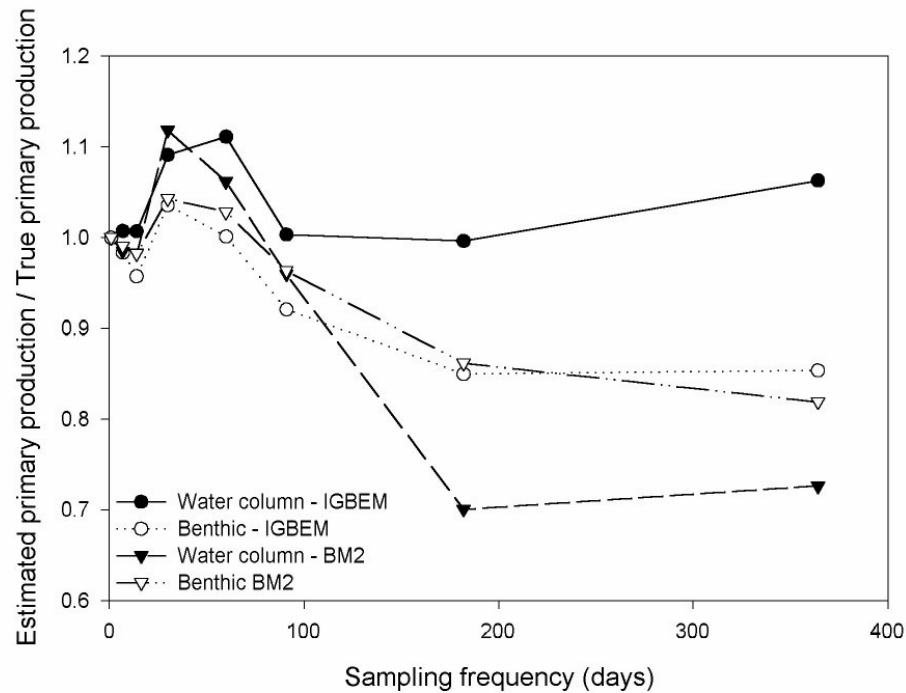


Figure 4.8: Ratio of the estimated and true values of pelagic (water column) and benthic primary production for Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) under various sampling frequencies.

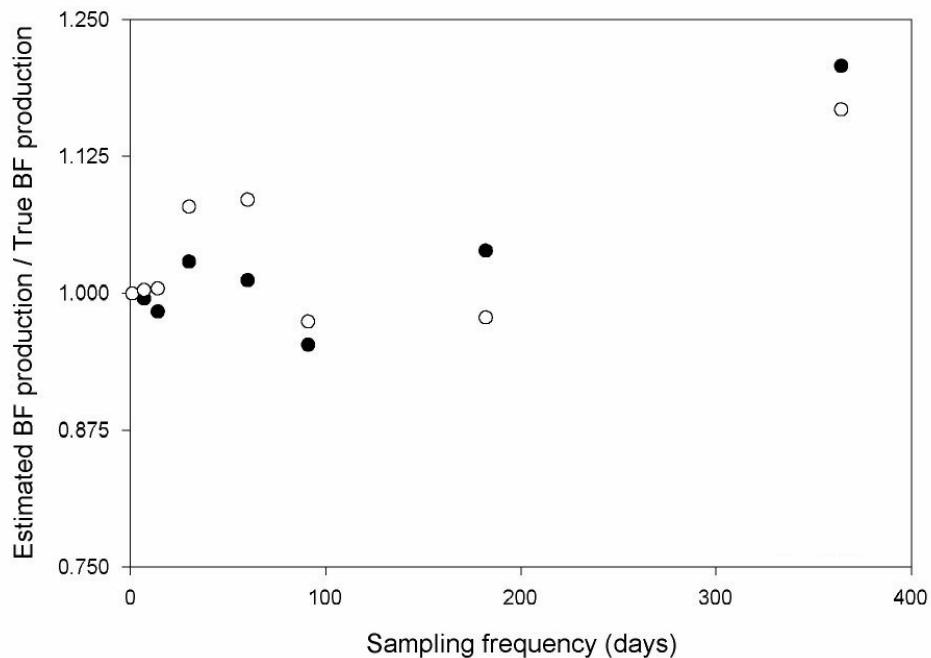


Figure 4.9: Ratio of the estimated and true values of production by benthic filter feeders (BF) for Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) under various sampling frequencies.

Table 4.7: Summary of the impact of changes in nutrient loading or fishing pressure on the effects of sampling frequency.

| Change in Conditions | Impact |
|----------------------------|--|
| Decreased nutrient loading | Reduced effect of sampling frequency as less variation translates to less inaccuracy when using longer sampling frequencies |
| Increased nutrient loading | Increase in the effects of sampling frequency, but only for the groups with fast-dynamics |
| Decreased fishing pressure | Increase in the effects of sampling frequency for the harvested groups and prey groups with fast-dynamics |
| Increased fishing pressure | Reduced effect of sampling frequency for the harvested groups. No change in the effects on other groups, unless the sampling frequency aligns (aliases) with fluctuations in prey biomass caused by the establishment, prior to fish-down, of new recruits to the fished stocks – this is particularly a problem with annual sampling. |

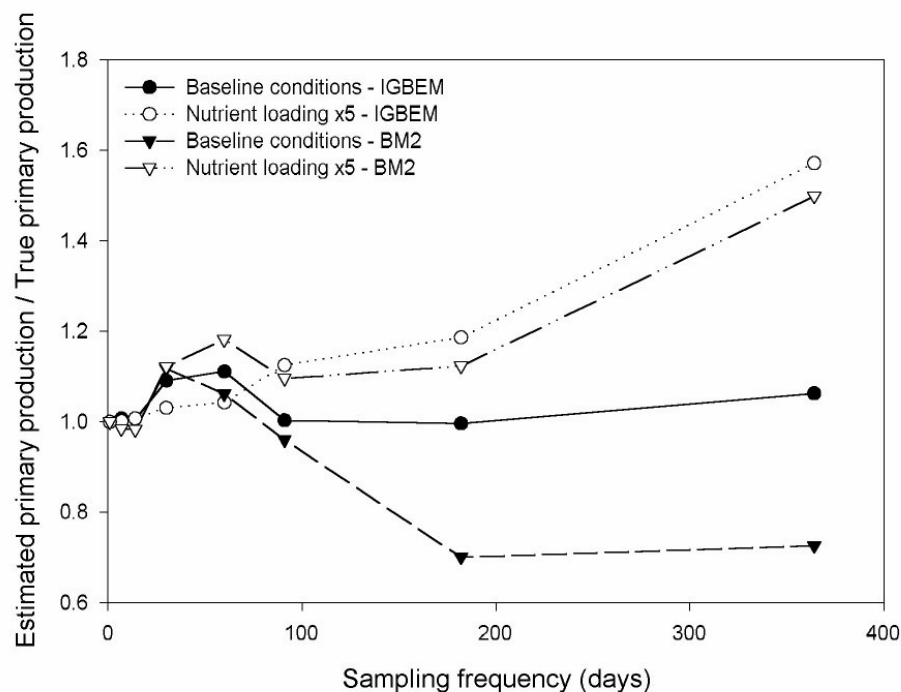


Figure 4.10: Ratio of the estimated and true values of pelagic primary production for the Integrated Generic Bay Ecosystem Model under various sampling frequencies with baseline nutrient conditions and a fivefold increase in nutrient load.

denitrification estimates. Again, this effect is stronger in IGBEM. Lastly, an increase in fishing pressure reduces the effects of using longer sampling frequencies, especially for the harvested groups, as their depleted biomasses show less variation through the year. Measures associated with prey groups, which may be released from predator control with an increase in fishing, do not show any increased effects of using longer sampling frequencies under higher fishing loads, except when annual sampling regimes are employed. At this point, aligning (aliasing) sampling times with peaks or troughs in the fish stocks can cause distortion of estimates, particularly for groups with fast dynamics. Under heavy fishing, if sampling coincides with a point just prior to recruitment, when stocks of fish are low, then estimates of the biomass or production of prey groups may be substantially overestimated (by as much as 50%). The converse holds if annual sampling coincides with the short period when recruits are of sufficient size to depress prey populations, but before fishing depletes their numbers to the point that their main prey groups recover.

4.4 Discussion

4.4.A Spatial structure

Harris et al. (1996) found that there is a decrease in local variation on less spatially resolved geometries for the original Port Phillip Bay Integrated Model (PPBIM). This matches the observation that BM2 and IGBEM display more short-term fluctuation when applied on more spatially resolved geometries. The mechanisms identified by Harris et al. (1996) for the behaviour of PPBIM also explains the corresponding behaviour of BM2 and IGBEM. The first of these is that more finely resolved spatial resolution results in a higher degree of local variation in environmental conditions due to changes in advection and mixing along broad-scale gradients produced by the location of the point source inputs. Secondly, point source inputs will

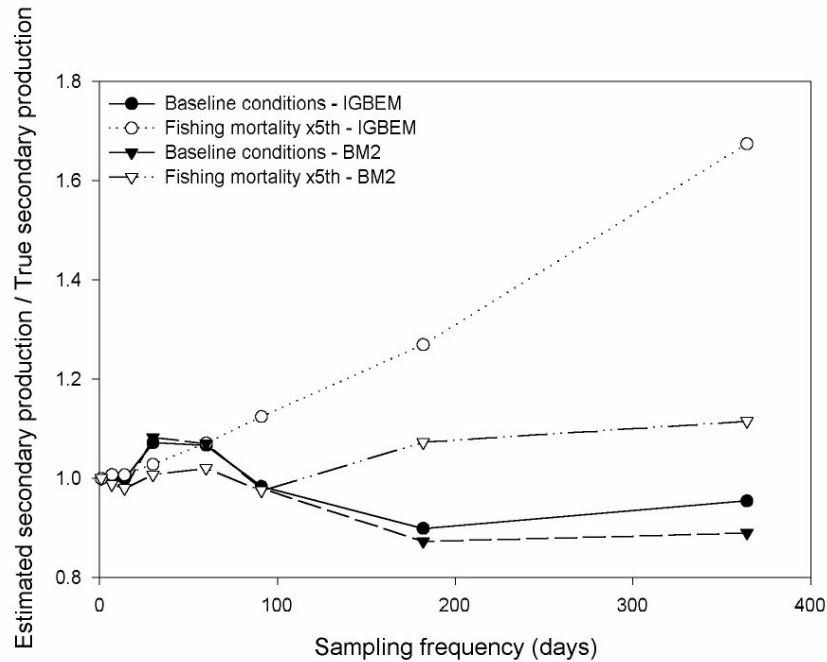


Figure 4.11: Ratio of the estimated and true values of pelagic secondary production for the Integrated Generic Bay Ecosystem Model under various sampling frequencies with baseline fishing conditions and a fivefold decrease in fishing pressure.

have a larger local, short-term influence when spatial resolution is finer as the inputs are not immediately diluted by mixing with sizeable proportions of the total capacity of the bay, as is the case on the coarser resolutions. Lastly, advection on the more detailed geometries continually brings local communities into contact with new levels of nutrients. Thus, these groups can never reach steady state as they are in a perpetual state of flux. As a result of these mechanisms, the less spatially resolved geometries underestimate local variation as they damp the many influences of environmental heterogeneity and allow the planktonic groups to inappropriately attain steady state.

The decrease in variation with coarser spatial resolution is reminiscent of the drop in the variation in the observed output of cellular-automata predator-prey models when increasingly large observation windows are used (e.g. Pascual and Levin 1999). However, Pascual and Levin's work differed from ours in that they considered the same

total number of cells and only changed the size of their observational windows, while this study considered different numbers of cells describing the same total area. Both methods remove heterogeneity. By averaging, Pascual and Levin (1999) smooth out local heterogeneity in population sizes at the time of “sampling”, while the models in this study remove heterogeneity in population sizes and local environmental conditions by using fewer larger cells in the less spatially resolved geometries.

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 changing spatial resolution produces systems with differing depth profiles and nutrient, chemical and hydrodynamic properties. Coarser geometries do not have the steep depth gradients 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). It was not possible to calculate flushing time for the 1-box model. However, it must be noted that, like the boxes at the mouth of the bay in more complex geometries, the 1-box model shows tidal aliasing and so the exchange between the boundary conditions of Bass Strait and the bay as a whole are over-stated. 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. That the differing geometries capture different physical environments is highlighted by the relative responsiveness of

the two models. BM2 requires retuning for numerical stability when the spatial resolution is changed, while IGBEM does not. This is in keeping with previous work that has found that BM2 needs more tuning as the underlying physical conditions change (chapters 2 and 3).

The “smearing” of the physical conditions with reduced spatial resolution has an additional biological effect. The removal of boxes and the general homogenisation of conditions removes refugia that allowed the persistence of some groups. For instance deposit feeders and meiobenthos, which are competitors but also predator and prey, are spatially disjunct in the 59-box case. 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 is completely excluded. This is a direct result of the use of differential equations in the model. Within each box competitors and predators are effectively “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. However, these refuges may be added 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. This effect of spatial resolution on trophic stability is particularly important given that many of the traditional models considering the effects of system complexity have omitted it (May 1974, Pimm 1982, Cohen and Newman 1988).

More recent work with spatial models shows different and multifaceted relationships between complexity, stability and invasiveness. As observed in nature, the relationships depend on network topology (the magnitude and direction of biological interactions between network members) (Dunstan and Johnson submitted). These recent

models still use assumptions that are unrealistic and there has been speculation over whether the findings from conventional consideration of the effects of trophic complexity would hold if more realistic conditions (including nutrient conservation, spatial structure and coupling, temporal forcing, omnivory, detrital infusion, ontogenetic diet shifts and mixotrophy) are included in the models (May 1974, Leibold 1996, Polis and Strong 1996, Keitt 1997). The models considered here include these processes.

Self-simplification of the food webs with a reduction in spatial resolution seen in this study suggests that a large number of trophic groups does not destabilise the system when environmental heterogeneity is present, but when the heterogeneity is removed the additional reticulation and detail in the food web cannot preserve the system and the web collapses. 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. Dunstan and Johnson (submitted) reach similar conclusions for competition systems, and modelling work by Keitt (1997) and Donalson and Nisbet (1999) also indicate that species persistence increases with system size and heterogeneity. They posit that larger systems have a greater capacity for ephemeral refugia, as physical and biological fluctuations in different regions can be out of phase. This is not possible in smaller systems so these systems go extinct. This is one of the mechanisms underlying the responses observed here.

The biological components included in the biogeochemical model of PPB (PPBIM) constructed as part of the Port Phillip Bay Environmental Study are largely from those groups that show the least impact of spatial structure, with macroalgae notable as the single exception. This is not surprising given that Murray and Parslow (1997) carefully selected the web structure in PPBIM to allow for maximum stability. It may also explain why Murray (2001) found a 1-box version of PPBIM very helpful during the development of the full model, whereas a similar approach would not be as

useful when trying to consider the full web that underlies IGBEM and BM2.

One area in which Murray (2001) and the findings here agree is in model divergence with changing conditions. Murray (2001) illustrated the limitations of the “simple modelling approach” by comparing the 1-box and 59-box versions of PPBIM under increasing nutrient loads. It was found that as conditions changed the 1-box model no longer reflects the dynamics of the 59-box model, 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). Similarly, 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. In the less spatially resolved cases seagrass biomass is reduced and the magnitude of interannual cycles is increased with increased nutrient loading, but only the 8-box model gives any indication that the distribution would contract and that the population would be in danger of disappearing from the bay. Thus, as is the case with PPBIM, complex system behaviour introduced by spatial heterogeneity cannot be ignored if the models are to be used to evaluate the impact of changing conditions.

4.4.B Sampling frequency

Despite differences in the models, and either damping or enhancing of variation by different sampling scenarios, there is a consistent pattern as to the usefulness of the various sampling frequencies (Table 4.8). At one extreme there are potentially large inaccuracies introduced by half-yearly or annual sampling, while at the other the noise inherent in daily sampling does not justify the immense storage requirements (or

expense) associated with computer generated or empirical observations of this detail. Under the circumstances considered here, of no observational error and complete knowledge, sampling frequencies of a week to a month are optimal. The lower end of this range agrees with field studies that have indicated that weekly sampling is best for measures such as primary productivity and sediment oxygen (Taylor and Howes 1994, Rantajärvi et al. 1998). These field studies do not find the monthly sampling as reliable as does the model study. The forcing files used in BM2 and IGBEM do not capture all of the temporal variability seen in real systems. The extra variation in natural systems may overwhelm the usefulness of monthly sampling suggested by the models.

The model and field studies point to similar conclusions regarding the effects of a poorly chosen sampling frequency. If longer sampling frequencies are implemented then estimates can be inaccurate and misleading with regard to understanding system dynamics. These concerns are particularly important when deciding on monitoring schemes as part of a system wide management strategy. Logistics may mean that sampling on the order of 7 to 14 days is impractical and prohibitively expensive. Unfortunately, evidence from field studies (Taylor and Howes 1994, Rantajärvi et al. 1998, Bennion and Smith 2000) and the work presented here indicates that opting for longer sampling frequencies is inadequate for informed management. This is particularly true for events that can happen very quickly, but have long lasting effects, such as oxygen-crises in the sediment. If longer sampling frequencies are to be successful in the future an index of overall system state which is robust to sampling frequency needs to be found. No such index was identified in this study, but it is likely that if one exists it will be a variable with slower dynamics.

Table 4.8: Summary of the utility of a range of sampling frequencies.

| Daily | Weekly | 2-weekly | Monthly | 2-monthly | Quarterly | Half-yearly | Annually |
|---|--|---|---|---|---|-------------|----------|
| Dominated by noise, which can mask underlying trends. This frequency does not add much to what can be captured by weekly sampling, except when trying to track oxygen stress events, which can occur for less than a week, but have long lasting impacts. | These frequencies are very similar with regard to the amount of information captured (and consequently any conclusions drawn). | Similar to weekly and fortnightly, but monthly sampling does lose some of the short-term variation. It is also important to be aware of potential aliasing problems. Overall, it still captures the seasonal trends well. | The loss of information is becoming evident for the groups with fast dynamics (seasonal trends are becoming “saw-toothed”). Satisfactory for groups with slow dynamics (much of the larger benthos) | Loss of information is evident for all groups, though those with fast dynamics are impacted the most. | These frequencies miss important events and much of the seasonal information. Aliasing is a critical problem. Sampling at these frequencies can lead to inaccuracies in estimates of annual denitrification, production and consumption of more than 25 – 50% depending on the ambient conditions. This is particularly true for measures associated with groups with fast dynamics (such as the plankton). | | |

4.5 Conclusions

Spatial and temporal 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 sampling on long time scales or using coarse spatial dimensions relative to the dynamics of the system, is a two edged sword. The scale at which sampling is undertaken not only impacts upon the costs of a field sampling program, it can also influence the processes detected and how they are interpreted. An observation scheme that reduces costs by concentrating on large spatial and temporal scales may miss crucial mechanisms that occur on a fine scale, but have far reaching impacts (e.g. oxygen crises). Moreover, modelling and field studies indicate that space itself is an important resource in an ecosystem and ignoring it can have a substantial impact on conclusions drawn.

The impacts of scale are not only an important concern in the field, but they can have substantial influences on modelling too. 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 characterize natural systems. Models need not be highly resolved, but to be informative the spatial and temporal resolution employed must allow for expression of the dominant gradients and dynamics in the system. 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.