

Chapter 5 Lump or chop: The effect of aggregating or omitting trophic groups on the performance of ecosystem models

Abstract

As ecosystem models become more commonly applied, questions regarding optimal complexity and parsimonious methods of simplification arise. Simplification of the underlying trophic complexity is one viable approach. Two potential methods of achieving this are to omit or aggregate components in the simulated food web. When applied to two biogeochemical ecosystem models, it was found that if the system is already aggregated to the level of functional groups then further aggregation will not work as well as the strategic omission of less important groups. The relationship between simplification and performance is nonlinear, but it is possible to identify two general principles. First, over-simplification of the web leads to poor model performance. Second, if important processes or couplings (such as between the pelagos and benthos in shallow coastal systems) cannot be included explicitly, simple forcing is unlikely to be a reliable alternative. Some form of robust empirical representation will be necessary.

The results of model simplification also have implications for the ecological stability-diversity debate. Shifts in the relative importance of different groups with changing ecosystem conditions, and dependence of the effect of simplification on ecosystem state, support the concept of the ecological “insurance hypothesis”. The models used here do not support the idea of a simple relationship between connectance or interaction strength and the stability of system behaviour. The biological details of the web, the trophic and non-trophic, direct and indirect interactions included are a crucial determinant of ecosystem and model behaviour that cannot be ignored.

Keywords: trophic complexity, trophic structure, aggregation, omission, stability, diversity, biogeochemical, ecosystem, model, IGBEM, BM2

5.1 Introduction

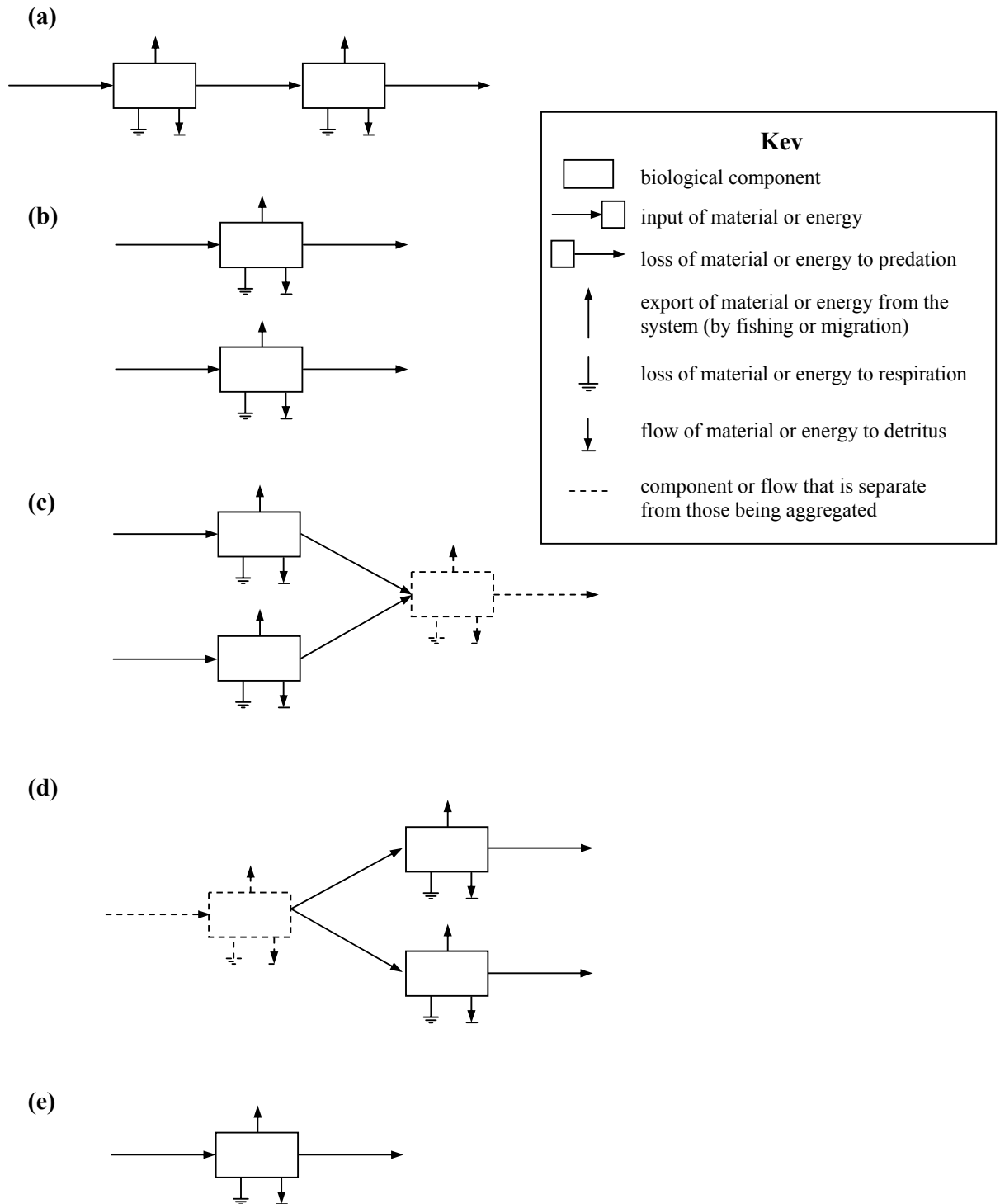
Natural ecological systems are inherently complex and it is neither possible nor desirable to model them exactly. Increasing focus on using ecosystem models as an integrated part of fisheries, water quality and general system level management has highlighted the importance of the issue of simplification. Simplified models have a number of desirable characteristics. They are often easier to comprehend (Iwasa et al. 1987), they can be economically or logistically attractive as they require less input information (Sugihara et al. 1984), and they are less computationally intensive (Lee and Fishwick 1998). Ludwig and Walters (1985) have also shown that simplified models can be more effective than more complex versions, as the simpler models do not suffer as much error propagation or sensitivity to parameterisation. Another potential advantage of simplified models, particularly aggregated ones, is that they are not tied to individual species and so, by definition, are more generic. Consequently, they may be more robust to change and amenable to application. Simplifications must be made and one way in which this can be done is by simplifying the underlying food web.

Model simplification by aggregation involves simplifying the model (and associated food web) by combining components that share common predators, prey or other characteristics. Given the universal use of aggregation in ecology it is not surprising that it has received some attention within the areas of theoretical systems ecology (O'Neill and Rust 1979, Iwasa et al. 1987) and biogeochemical modelling (Zeigler 1976, Cale and Odell 1980, Gardner et al. 1982, Cale et al. 1983). A common finding across many studies is that components of a system may be aggregated with little error if the property being scaled is highly correlated among the components

(Bartell et al. 1988), or if their rate constants are similar (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et al. 1982, Cale et al. 1983, Iwasa et al. 1987), or if one of the components is consistently comparatively rare (O'Neill and Rust 1979, Cale et al. 1983). However, it is also recognised widely that because an aggregate is not capable of producing exactly the same behaviour as the constituent components, errors due to inappropriate aggregation can be excessive (O'Neill 1979, Cale and Odell 1980, Gardner et al. 1982, Cale and O'Neill 1988, Iwasa et al. 1987, Rastetter et al. 1992). For example, aggregating components that are serially linked (Figure 5.1a) is ill advised in most cases, while aggregating components that are in parallel (Figure 5.1b), or share a common predator or prey (Figures 5.1c and 5.1d), is usually acceptable if their rate constants are within two- or threefold of each other (Gardner et al. 1982). It has also been found that if aggregated parameters cannot be measured accurately then the compounding effects of aggregation and measurement error result in significant output error and poor model performance (Gardner et al. 1982, Rastetter et al. 1992).

An alternative method of model simplification is reduction in model complexity by omitting, rather than aggregating, components. This method follows from the suggestion that system behaviour may be characterised by the dynamics of dominant, or representative, species. Despite being central to the concept and use of indicator species, this approach has not received the same level of theoretical and modelling attention as simplification by aggregation. There is little work that directly considers the effects of omitting groups on model performance, and the implication for the use of models simplified in this way. The work that has been done has largely concentrated on models using randomly constructed food webs to investigate the effects of diversity on system stability (May 1973), or food chain models where entire trophic levels are considered rather than individual species or guilds (Carpenter and Kitchell 1993), or models of plankton ecology (Yool 1998, Edwards 2001). Conclusions pertaining to more complete

Figure 5.1: Diagrams of the most common system configurations that are simplified by aggregating groups: (a) in series, (b) in parallel, (c) triangular with a shared predator, (d) triangular with a shared prey and (e) the aggregated form (identical for all).



or realistic ecosystem models may be drawn by considering changes in model performance as models are constructed incrementally (e.g. ERSEM I vs ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997)). The “insurance” or “redundancy” hypothesis (Yachi and Loreau, 1999) suggests that without any change in ecosystem conditions at least some of the redundant species or groups could be removed without the system changing substantially. However, the idea that overall mean interaction strength is closely linked to system behaviour implies that removing a single species could cause a significant shift in system dynamics (McCann 2000). Work by Yodzis (2000) on the diffusion of the effects of interactions through food webs supports the idea that, at least in some ecosystems, considering only a small subset of the food web is inappropriate as even the influences of small perturbations will not be represented accurately. However, the issue is far from resolved. Those studies considering the effect of trophic complexity on models of plankton ecology indicate that some simplification is possible, e.g. models that omit bacteria and certain nutrient groups still perform well (Yool 1998), but the effects of simplification can be dependent on the linkages captured in the modelled web (Edwards 2001). However, because the food webs included in the full versions of these plankton models are very simple, more work considering larger and more realistic food webs is necessary.

The greatest interest in the effects of trophic complexity on ecosystem models was born of the modelling efforts associated with the International Biological Program (e.g. O'Neill 1975, Watt 1975 and Wiegert 1975). However, it has a wider place within theoretical ecology in the long running debate over the relationship between stability and diversity in food webs. Historically, field studies suggested that an increased number of biological components would confer greater stability on a community (Odum 1953, MacArthur 1955, Elton 1958). In contrast, some mathematical studies suggested the opposite and indicated that randomly constructed model communities tended to

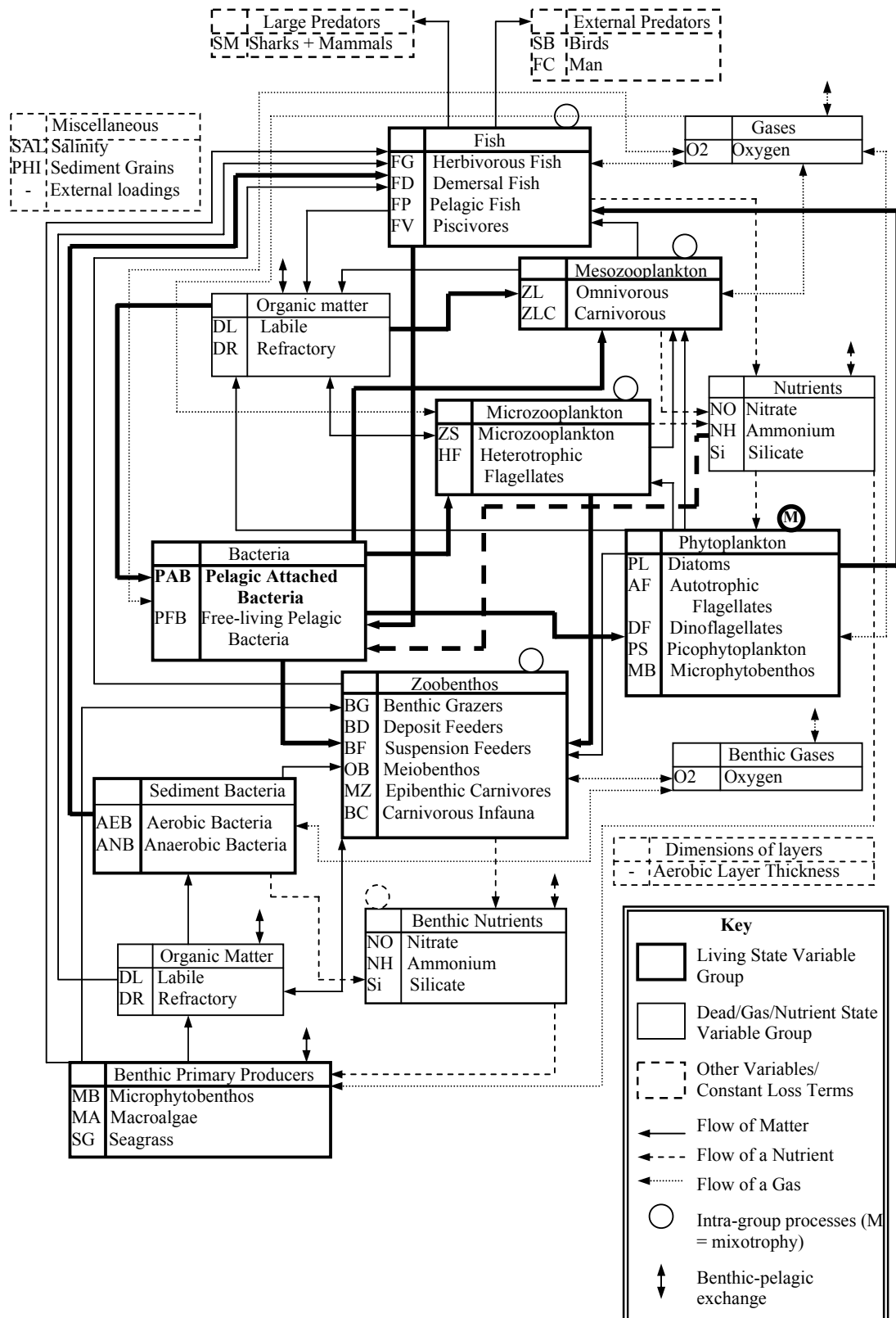
destabilise as they became more complex (Gardner and Ashby 1970, May 1973, Pimm and Lawton 1978). Later studies have shown that these two sides of the problem are not inconsistent as natural systems are not constructed randomly and are characterised by a large number of buffering mechanisms, as well as material conservation and external dependencies or linkages (De Angelis 1975, Yodzis 1981, Tilman and Downing 1994, Sterner et al. 1996, McCann et al. 1998, Harding 1999). However, the debate is not yet resolved and the consideration of models using more realistic food webs, constraints (e.g. material conservation) and physical forcing still has much to offer, given that it is doubtful that there is a simple relationship between diversity and stability when more realistic systems are considered. If theories such as the “weak interaction effect” (McCann 2000) are correct, it is likely that simplification of a system will take the system through alternating periods of increased and decreased stability as the ratio of strong:weak interactions is modified in one direction or another. Monitoring the behaviour of models under a series of simplifications may help to give some insight on this topic.

Here we report the effects of model simplification by aggregating or omitting groups in two biogeochemical ecosystem models. The work and ecosystem models used are part of a larger study on the effects of model structure and complexity on the performance and behaviour of ecosystem models.

5.2 Methods

To investigate the effects of trophic complexity on model performance the food web (Figure 5.2) implemented in two biogeochemical ecosystem models is modified in a number of ways, while other features of the models (e.g. spatial resolution, stoichiometry, processes included) are left unchanged. The two models are Bay Model 2 (BM2) (chapter 2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (chapter

Figure 5.2: Food web diagram for the ecosystem models Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). The Pelagic Attached Bacteria and any flows marked in bold are present in BM2, but not in IGBEM.



1). The two models share a similar list of biological components (Table 5.1), which represent the typical list of functional guilds found in a temperate bay system. Both models include the same biological, physical and chemical processes, but in differing degrees of detail (Table 5.2).

Table 5.1: List of the biological components in the full versions of Bay Model (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Component	Codename
Diatoms	PL
Autotrophic flagellates	AF
Picophytoplankton	PS
Dinoflagellates	DF
Free-living pelagic bacteria	PFB
Pelagic attached bacteria (BM2 only)	PAB
Heterotrophic flagellates	HF
Microzooplankton	ZS
Large omnivorous zooplankton	ZL
Large carnivorous zooplankton	ZLC
Planktivorous fish	FP
Piscivorous fish	FV
Demersal fish	FD
Demersal herbivorous fish	FG
Macroalgae	MA
Seagrass	SG
Microphytobenthos	MB
Macrozoobenthos (epifaunal carnivores)	MZ
Benthic (epifaunal) grazers	BG
Benthic filter feeders	BF
Infaunal carnivores	BC
Benthic deposit feeders	BD
Meiobenthos	OB
Aerobic bacteria	AEB
Anaerobic bacteria	ANB

Table 5.2: Processes and structure 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

Briefly, IGBEM is a physiologically explicit biogeochemical process model, which follows the carbon, nitrogen, phosphorus and silicon pools of its biological components (chapter 1). It was constructed using the physical and biogeochemical submodels of the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow

1997, 1999a) and the biological groups of the European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997). The benthic primary producers included in PPBIM were retained in IGBEM, as there was no analog present in ERSEM II. In addition, herbivorous benthic invertebrates and fish were added, using the same general formulation structure as ERSEM, to exploit the benthic primary production and complete the food web.

In comparison with IGBEM, BM2 has much less process detail, using relatively simple general equations of assimilation and waste handling, and only representing the nitrogen and silicon pools of the biological components. This formulation was the one used in PPBIM, and BM2 was developed by extending that formulation to cover all of the groups in IGBEM (chapter 2).

5.2.A Aggregating functional groups

When components and their associated links are aggregated all the original linkages to the separate components are kept but directed to the aggregated group. The parameter values used for the aggregated group represent the weighted average of the parameters for the constituent components. Thirty-three simplifications of the web structure are made by aggregating components (Table 5.3). These simplifications reflect aggregations made in other field and model studies (for example “other benthos” is a common feature of the ECOPATH models primarily concerned with finfish, but which attempt to include a broad picture of the entire web (Christensen 1992)). We consider a range of intensity of amalgamation, from slightly aggregated cases to a massively reduced web with only phytoplankton, zooplankton, fish, benthos and macrophyte aggregated groups. The aggregated webs also span cases where only the pelagos or benthos is considered. Thus, some runs include only pelagic components, while others have only benthic components (apart from a pelagic food group, which is a forcing

Table 5.3: List of the trophic simplifications of the food web made by aggregating groups. Bars indicate groups lumped together in constructing aggregated groups. Codes for the base groups are given in Table 5.1. “Pelagic only” runs only include the pelagic fraction of the food web, “Pelagic and benthic” runs include pelagic and benthic groups, and “Benthic only” runs only include the benthic fraction of the food web. Note that all the groups above the dotted line are considered to be pelagic components and all the groups below the dotted line are considered to be benthic components.

Codes for model runs in which groups are aggregated																																			
Group Code	Pelagic and benthic																Benthic only																		
	LP1	LP2	LP3	LP4	LP5	LP6	LP7	LP8	LA1	LA2	LA3	LA4	LA5	LA6	LA7	LA8	LA9	LB1	LB2	LB3	LB4	LB5	LB6	LB7	LB8	LB9	LB10	LB11	LB12	LB13	LB14	LB15	LB16		
PL																																			
AF																																			
PS																																			
DF																																			
PFB																																			
PAB ⁺																																			
HF																																			
ZS																																			
ZL																																			
ZLC																																			
FP																																			
FV																																			
FD																																			
FG																																			
MA																																			
SG																																			
MB																																			
MZ																																			
BG																																			
BF																																			
BC																																			
BD																																			
OB																																			
AEB																																			
ANB																																			

* A generic water column food group for the benthic feeders that is a forcing function and not a dynamic group.

⁺ Bay Model 2 only. In the Integrated Bay Model the Pelagic Free Bacteria alone were present in the “pelagic bacteria metagroup”.

function). For ease of reference, each of the runs using aggregated webs has a code (listed in Table 5.3). These codes begin with L, the second letter indicates the fraction of the ecosystem considered (P for pelagic only, B for benthic only, and A for benthic and pelagic), and the number represents the degree of aggregation (the lower the number the more highly aggregated the model web).

5.2.B Omitting functional groups

When a group is omitted from the web there are no re-parameterisations of the remaining components or changes in model formulations, with two exceptions. When a predatory group is removed from the web, the mortality parameters of its prey groups are adjusted to implicitly include the predation pressure that was explicit when the predator was still active in the web. Second, when bacteria are omitted from BM2 runs, the empirical model of denitrification proposed by Murray and Parslow (1999a) for PPBIM is used in place of the sediment chemistry module that was dependent on bacteria. This empirical sediment chemistry model is standard for all runs of IGBEM. Overall, twenty-one simplified forms of the original web are made by omitting groups (Table 5.4). These range from the complete omission of all but two of the components to the omission of only a few components, primarily those that are not as commonly included in system models. One special class of omission is truncation. The most common form of truncation is when either the lower or top ends of the trophic web are removed (e.g. consider the pelagic groups of OP1, where every group above zooplankton is omitted). The list of simplified forms includes examples of truncation. Another form of truncation is when an entire subweb is dropped, restricting the coverage of the web to certain habitat types. For example, some runs include only pelagic biological components (though the sediment chemistry and detritus pools remain), while others have only the benthos as dynamic components (a pelagic food

Table 5.4: List of the trophic simplifications of the food web made by omitting groups. “Y” indicates inclusion of the group in that version of the modified food web. The codes for the groups are given in Table 5.1. “Pelagic only” runs only include the pelagic fraction of the food web, “Pelagic and benthic” runs include pelagic and benthic groups, and “Benthic only” runs only include the benthic fraction of the food web. Note that all the groups above the dotted line are considered to be pelagic components and all the groups below the dotted line are considered to be benthic components.

Codes for model runs in which groups are omitted																					
Group Code	Pelagic only										Pelagic and benthic										
	OP1	OP2	OP3	OP4	OP5	OP6	OP7	OA1	OA2	OA3	OA4	OA5	OB1	OB2	OB3	OB4	OB5	OB6	OB7	OB8	OB9
PL	Y	Y			Y	Y	Y	Y	Y	Y	Y	Y	Y*	Y*	Y*	Y*	Y*	Y*	Y*	Y*	Y*
AF				Y	Y	Y	Y		Y	Y	Y	Y									
PS			Y	Y	Y	Y	Y		Y	Y		Y									
DF					Y	Y	Y														
PFB							Y					Y									
PAB ⁺							Y ⁺					Y ⁺									
HF																					
ZS				Y	Y	Y	Y		Y	Y	Y	Y									
ZL	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y									
ZLC																					
FP		Y	Y	Y		Y	Y	Y	Y	Y	Y	Y									
FV						Y	Y	Y													
FD							Y	Y	Y	Y	Y	Y			Y			Y	Y	Y	Y
FG								Y	Y	Y	Y	Y			Y			Y	Y	Y	Y
MA								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
SG										Y	Y	Y				Y	Y	Y	Y	Y	Y
MB											Y					Y		Y		Y	Y
MZ								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
BG											Y	Y				Y		Y	Y	Y	Y
BF								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
BC										Y	Y	Y				Y	Y	Y	Y	Y	Y
BD										Y	Y	Y				Y	Y	Y	Y	Y	Y
OB												Y					Y	Y	Y	Y	Y
AEB												Y					Y	Y	Y	Y	Y
ANB												Y					Y	Y	Y	Y	Y

* A generic water column food group for the benthic feeders that is a forcing function and not a dynamic group.

⁺ Bay Model 2 only.

group is present in these runs, but it is only a forcing function in this case). As for the runs using webs produced by aggregating groups, each of the runs using a web produced by omitting groups has a code (listed in Table 5.4). These codes begin with O, the second letter indicates the fraction of the ecosystem considered (as before, P for pelagic only, B for benthic only, and A for benthic and pelagic), and the number represents the relative amount of omission used (the lower the number the more groups that have been omitted from the model web).

5.2.C Altered ecosystem conditions

Some of the runs (Table 5.5) were repeated with nutrients, or fishing pressure, increased fivefold. These runs were chosen to span the range in magnitude of simplification by omission and aggregation. This allows for consideration of the effects of ecosystem change on the relative performance of models with varying trophic complexity.

Table 5.5: List of the trophic simplifications (models) considered under a fivefold increase in nutrient load or fishing pressure. Codes are as in Table 5.3 for models with aggregated groups and in Table 5.4 for models with omitted groups.

Models with aggregated groups	Models with omitted groups
LP2	OP1
LP5	OP2
LA1	OP6
LA3	OA1
LA6	OA4
LA8	OB1
LB4	OB3
LB8	OB6
LB14	OB8

5.2.D Analysis

Summarising the overall effects of model simplification

To summarise the range of system structures encompassed by the simplifications we examine, the number of links and connectance (C) of the system is plotted against the number of groups in each case. C was calculated as given in Putman (1994):

$$C = \frac{L}{N(N-1)} \quad (5.1)$$

where C is connectance, L is the number of links in the web and N is the number of separate “species” in the web (in this case either the original components or the aggregated groups). A number of indices (chlorophyll a, levels of sediment oxygen, denitrification and the biomass, production and consumption of each of the components in the models) are used to judge the relative performance of the models. In each case the runs are compared by considering the absolute relative value of the difference between the averages (over the entire bay for the final four years of each run) of the simplified and standard (full version) runs of the model. Finally, the following measure was taken as an overall indicator of performance:

$$V = \sum_j \frac{|I_j^{std} - I_j^{simplif}|}{I_j^{std}} \quad (5.2)$$

where I_j is the j th relevant indicator (i.e. V 's calculated for runs containing pelagic components only are based only on pelagic indicators) and “std” and “simplif” indicate the value of the j th indicator for the standard run and simplified run respectively. The simplified model with the smallest value of this overall measure V is considered to have the best overall performance. It is recognised that a very low contribution for a single indicator (I_j) by a run with generally poor performance could better a consistent performance by another run. Fortunately this situation does not arise here. For models that omitted groups, the models that produced the minimum values of V are also the ones that are consistently sound performers (within the top 25%). The relative quality of

each run, as specified by the indicators, is not as consistent for models with aggregated groups as for models with omitted groups. However, the use of V as an overall summary statistic is still acceptable as the “best” run was usually within the top 35% for every indicator.

Summarising the fine scale spatial and temporal effects of model simplification

The output is also considered on a cell-by-cell basis, not just for the bay as a whole. This allows for detection of effects of model simplification on the spatial details of the output.

To judge the effects of model simplification on the fine scale spatial dynamics of the models the relative spatial distributions of each component was tracked over the final four years of each run. The quality of the match at each point is based on the number of boxes for which the distribution in the run using a simplified web differs from the distribution predicted in the standard run. To summarise these results across runs, three broad categories of responses are recognised:

- the spatial distribution of the component matches the spatial distribution in the standard run for the majority of the runs using simplified webs
- there is no match between the spatial distribution of the component in the standard run and any of the runs using simplified webs
- there is only a match between the spatial distribution of the component in the standard run and the runs using simplified webs that have the lowest values for V (as defined above).

A simple comparison of the time series of each component (achieved by overlaying the time series from simplified runs on the time series from the standard run) is used to judge the effects of model simplification on the temporal dynamics of the model.

5.3 Results

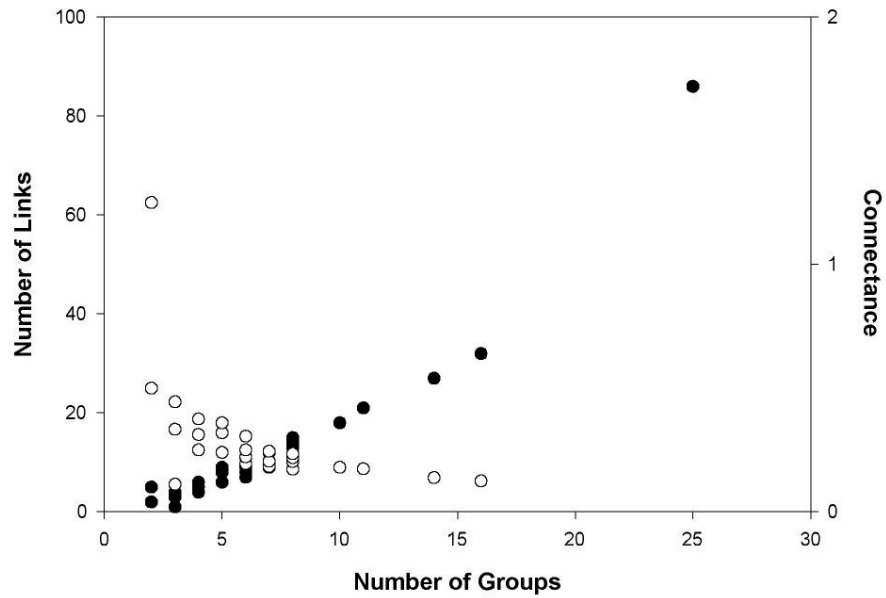
When simplification of the food web is produced by aggregating components there is a clear increase in connectance as the number of nodes (individual components or aggregated groups) is decreased (Figure 5.3). This reflects the marked decrease in the number of links remaining in the web as the number of nodes is reduced (Figure 5.3). Results for simplified food webs produced by omitting groups are similar (Figure 5.4), but the relationships are not as tight. In both cases (omission and aggregation of groups) the small differences in web structure between BM2 and IGBEM (BM2 has an additional pelagic bacteria group) have little effect on the results (Figure 5.3(a) vs. 5.3(b), and Figure 5.4(a) vs. 5.4(b)).

Effects of aggregating groups

In both IGBEM and BM2, a number of the models with aggregated groups that only consider the benthos (the LB models) show trophic self-simplification through the extinction of some functional groups. Some of the simplified versions of BM2 that are the most highly aggregated (runs LB2 – LB4, see Table 5.3 for definitions of the codes) lose the composite “all benthos” component, as does the LB4 run of IGBEM. While no groups go extinct in the less aggregated LB runs of BM2, some groups are lost in IGBEM with the same level of aggregation. The LB8, LB9 and LB12 runs of IGBEM all suffer some form of trophic self-simplification. All of these runs have an aggregated demersal fish group, microphytobenthos and infauna and epifauna groups that are aggregated to slightly different degrees. In LB8 all but the microphytobenthos drop to negligible levels of biomass; LB9 loses the lumped “all infauna” group; and LB12 loses the “large infauna” aggregated group. It is noteworthy that these models undergo trophic self-simplification in IGBEM when they do not in BM2 and that even other versions of IGBEM with very similar levels of aggregation (e.g. LB10 and LB11) do

Figure 5.3: Plot of connectance (C) (open circles) and the number of links (solid black circles) in the simplified food webs produced by aggregating components, against the number of groups (individual functional groups or aggregated groups) in the webs.

(a) Bay Model 2 (BM2)



(b) for the Integrated Bay Ecosystem Model (IGBEM)

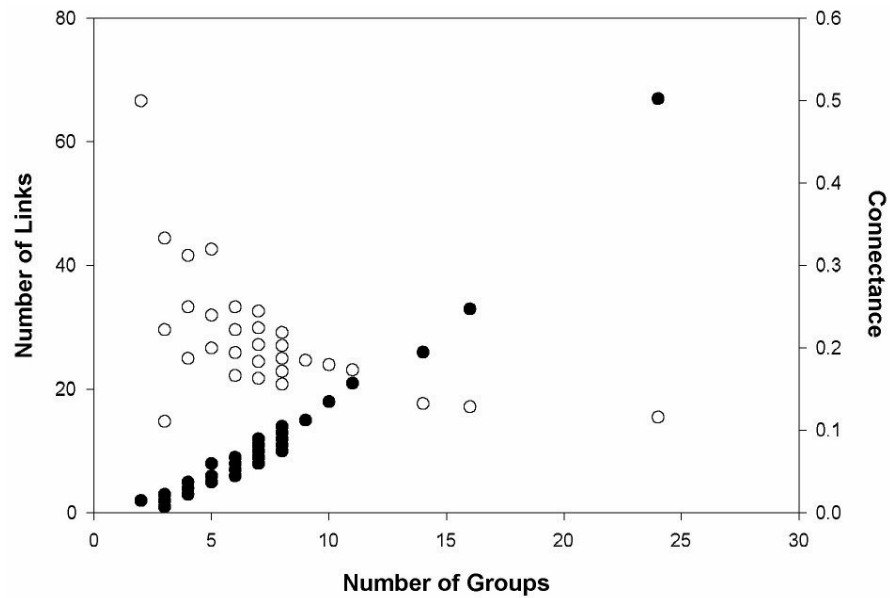
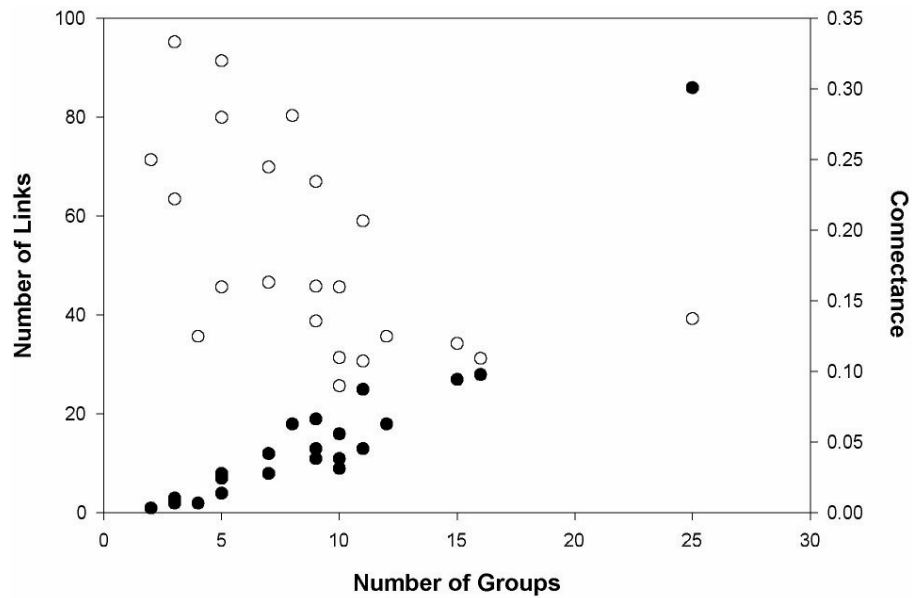
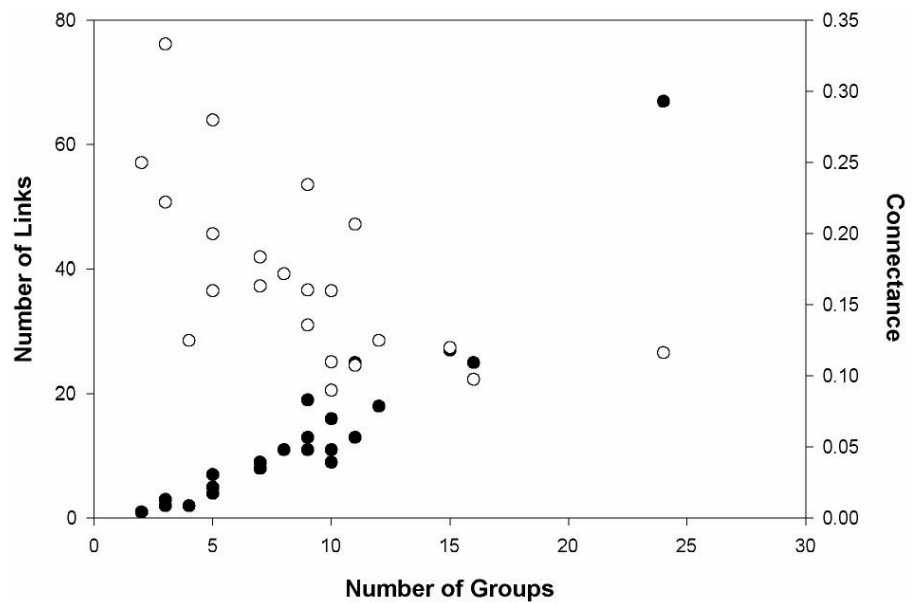


Figure 5.4: Plot of connectance (C) (open circles) and the number of links (solid black circles) in the simplified food webs, produced by omitting components, against the number of functional groups in the webs.

(a) Bay Model 2 (BM2)



(b) the Integrated Bay Ecosystem Model (IGBEM)



not self-simplify in this way. Two of the runs that use aggregated food webs that span pelagic and benthic components also predict the extinction of some groups. In the LA8 run of BM2 the benthic consumers, except the “mobile epifauna”, decline to negligible levels, and the LA9 run of IGBEM loses the diatoms and the aggregated group “small zooplankton”. There are also a number of versions of IGBEM with aggregated groups where the system approaches numerical instability (these are LA3 and all of the LB runs that include the aggregated groups “macrophytes” or “all phytobenthos”).

It is possible to compare indices across the models despite extinction of some groups and potential instabilities. A majority of the indices show no clear patterns when the absolute relative differences in the values for the simplified and standard runs are plotted against the number of groups in the run (Figure 5.5). Only denitrification shows a clear effect of aggregating groups, and that is that the upper bound of the absolute relative difference in predicted denitrification in the simplified vs full models increases as more groups are aggregated (Figure 5.5). None of the indicators shows any clear patterns when plotted against connectance for either BM2 or IGBEM.

A final way of considering the baywide averages for the indices is to evaluate them in relation to the subwebs that are preserved in each run, that is to explicitly consider the results per run. Considering the results of each run in this way, it is clear that the behaviour of models with aggregated groups are frequently very different to those of the full versions without aggregation. Deviations from the non-aggregated models of the predicted values of the various indicators are often greater for versions of BM2 and IGBEM with aggregated groups than for versions with omitted groups (Table 5.6). The amount of deviation has a non-linear relationship with the level of aggregation used. For each indicator there is usually one or more runs with intermediate levels of aggregation for which the amount of deviation is smaller than for other runs with higher or lower levels of aggregation (e.g. chlorophyll a in the LP runs, Figure 5.6). This

Figure 5.5: Plots of the absolute relative differences in the predicted values of indices between the simplified (with aggregated trophic groups) and full versions of the models in relation to the number of groups (individual functional groups or aggregates) included in the models. (Note: the larger the number of components the lower the degree of aggregation.) The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles. The indices are: (a) chlorophyll a in the water column, (b) chlorophyll a on the sediments, (c) denitrification, (d) concentration of oxygen in the sediments, (e) water column primary production, (f) total consumption in the water column, (g) benthic primary production, (h) total benthic consumption, (i) biomass of macrophytes, (j) biomass of zooplankton, (k) biomass of benthos, and (l) biomass of fish.

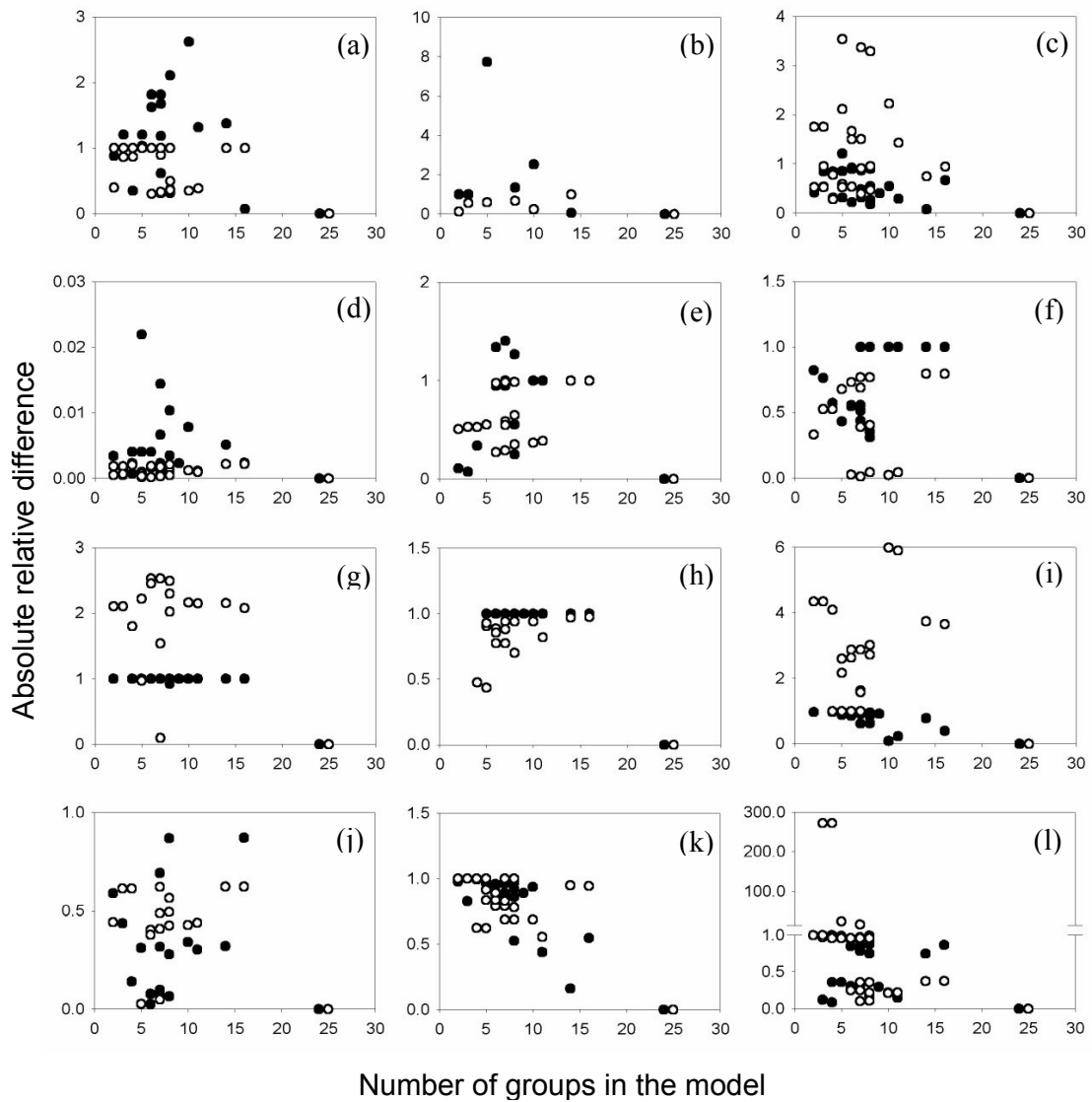


Table 5.6: Comparison of the magnitude of average relative deviation from the full models of the indices from runs produced by aggregation and omission of groups for Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM). Values in the table are the average ratio of the deviation for models with aggregated groups: the deviation of models with omitted groups with the same degree of simplification.

Index	BM2	IGBEM
Biomass of fish	59.3	1.0
Biomass of macrophytes	7.7	2.2
Biomass of zooplankton	0.8	0.9
Biomass of benthos	0.5	0.5
Chlorophyll a	0.5	1.4
Consumption (water column)	1.0	1.2
Consumption (sediment)	1.5	2.2
Denitrification	1.2	1.8
Primary Production (water column)	2.3	1.3
Primary Production (sediment)	3.7	2.0
Sediment Oxygen	0.3	1.3

general pattern is also evident in the overall V statistics for models with aggregated groups (Table 5.7). Consideration of the structure of the food web in each of the models with aggregated groups (Table 5.3) that have the lowest V values (Table 5.7) suggests that retaining broad trophic level and size structure is necessary for reasonable model performance.

Considering fine-scale spatial and temporal resolution rather than baywide averages, there are still strong effects of aggregating groups. Overall, there are relatively few processes with a fairly consistent distribution over all the runs and these are driven largely by production and consumption by the fish (Table 5.8). There are many more components and processes for which the relative spatial distributions in the runs with aggregated groups do not match the relative spatial distribution of the non-aggregated model (Table 5.8). Many of these processes and measures are associated with bacteria. A notable exception is the biomass of zooplankton. None of the runs with aggregated groups predict a relative distribution for this measure which matched the relative distribution in the full versions of BM2 or IGBEM. In comparison to the number of components and processes that do not match the relative distribution of the standard run, a similar number have relative spatial distributions that only match those of the standard

run for the models with aggregated groups that have the lowest V values (e.g. LA5 for BM2). For many of the benthic components and processes in this category there is a discernible degradation between the match of the relative spatial distribution in the runs with aggregated groups and the distribution in the full version as the amount of aggregation is increased. Generally there is a sharp transition in performance at the point when the aggregation of groups removes the size structuring of the benthic primary producers and the distinction between infauna and epifauna.

Table 5.7: Overall performance indicators (V) for the simplified versions of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM), when simplification was by aggregating trophic groups. The lower the value of V the better the overall performance of the run relative to the full model.

Run	Pelagic Only		Pelagic and Benthic		Benthic Only	
	BM2	IGBEM	BM2	IGBEM	BM2	IGBEM
LP1	1.68	2.40				
LP2	274.56	2.60				
LP3	275.04	1.48				
LP4	3.08	3.54				
LP5	1.25	4.25				
LP6	1.27	4.24				
LP7	3.74	4.55				
LP8	3.68	2.08				
LA1			35.21	15.25		
LA2			24.06	14.99		
LA3			24.91	7.04		
LA4			10.71	8.42		
LA5			9.44	12.34		
LA6			11.47	10.30		
LA7			11.18	7.68		
LA8			11.20	6.53		
LA9			11.31	6.93		
LB1					3.53	3.37
LB2					4.53	4.85
LB3					4.76	3.40
LB4					5.73	3.67
LB5					4.95	4.85
LB6					4.75	3.67
LB7					3.34	4.55
LB8					5.13	3.48
LB9					4.29	4.43
LB10					3.37	3.59
LB11					5.03	3.47
LB12					4.22	4.67
LB13					4.42	3.21
LB14					5.03	4.22
LB15					4.58	4.23
LB16					3.91	3.47

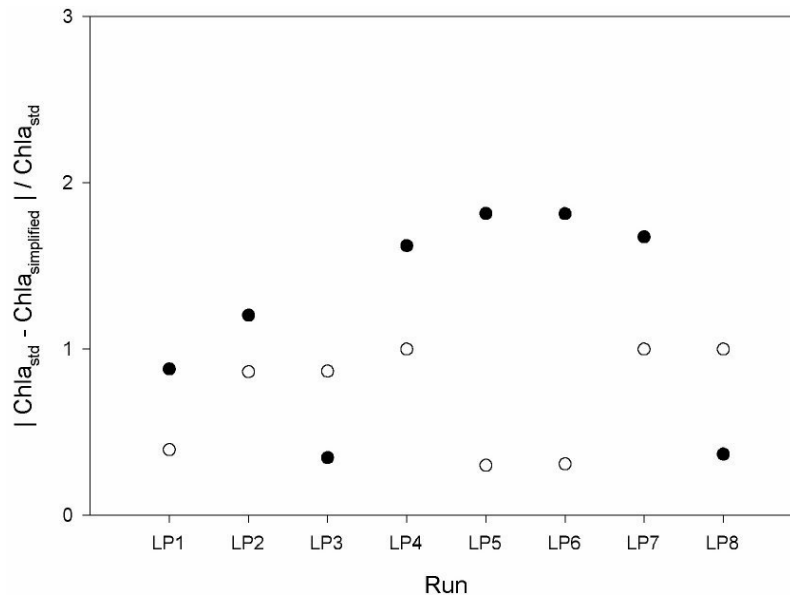


Figure 5.6: Relative differences between the chlorophyll a concentrations provided by the simplified (with aggregated trophic groups) and full (std) models. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

Table 5.8: Categories of the effects of aggregating groups on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Codes are as in Table 5.1, and the standard distribution is the spatial distribution in the full model.

Match standard distribution for most runs	No match with standard distribution	Match standard distribution only for runs with lowest V values (see Table 5.7)
<ul style="list-style-type: none"> • Total water column secondary production and consumption • Total production and consumption by pelagic, piscivorous and demersal fish • Total denitrification (BM2 only) 	<ul style="list-style-type: none"> • Biomass of zooplankton • Biomass of pelagic bacteria • Biomass of sediment bacteria • Total production and consumption by pelagic bacteria • Total production and consumption by sediment bacteria • Biomass of phytobenthos (BM2 only) • Biomass of epifauna (BM2 only) • Total benthic primary production (IGBEM only) 	<ul style="list-style-type: none"> • Chlorophyll a • Total water column primary production • Total benthic secondary production and consumption^T • Biomass of infauna^T • Total biomass of the benthos^T • Total biomass of fish^T • Biomass of phytobenthos (IGBEM only)^T • Biomass of epifauna (IGBEM only) • Total denitrification (IGBEM only)

^T Threshold effect: with a decrease in aggregation there is a sharp transition between displaying very poor relative spatial distributions and approaching the relative spatial distribution of the full model.

The temporal dynamics displayed by the models with aggregated groups are more often like each other than the corresponding components in the standard run of BM2 or IGBEM. For example, for BM2 the time series for “large zooplankton” in LP2 is similar to the time series produced by adding the time series for “small zooplankton” and “large zooplankton” in LA6, but is markedly different from the time series produced by adding the time series for all the zooplankton groups in the standard run (Figure 5.7). The general forms of the dynamics of aggregated and non-aggregated models is more similar when the amount of aggregation is lower, though even then critical details such as bloom peaks are not predicted accurately in versions with aggregated groups (Figure 5.8). If the degree of aggregation is high then there is little, if any, resemblance between the temporal dynamics of the standard and simplified runs for a large number of the trophic groups, particularly the fish, benthos and macrophytes.

Effects of omitting groups

BM2 demonstrates trophic self-simplification, in which functional groups went extinct in the run, in 5 cases. In OA2 (see Table 5.4 for definitions of the codes), macroalgae was lost from the system, while in OB4, OB6, OB8 and OB9 the biomass of the benthic deposit feeders fell to negligible levels. In contrast, for IGBEM, macroalgae and the benthic deposit feeders show a reduced spatial distribution for some of the runs, but no component is entirely lost from the system.

There are a number of runs where the system becomes susceptible to the effects of increased short-term nutrient loading (e.g. flooding of the Yarra River, which is a key point source of inputs in the model). As a result the system exhibits extreme behaviours (such as high amplitude oscillations in some components) or approaches numerical instability. This is more common in IGBEM than in BM2. In BM2 only OA5 exhibits this problem, while for IGBEM the runs OB2 – OB9 (inclusive) also display this behaviour.

Figure 5.7: Comparison of the temporal dynamics of “large zooplankton” in LP2, the time series produced by adding the time series for “small zooplankton” and “large zooplankton” in LA6 and the time series produced by adding the time series for all the zooplankton groups in the standard (full) version of Bay Model 2 (BM2). The codes for the runs simplified by aggregating groups (LP2, LA6) are given in Table 5.3 and all time series come from the same cell of the model (close to the mouth of the modelled bay).

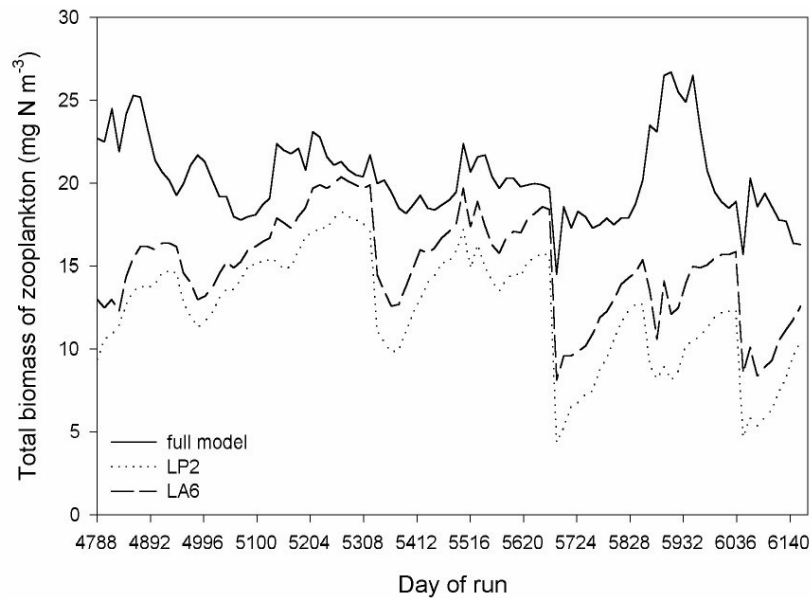
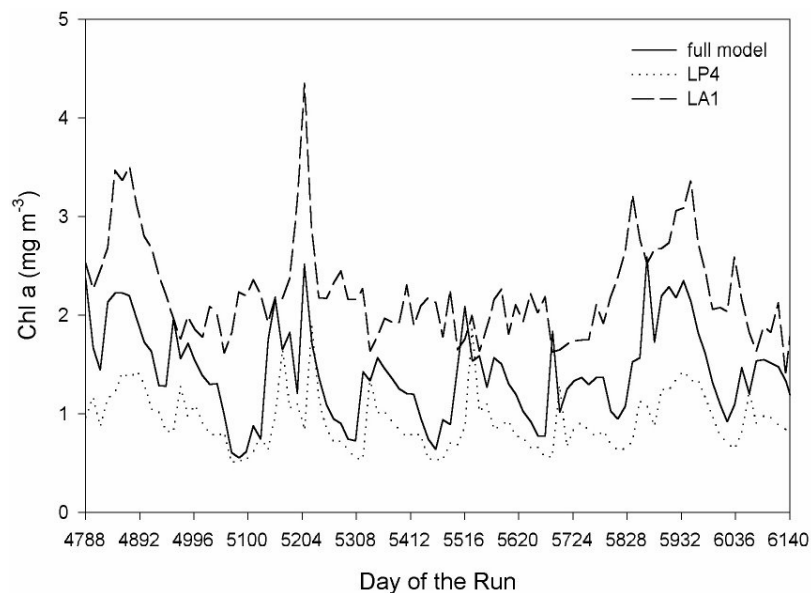


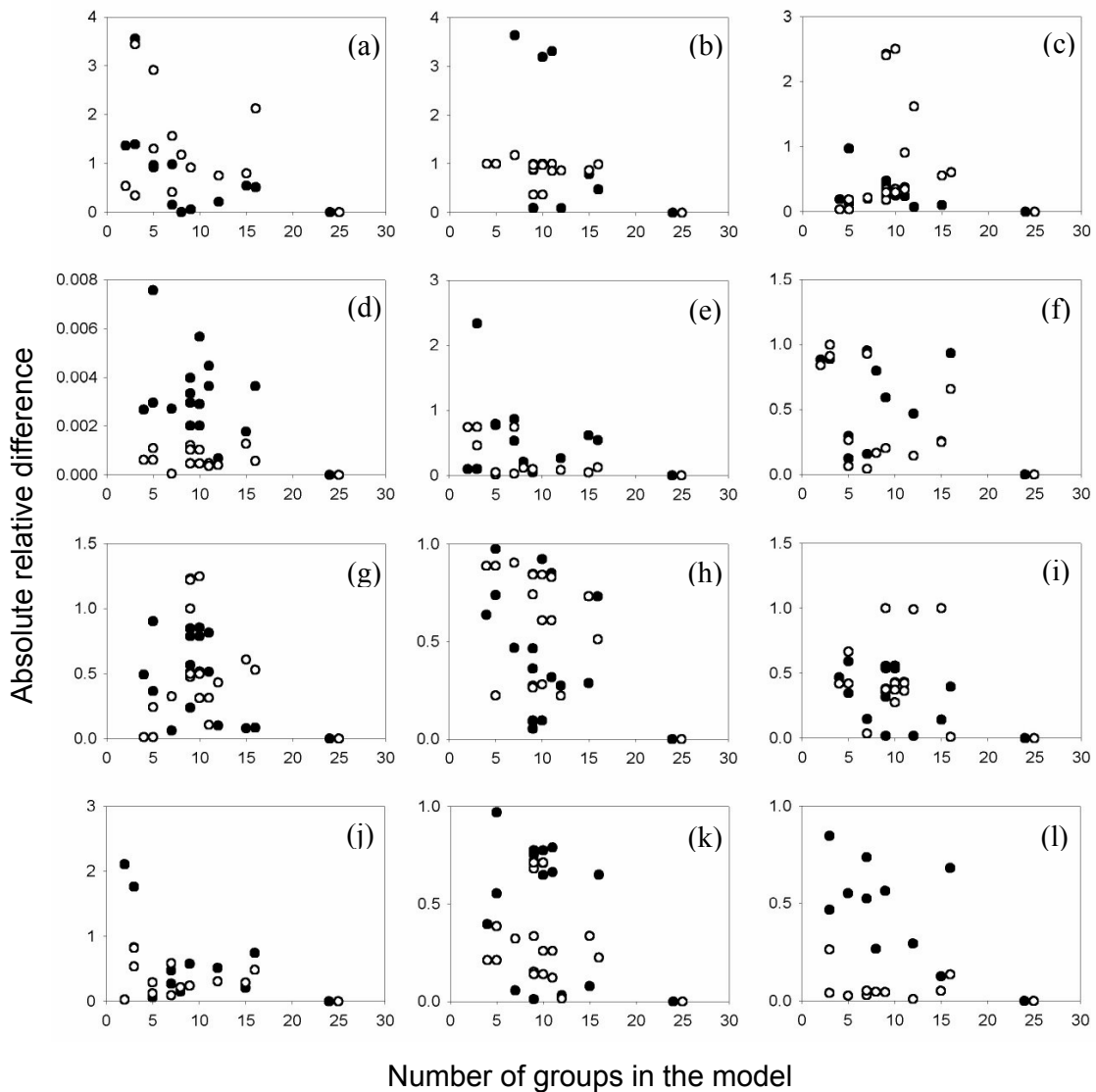
Figure 5.8: Comparison of the temporal dynamics of chlorophyll a (Chl a) in one cell (covering an input point from a sewage treatment plant) of the standard (full) model and versions of Bay Model 2 with aggregated groups. For clarity, only a selection of the simplified models are displayed, but all the simplified models produced levels of Chl a between the extremes presented here.



Despite the extinction of some groups and instabilities, it is possible to compare indices across the models. When the absolute relative differences between the simplified versions (with omitted groups) and the standard (full) model are plotted against the number of groups, there are some clear results and these patterns are stronger for IGBEM than BM2 (Figure 5.9). For BM2 there is no clear overall pattern of the effect of omitting groups on the levels of oxygen (Figure 5.9d) or chlorophyll in the sediment (Figure 5.9b), or the predicted average biomass of planktivorous fish (Figure 5.9l) or macroalgae (Figure 5.9i). There is a clear pattern for the rest of the indices for BM2, but it is not usually as marked as that shown by IGBEM. The general pattern of the effect of omitting groups is that the upper bound on the absolute relative difference between the simplified and full versions of the model increases as more groups are omitted (Figure 5.9). The pattern is not equally strong across all indices, even in IGBEM, and is clearest for water column variables, such as chlorophyll a (Figure 5.9a), the biomass of large omnivorous zooplankton (Figure 5.9j), and denitrification in the sediments (Figure 5.9c). This relationship, between the absolute relative difference between the models and the number of groups omitted, is less evident for the biomass of the benthic groups, for example benthic filter feeders (Figure 5.9k). In contrast to the consistent patterns between performance of reduced models and the number of groups they contain, there is no clear relationship between any of the indices and connectance for either BM2 or IGBEM.

Considering the results of each run individually shows that there are crucial links that have to be included if the behaviour of the simplified models is to approach that of the full version of BM2 or IGBEM. This is indicated clearly by estimates for primary production and consumption (Figures 5.10 and 5.11). If few groups are included in the simplified web then the productivity estimates from simplified models usually diverge from equivalent estimates from the full model by as much as 50-85%. The effect is

Figure 5.9: Plot of the absolute relative differences in the predicted values of indices between the simplified (with omitted trophic groups) and full versions of the models in relation to the number of groups included in the models. (Note: the larger the number of components the fewer groups that have been omitted.) The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles. The indices are: (a) chlorophyll a in the water column, (b) chlorophyll a on the sediments, (c) denitrification, (d) concentration of oxygen in the sediments, (e) water column primary production, (f) total consumption in the water column, (g) benthic primary production, (h) total benthic consumption, (i) biomass of macroalgae, (j) biomass of large omnivorous zooplankton, (k) biomass of benthic filter feeders, and (l) biomass of planktivorous fish.



particularly severe in the “benthic only” runs, where benthic primary production is consistently more than 35% from the value given by the full model, except for some of the simplest of the BM2 cases (OB1 and OB3) where it is within 2% of the standard estimate (Figure 5.10). The results for consumption (Figure 5.11) are largely similar to those for production. Runs with only a few groups in them produce estimates of consumption that deviate most from the standard estimate (by as much as 90%). Notably the consumption estimate from the run with the fewest omitted groups usually also performs poorly (as poorly as the most simplified runs). This suggests that the inclusion of bacteria may not be appropriate in simplified webs.

Consideration of food web structure (Table 5.4) in each of the runs with the lowest values of the V statistic (Table 5.9) indicates that some representation of size structure is required in simplified food webs and that benthic subwebs may need to be more highly resolved than pelagic subwebs. Further, the results suggest that representing many of the microfaunal functional groups may not be necessary.

As might be expected given the overall responses of the model to omitting groups, the fine scale output of the models is also affected by omitting groups. As occurs in the overall indices, not all components and processes in the models are affected to the same degree by the omission of groups. Generally, the relative spatial distribution of some microfauna (meiobenthos and the pelagic bacteria) does not match the standard case for any of the simplified runs in which they are included (Table 5.10). In contrast, the distribution of fish, picoplankton and total water column production is virtually identical to that of the full model for all runs of the simplified versions of BM2 and IGBEM (Table 5.10). There are also a couple of components (macroalgae in BM2 and anaerobic bacteria in IGBEM) for which the relative spatial distributions in the simplified and standard runs are close matches in only one of the two models. It is not surprising that the relative spatial distributions of the fish are close matches in all the

Figure 5.10: Absolute relative differences between estimates of primary production between models with omitted groups (simplif) and the full (std) model. (a) Water column primary production, and (b) benthic primary production. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

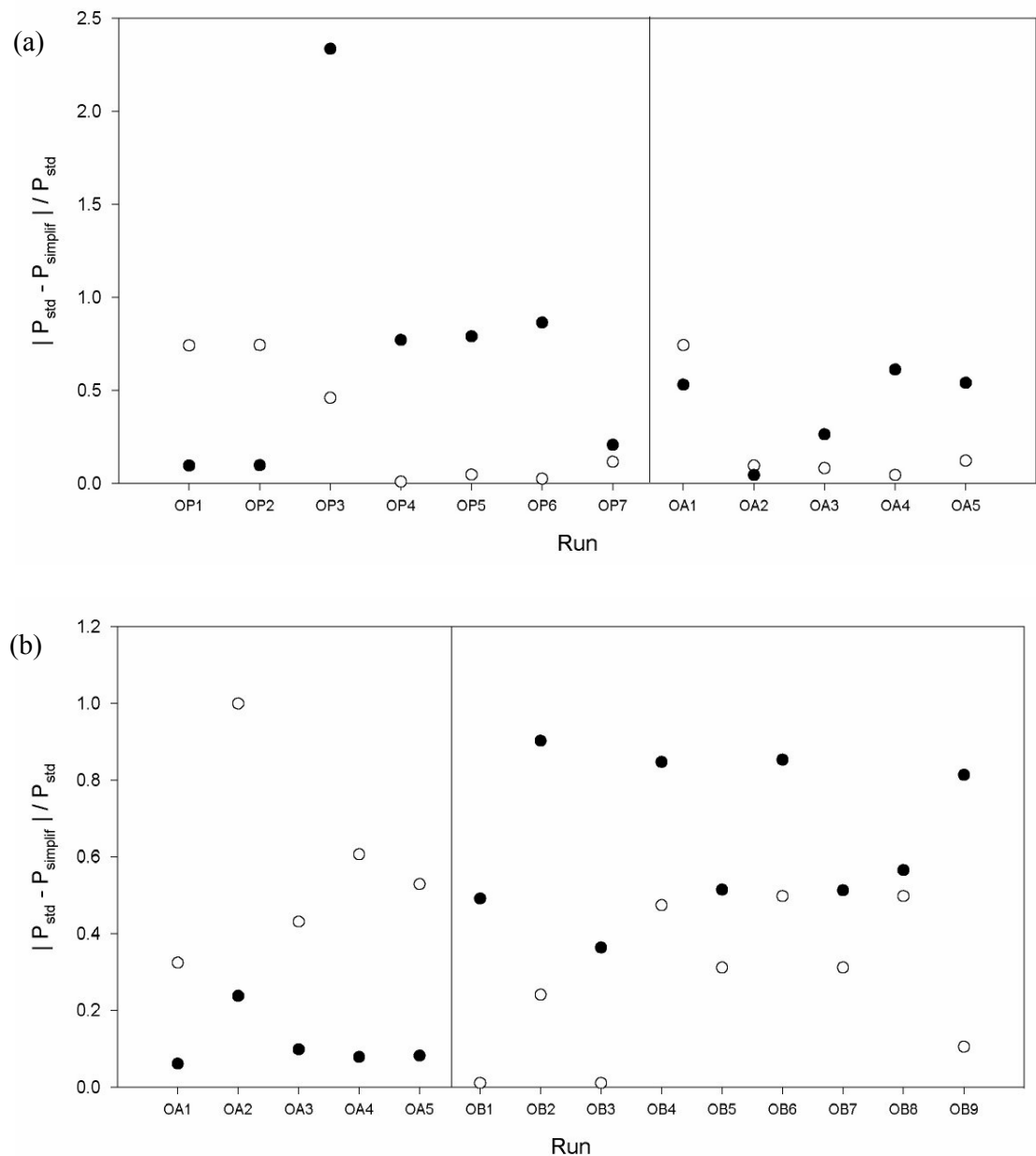


Figure 5.11: Absolute relative differences between estimates of consumption between models with omitted groups (simplif) and the full (std) model. (a) Water column consumption, and (b) benthic consumption. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

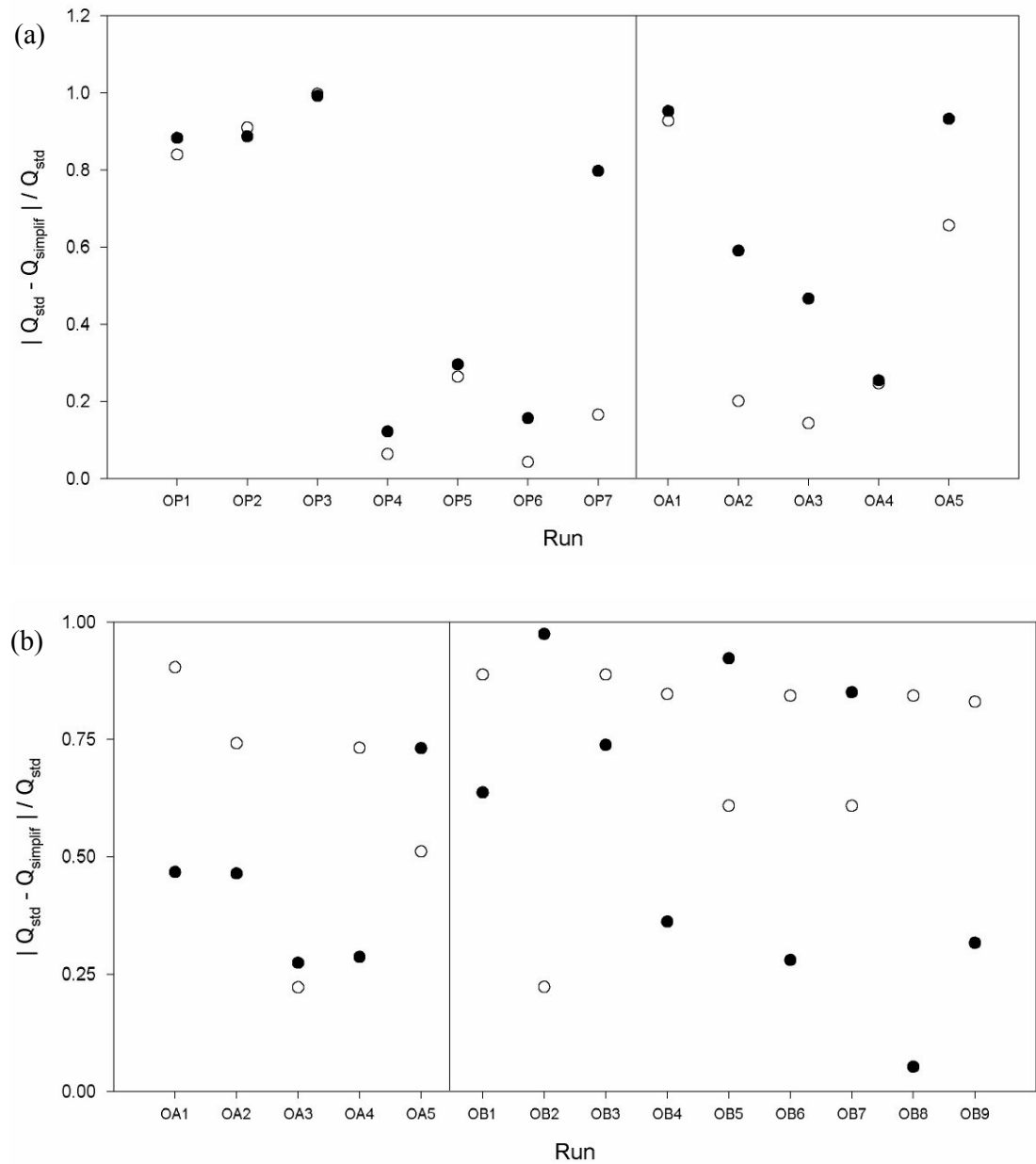


Table 5.9: Overall performance indicators (V) for runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM), with groups omitted from the models. The lower the value of V the better the overall performance of the run relative to the full model.

Run	Pelagic Only		Pelagic and Benthic		Benthic Only	
	BM2	IGBEM	BM2	IGBEM	BM2	IGBEM
OP1	3.00	4.45				
OP2	3.49	4.61				
OP3	6.98	8.57				
OP4	1.62	2.47				
OP5	3.82	2.07				
OP6	1.83	3.00				
OP7	1.92	1.42				
OA1			7.63	7.22		
OA2			6.87	3.20		
OA3			6.40	2.45		
OA4			6.81	3.37		
OA5			14.58	6.69		
OB1					2.57	3.89
OB2					2.71	6.26
OB3					2.58	3.41
OB4					3.09	3.92
OB5					2.96	6.20
OB6					2.54	3.81
OB7					2.95	6.49
OB8					2.54	3.22
OB9					3.20	3.72

Table 5.10: Categories of the effect of omitting groups on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Codes as are as in Table 5.1, and the standard distribution is the spatial distribution in the full model.

Match standard distribution for nearly all runs	No match with standard distribution	Match standard distribution only for runs with lowest V values (see Table 5.9)
<ul style="list-style-type: none"> • FD*, FG*, FP*, FV*, PS, • Total water column primary production, • Total production and consumption by FD and FV, • ANB (IGBEM only), • Macroalgae (BM2 only) 	<ul style="list-style-type: none"> • OB, PB (PAB and PFB for BM2), • Total production and consumption by pelagic bacteria, • DF (BM2 only) 	<ul style="list-style-type: none"> • AEB, BC, BD, BF, BG, MB, MZ, PL, SG, ZL, ZS, Chlorophyll a, • Total benthic primary production, • Total benthic secondary production and consumption, • Total water column secondary production and consumption, • Total denitrification, • Total production and consumption by benthic bacteria, • Total production and consumption by FG and FP, • ANB (BM2 only)

* A fixed migration matrix gives the spatial distribution of the biomass of these groups. However, the distribution of production and consumption by these groups is not fixed as that depends on the local density of their food groups.

runs because a migration matrix fixes their distribution. However, it is noteworthy that the relative spatial distributions for the picophytoplankton, and the macroalgae in BM2 are close matches in all the runs. Nevertheless, only a minority of the components in the runs with omitted groups have relative spatial distributions that either match the distribution in the full model closely or not at all. The relative spatial distribution of the majority of components and processes only approaches that of the standard run for those models with omitted groups that are identified by the overall indicator (V) as being close to the standard output (e.g. OA3).

The temporal dynamics of the models with omitted groups indicated that the turnover time of a component is one of the central factors determining the degree to which omitting groups degrades the model performance. The slower growing components usually show little change in temporal patterns as a result of omission (e.g. biomass of the epifaunal carnivores, Figure 5.12), while the greatest changes are associated with groups with rapid dynamics (e.g. diatoms, Figure 5.13).

Influence of changes to the ecosystem conditions on the effects of simplifying models

Increasing nutrient load or fishing pressure does not change the general pattern of effects of simplification based on baywide measures reported above, but there are some quantitative differences. The upper bound of the difference between the simplified runs and the full models declines as the total number of groups in the models increased. As for the results under baseline conditions, this pattern is stronger for IGBEM than for BM2. Again, there is no relationship between the differences of the simplified and standard runs and connectance.

In contrast to the baywide results, the quality of the matches of the relative spatial distributions of the simplified and full models changes substantially for some of the groups and processes when ecosystem conditions are altered. Within models that have either omitted or aggregated groups, the changes tend to be the same whether it is

Figure 5.12: Comparison of the temporal dynamics of epifaunal predators (MZ) in one cell (offshore from a sewage treatment plant) of the full Integrated Generic Bay Ecosystem Model and versions with omitted groups. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of MZ between the extremes presented here.

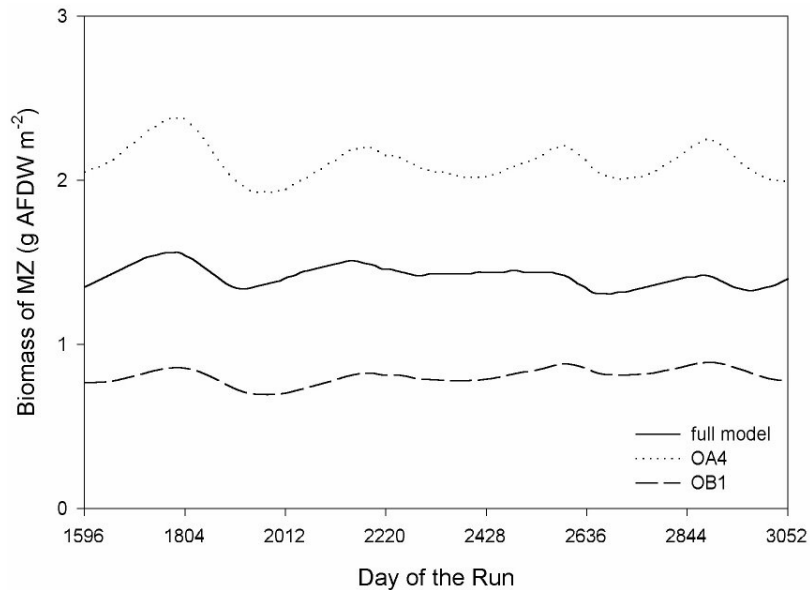
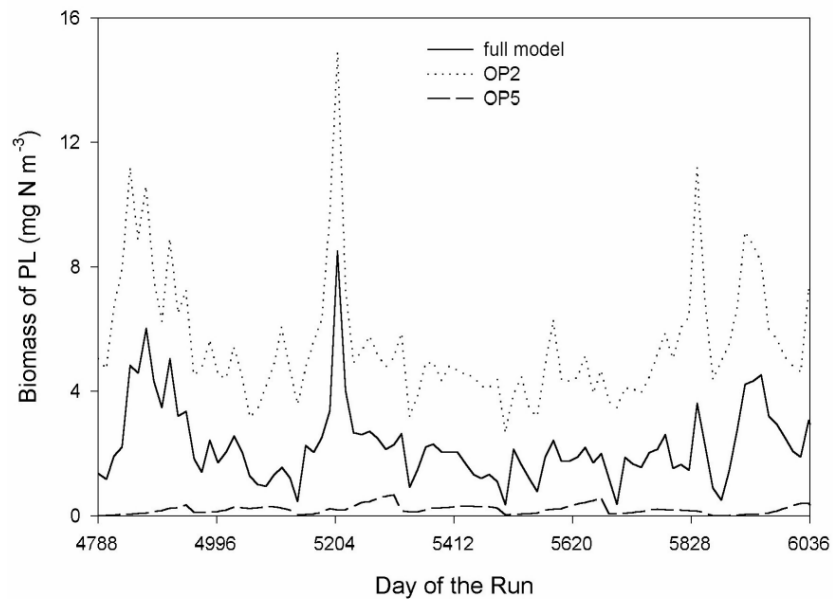


Figure 5.13: Comparison of the temporal dynamics of biomass of diatoms (PL) in one cell (covering an input point from a sewage treatment plant) of the full Bay Model 2 model and versions with omitted groups. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of PL between the extremes presented here.



fishing pressure or nutrient loading that changes. However, comparing the changes across models that use different forms of simplification, it is clear that the direction of change is often similar, but the groups and processes affected are different for models that aggregate groups (Table 5.11) and models that omit groups (Table 5.12). The effects of aggregating groups on relative spatial distributions does not change with changing ecosystem conditions for many groups and processes. The majority of the groups and processes for which the effects of aggregation on spatial distributions do change with changing ecosystem conditions move from occasionally matching the distribution in the full model to never matching it (Table 5.11). A similar pattern of change in the results occurs for models with omitted groups when ecosystem conditions are altered. The majority of the components that only show occasional agreement with the full version under baseline conditions now show no agreement (Table 5.12). However, the match for denitrification, benthic primary production and the production and consumption by planktivorous and herbivorous fish improve with altered ecosystem conditions, and many of the components that display relatively consistent spatial distributions across all of the models with omitted groups under baseline conditions continued to do so (Table 5.12).

The same temporal patterns of behaviour, in the simplified models relative to the full model, hold under changed conditions, except that the deviations from the standard run are more exaggerated (e.g. diatoms, Figure 5.14). This is due to the higher levels of resources available to primary producers, or lower predation pressure on the fish prey groups, under the new conditions. These deviations arise when groups are either aggregated or omitted, but are much worse in the former. There are a few cases in the models with aggregated groups where the effects of changing ecosystem conditions are opposite to those predicted by the full model. For example, the overall behaviour of the “macrophyte” group more closely resembles the behaviour of the seagrass in the full

Table 5.11: The effects of model simplification by aggregation on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) when the nutrient load (x5) or fishing pressure (Fx5) is increased to five times that of the “baseline” conditions. Codes are as in Table 5.1, and the standard distribution is the spatial distribution in the full model under the same nutrient load and fishing pressure.

Match standard distribution for most runs			Never match standard distribution		Occasionally match standard distribution	
Fx5	x5		Fx5	x5	Fx5	x5
• Total biomass of fish	• Total biomass of fish	• Biomass of epifauna	• Biomass of epifauna	• Biomass of zooplankton	• Biomass of zooplankton	• Biomass of zooplankton
• Total denitrification	• Total denitrification	• Chlorophyll a	• Chlorophyll a	• Biomass of infauna	• Biomass of infauna	• Biomass of infauna
• Total production and consumption by pelagic, piscivorous and demersal fish	• Total consumption by pelagic, piscivorous and demersal fish	• Biomass of phytobenthos	• Biomass of phytobenthos	• Total biomass of benthos	• Total production by pelagic, piscivorous and demersal fish	• Total production by pelagic, piscivorous and demersal fish
		• Total benthic primary production	• Total biomass of benthos	• Total water column primary production,	• Total benthic secondary production and consumption	• Total benthic secondary production and consumption
			• Total water column primary production	• Total benthic secondary production and consumption	• Total water column secondary production and consumption	• Total water column secondary production and consumption
			• Total benthic primary production	• Total water column secondary production and consumption		

model than the macroalgae. Consequently, when nutrients rise the “macrophyte” group is lost from the system in the models with aggregated groups, while the biomass of macrophytes (the sum of the biomasses of macroalgae and seagrass) persists and even rises in the standard form of BM2 (Table 5.13).

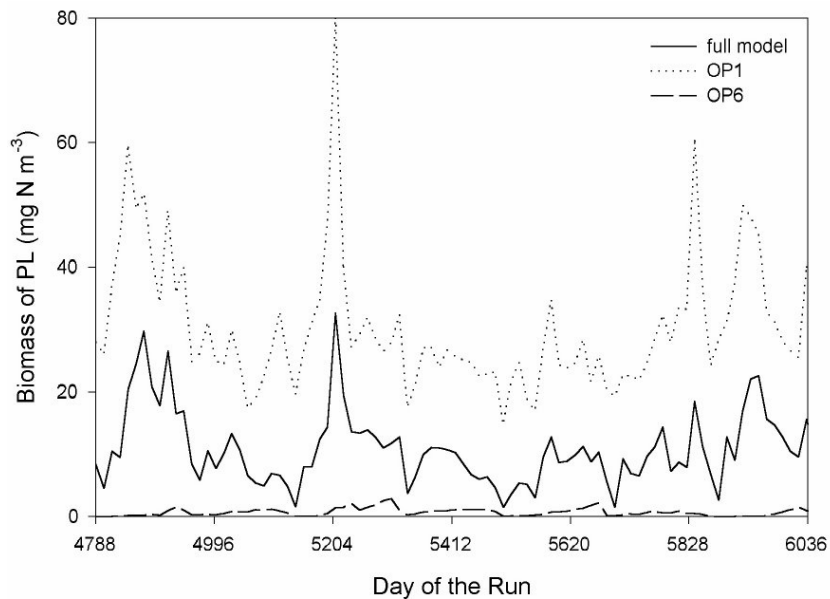
5.4 Discussion

It is possible to make a number of generalisations from the relative performance of the various kinds of simplified models. First, groups with the fastest dynamics often show the greatest effects of reduced model complexity (e.g. consider the temporal dynamics of the various components of the models). This is due to the greater ability of groups with fast dynamics to respond to changes in ambient physical and ecological conditions. The resources and forces on these groups are in a constant state of flux (due to advection and diffusion). As a result, small variations in effective predation pressure and competition can lead to large deviations as they build upon potentially large short-term changes in resources, the outcomes of these interactions can then accumulate or compound. However, as with all groups, the exact form of these responses to differing ecological and physical conditions are due to a mixture of trophic and non-trophic, as well as direct and indirect interactions. Thus, the greatest deviations are often seen when the simplified models are linear chains and furthest in form from the web of the standard case.

The relationship between trophic complexity and performance

Our findings that a high degree of simplification, whether by aggregating or omitting groups, leads to poor model performance is consistent with earlier studies (Sugihara et al. 1984, Costanza and Sklar 1985, Pahl-Wostl 1997). Simplification of trophodynamic models is possible, but thresholds exist beyond which insufficient detail

Figure 5.14: Comparison of the temporal dynamics of the biomass of diatoms (PL) in one cell (covering an input point from a sewage treatment plant) of the full Bay Model 2 model and versions with omitted groups when nutrient loads have been increased by fivefold. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of PL between the extremes presented here.



remains to effectively reproduce the dynamics of complex systems. This is particularly crucial when successional or other sequential details are important. For example, without explicit representation of the size classes of phytoplankton, accurate bloom dynamics (and thus primary production) cannot be reproduced satisfactorily (Murray and Parslow 1997).

Unfortunately, the relationship between trophic complexity and performance is not linear, and is usually not even asymptotic. The overall measure V , as well as the relative spatial distributions and other indices, frequently suggest a more parabolic form to the pattern of performance over the entire range of simplification. This concurs with the findings of others (e.g Costanza and Sklar (1985)) for overall model performance with increasing complexity, as well as other studies of the effects of aggregating groups

(e.g. Gardner et al. 1982). The other relationship observed between trophic complexity and performance of the models is a threshold-triggered step-function. In the simplified models with aggregated groups, there is often a clear and sudden transition from a poor to a good performance when considering the relative spatial distributions of the components and processes (Table 5.8). This suggests that in these cases there is some minimum set required or some specific linkages that must be explicit for model behaviour to approach that of the full model. The most important of these triggers or critical requirements is the inclusion of both seagrass and macroalgae and the addition of benthic deposit feeders. This is not surprising given the overwhelming importance of these groups in large shallow marine systems (Harris et al. 1996) like the one modelled here.

Some mechanisms responsible for the shape of the response surfaces relating complexity and performance reported in previous studies (Gardner et al. 1982, Sugihara et al. 1984, Costanza and Sklar 1985, Rastetter et al. 1992) do not apply in our study. For example, in previous studies decline in performance with an increase in the number of components in the models was thought to be due to increasing effects of measurement error as more and more parameters were included. The models used here are all built with “perfect knowledge” of the standard system. Apart from the adjustments made to account for mortality due to groups no longer explicitly included in the simplified models, there is no adjustment of model parameters. It could be argued that model recalibration would be necessary even for models that omit groups, as the retuning represents “compensation” for the removal of explicit non-trophic interactions. However, these interactions can be exceedingly difficult to quantify even in a model setting. Moreover, an investigation of the effects of trophic simplification on model performance is more transparent without retuning. As there is no retuning and no measurement error to influence the behaviour of the simplified runs, the relative

performances can only be explained in terms of the adequate representation of the true web.

Empirical representation of subwebs

The explicit inclusion of a number, or even a majority, of the members and interactions of a particular subweb may not guarantee satisfactory model performance. If the subweb under consideration is strongly linked with another web, or if it is dependent on inputs from another web, then that other web must also be represented sensibly. For example, in large (1930 km²) and shallow (≤ 24 m) systems such as the one modelled here, the inclusion of pelagos is a necessary requirement for an accurate representation of the benthos. The links between the pelagic and benthic communities in these systems are strong and consist of a number of trophic (predator-prey) and non-trophic (competitive) interactions. Consequently, simple forcing functions will not suffice, as evidenced by the poor performance of the OB and LB runs here. However, robust empirical representations of the pelagic-benthic link may be satisfactory. A good deal of attention has been paid to representing benthic returns to pelagic models (Fransz et al. 1991, Silvert 1991, McCreary et al. 1996), but empirical and explicit representation of the reverse needs more thought. The relative performance of the BM2 runs with and without explicit handling of the bacteria is evidence of how well an empirical sub-model can compensate for not explicitly representing a poorly, or incompletely, known component that has a potentially crucial role in the system. There is little if any improvement in overall model performance with the addition of bacteria to the simplified runs. In this case, given the effects of the other trophic simplifications on the model structure, the explicit inclusion of bacteria does not seem warranted. This is in contrast with the impressive increase in performance of the standard models after the addition of bacteria and an interactive form of the denitrification submodel (chapter

2).

Aggregation vs omission of groups

While the same broad effects of simplification are evident whether aggregating or omitting groups, omitting groups frequently has much less impact on performance than does aggregating groups. Previous consideration of the standard models has shown they reasonably reflect the biomass and dynamics of real systems (chapters 1 – 3). The standard models use food webs resolved to the level of functional groups (groups which share predators and prey, have similar degrees of mobility and metabolic rate constants within two to threefold of one another). The performance of the standard models implies that aggregation up to the level of functional groups is a valid method of handling complex systems. However, our results that aggregation of functional groups leads to poor model performance compared with omitting functional groups, indicates the presence of non-linear responses to aggregation of trophic complexity. It also indicates a “natural” level of aggregation. Thus, when simplifying a food web already aggregated to the level of functional groups, judicious choice and retention of the most important functional groups in a system appears to be a much more reliable method of constructing simplified webs than aggregating across functional groups in an effort to represent everything. One reason for this may be that aggregating functional groups breaks the “aggregation rules” laid down in previous studies. The web-like structure of natural systems means that aggregating functional groups produces an increasing number of instances where “serially-linked” aggregation cannot be avoided. This form of aggregation is known to be ill advised even at low levels of aggregation (Gardner et al. 1982). Further, aggregating functional groups often entails aggregating groups with rate constants more than two to threefold different to each other, which also appears to be ill advised (Wiegert 1977, O’Neill and Rust 1979, Cale and Odell 1980, Gardner et

al. 1982).

Changing ecosystem conditions and the stability-diversity debate

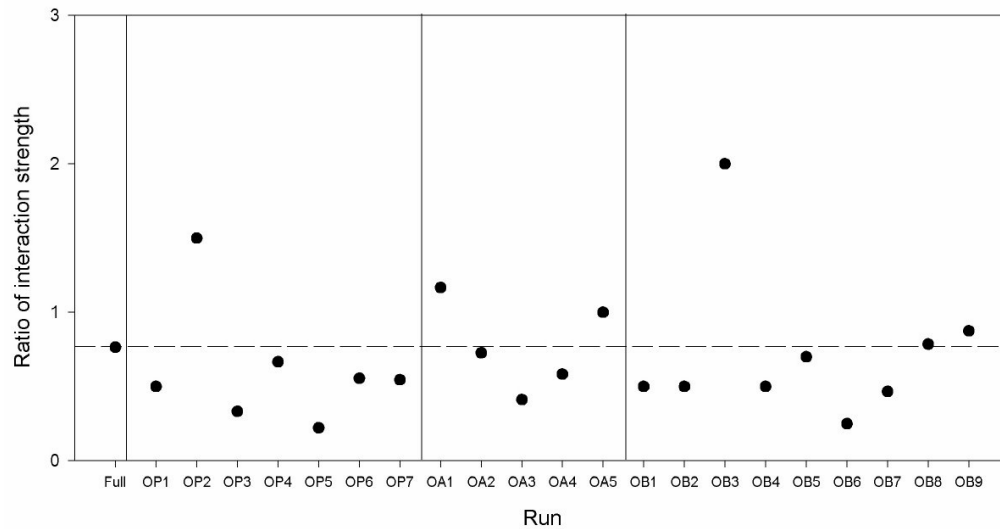
There are limitations to the approach of simplifying food webs by aggregating species to the level of functional groups and then omitting the least important functional groups. Predictions about system behaviour are often most wanted when there are large scale changes in external forcing, but this is when models that are too simplified fail to continue to faithfully reproduce system behaviour. Further, groups that may not have been important when the system was in one state may have a much greater role when conditions change. This is one of the fundamental ideas behind the ecological insurance hypothesis (Yachi and Loreau 1999). Formal consideration of which model with omitted groups performed the best under altered conditions is not possible, but it is nonetheless clear that the dynamics of models that are the least simplified are closest to the dynamics of the full models under changed nutrient loads. While the results are not as clear-cut in the scenario where fishing pressure is increased, the majority of the indices are closer to the standard for those runs with a minimum of simplification. This lends strong support to the suggestion that diversity provides natural communities with a buffer against change (Naeem and Li 1997, Naeem 1998, Yachi and Loreau 1999). Removing a few species will usually make little difference provided that the functional groups remain, as evidenced by the reliable performance of the standard runs, which only represent functional groups. Any further simplification of the system will have some effect, but it may be minimal if non-critical groups and interactions are lost. However, the full force of the effects of a loss in diversity will not present themselves until conditions have changed, as may arise given anthropogenic impacts on the environment. Thus, the behaviours of our simplified models are in agreement with the ecological insurance hypothesis.

The consideration of the effects of simplification by omission provides insight into another facet of the diversity-stability debate. It has been posited that connectance is a key factor in determining stability, but whether it improves (MacArthur 1955) or reduces (Gardner and Ashby 1970) stability is a matter of debate. There are no clear patterns of stability or performance in relation to connectance in the simplified models. This suggests that in webs that more closely resemble those in nature, it is not connectance *per se* but the identity of the links included that is important. Furthermore, the standard runs (that is the most complex runs) are stable, while other runs with fewer groups (but not the fewest) undergo self-simplification. Thus, the absolute number of components included in a model doesn't determine stability either, as was suggested in the early phases of the stability-diversity debate (Elton 1958, May 1973). One possible mechanism determining the system characteristics is the ratio of strong:weak interactions. Those runs with higher ratios of interaction strength (Figure 5.15) often exhibit instabilities, or trophic self-simplification or substantial departures in predicted distributions or total biomass for one or more groups. Moreover, the runs with the best overall performance are usually among those that had lower ratios of interaction strength (Figure 5.15). However, by itself the ratio of interaction strength is not a complete explanation as there are runs with low ratios that do not perform as well (e.g. OP3) and runs with high ratios that work reasonably well (e.g. OB3). Simple rules of thumb do not completely describe behaviour of the models, at least not in this case. The details of the links and components included are also important.

5.5 Conclusions

By definition, ecosystem models are simplified versions of the real world systems they are designed to represent. The use of trophospecies or functional guilds has been a successful method for capturing system dynamics without requiring species runs simplified by omitting groups. The strength of each interaction was assessed using

Figure 5.15: Plot of the ratio of interaction strength (strong:weak) for the Bay Model 2 the availability parameters of the grazing term; availabilities greater than 0.5 were classed as strong interactions.



level detail (Fransz et al. 1991, Baretta et al. 1995, Murray and Parslow 1997, Baretta et al. 1998, chapters 1 – 3). However, even at this level models can be highly complex structures and for reasons of logistics, computational demands and intelligibility, further simplification can be attractive. The results of the simplifications performed here suggest that there are no simple answers to questions about trophic complexity and model performance. There is a clear indication that once the system has been aggregated to the level of the functional group further aggregation is unwise and complete omission of less important groups is a better option. Unfortunately, during model validation multiple models with varying levels of simplification will still be required to check whether critical components and links have been omitted. Even then the relative performance of the final simplified model may be inaccurate if the system is subject to large shifts in nutrient loads or exploitation levels. Our results suggest two general guides:

- 1) Reducing the complexity of a model web (which represents the food web of an

entire system aggregated to the level of functional groups) to less than 20 – 25% of its original size (whether through omission or aggregation of groups) is rarely beneficial. Overly simplified models lose too many of the feedbacks, and the trophic and non-trophic interactions that characterise the system and structure its behaviour. Representing the distinctions between the large and small flora and fauna, or mobile and sedentary fauna, may be crucial for success.

- 2) If an important process (e.g. denitrification) or linkage (e.g. pelagic-benthic coupling) is to be omitted from the model, then an empirical representation must be included if model performance is to be satisfactory.

These guides are in addition to any that have been stated elsewhere that deal with the added problems of measurement error and imperfect knowledge (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Innis and Rextad 1983, Halfon 1983 a and b, Gardner et al. 1982, Iwasa et al. 1987).

That it is not possible to find simple rules relating diversity with stability and other aspects of system behaviour in this study suggests that there may be no general solution to the stability-diversity debate. The results lend further credence to the ecological insurance hypothesis, but they do not suggest any simple relationship between connectance, or the ratio of interaction strength, and system behaviour and stability. Rather they imply that the biological details of the web, trophic as well as non-trophic, can be very important.