

Chapter 6 Mortality and predation in ecosystem models: is it important how it is done?

Abstract

The effects of the form of the grazing and mortality terms used in plankton models are well known. The same cannot be said for ecosystem models. As ecosystem models become an increasingly utilised scientific tool more must be known about the effects of model formulation on model behaviour and performance. The impact of the form of the functional response and mortality terms used in a biogeochemical ecosystem model are considered here. We show that in the large and inter-linked webs used in ecosystem models, model behaviour is far more sensitive to the form of the grazing term than to that of the mortality terms used to close the modelled food web. In comparison with the simpler Holling disk equation, the most dynamic and sophisticated functional responses describing grazing require extra parameters and validation, but usually still lead to the same general conclusions about system state and the effects of changes in forcing functions. Thus, the use of more complex functional responses is not necessarily warranted in many cases. Similarly, the extra effort and data required to explicitly represent the top predators (sharks, mammals and birds) is not generally necessary, as a quadratic mortality term applied to intermediate predators (such as piscivores) is sufficient to achieve sensible model behaviour. However, it should be noted that some degree of sophistication is required in the grazing and mortality terms. Use of simple linear functional responses and mortality terms is unsuitable for models used to consider a range of nutrient loading or harvesting scenarios.

Keywords functional response, mortality term, model closure, biogeochemical, ecosystem, model, IGBEM, BM2

6.1 Introduction

Modern marine resource management is increasingly focused upon multiple use and sustainable management of marine systems. An important aspect of such a management approach is the use of appropriate tools. This is one of the driving forces behind the recent interest in ecosystem models (Walters et al. 1997, Hollwed et al. 2000, Sainsbury et al. 2000). These models, whether primarily biogeochemical or ecological, have a lot of potential, but several areas of their performance and structure need investigation.

While there are only a few accepted ways of handling the mechanics of hydrodynamics, biological processes can be formulated in a multitude of ways (Gao et al. 2000). In eutrophication models the issue of the effect of the formulation of biological processes on model performance has begun to be thoroughly analysed (Fransz et al. 1991, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000, Gao et al. 2000, Tett and Wilson 2000). However, this has not been the case for ecosystem models that encompass whole food webs.

Due to their aims and scope, ecosystem models can often be quite large, highly detailed and potentially unwieldy. A comprehensive sensitivity analysis of parameters used in these models is often a daunting, if not impossible, task. Thus, the effects of alternative formulations of key processes may seem even less likely to be tackled. However, the work of Steele and Henderson (1992, 1995), Murray and Parslow (1999b) and Gao et al. (2000), amongst others, indicates that the behaviour of eutrophication models can be strongly dependent on these formulations. With the additional groups and linkages found in ecosystem models, it is unlikely that the effect of formulation is any less important.

Over the last quarter of a century theoretical and model studies have shown that the form of predation incorporated into models can have a large effect on their

performance (including stability) and predictions (May 1976, Hassel 1978, Hassell and Comins 1978, Begon and Mortimer 1986, Steele and Henderson 1992, Edwards and Brindley 1999, Gao et al. 2000). There are two areas in which predation and its formulation must be considered in biogeochemical models with multiple biological components. The first is the grazing terms used, which functional responses are implemented and whether these responses reasonably represent animal behaviour. The second is the formulation of the mortality terms for the species or groups at the highest trophic level of the web explicitly represented in the model. Natural mortality is applied to all biological components of models, but at the highest trophic levels in a model extra assumptions may be necessary. One important consideration is whether the effect of predators not explicitly covered in the web is constant or reacts to the size of the prey population, as one would expect populations of predators to respond. As a result, linear and quadratic mortality terms are the most common means of handling model closure (i.e. the mortality terms used for the top predators represented in the model). However, it is important to assess whether the model's behaviour is sensitive to the form of the mortality term used (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b).

Examination of water quality models has indicated that the form of the grazing term used is not as important a determinant of model behaviour as the form of model closure employed (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000). These investigations of the performance of water quality models also indicate that quadratic mortality is the most appropriate form of closing the food web in a model. Studies of the performance of water quality models also indicates that quadratic mortality appears to be the most appropriate form of closing the food web. Such studies have been restricted to planktonic webs and as there is little (if any) consideration of this topic in other areas of ecological modelling so

extension of these findings to larger webs is open to doubt.

Linear mortality is used in the majority of published ecological models without mention of its potential effects. In contrast, the effect of functional responses has received more widespread attention. Holling (1959) classified the range of relationships between consumption rate and prey density observed in nature into three “types”: type I (linear increase in consumption rate with prey density up to some threshold density where consumption rate becomes constant); type II (smooth increase to an asymptote); and type III (sigmoidal). These three types are still widely used (Büssenschütt and Pahl-Wostl 2000), though they have been criticised for their simplicity and dependence on prey abundance. Much of the criticism has resulted from (1) the “boom and bust” predictions of models which use type I or II responses (Büssenschütt and Pahl-Wostl 2000); (2) the problem of the paradox of enrichment (where models predict only top predators will benefit from increased primary production, while empirical observations suggest all trophic levels benefit) (Hairstone et al. 1960, Arditi and Ginzburg 1989, Ginzburg and Akçakaya 1992); and (3) unrealistic behaviour at high predator abundance (Abrams 1993). As a result, other more complicated responses have been proposed. A review of all of these responses is beyond the scope of this paper, but it can be said that there have been mixed results and that the debate is far from over. For example, ratio-dependent responses were initially promising (Arditi and Ginzburg 1989, Matson and Berryman 1992), but their usefulness in general models (like the one considered here) has been questioned (Gleeson 1994, Sarnelle 1994, Abrams 1994, Abrams and Ginzburg 2000, Büssenschütt and Pahl-Wostl 2000). Nonetheless, functional responses, such as the one included in ECOSIM (Walters et al. 2000), which attempt to incorporate the pressure on an organism to maximise foraging time while minimising predation risk, are useful.

During the development of two biogeochemical ecosystem models, Bay Model 2

(BM2) (chapter 2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (chapter 1), it became clear that the way in which feeding and mortality is modelled can be critical to model behaviour. For example, using only linear mortality terms for the fish groups in IGBEM (linear model closure) can result in unstable behaviour under some conditions (chapter 1). The work here examines some aspects of the effect of the form of the grazing terms and model closure on the dynamics and performance of an ecosystem model. This work is one part of a wider model study considering the effects of model structure and formulation on model behaviour.

6.2 Methods

To consider the effects of the formulation of the grazing term and model closure on model dynamics and performance, alternative forms of these terms are considered in the ecosystem model BM2. BM2 is a biogeochemical ecosystem model constructed at the level of trophic guilds. It follows the nitrogen and silicon pools of 21 living groups (pelagic and benthic) and a number of detrital and nutrient pools (Table 6.1). The food web (Figure 6.1) and associated processes are for a generic temperate bay system, rather than any particular bay. For convenience the physics used is a transport model built for Port Phillip Bay, in southern Australia, but the model captures the dynamics typical of many temperate coastal systems (chapter 2). An 8-box form of this model is used to investigate the alternative formulations considered. This spatial resolution provides a balance between computational requirements and potential impacts of model trophic self-simplification due to system homogeneity and refuge losses (chapter 4). There are some effects of self-simplification in the 8-box compared with the complete 59-box spatial configuration usually used with BM2 (Figure 6.2), but they are small and so the benefits of much shorter run times outweighs potential costs.

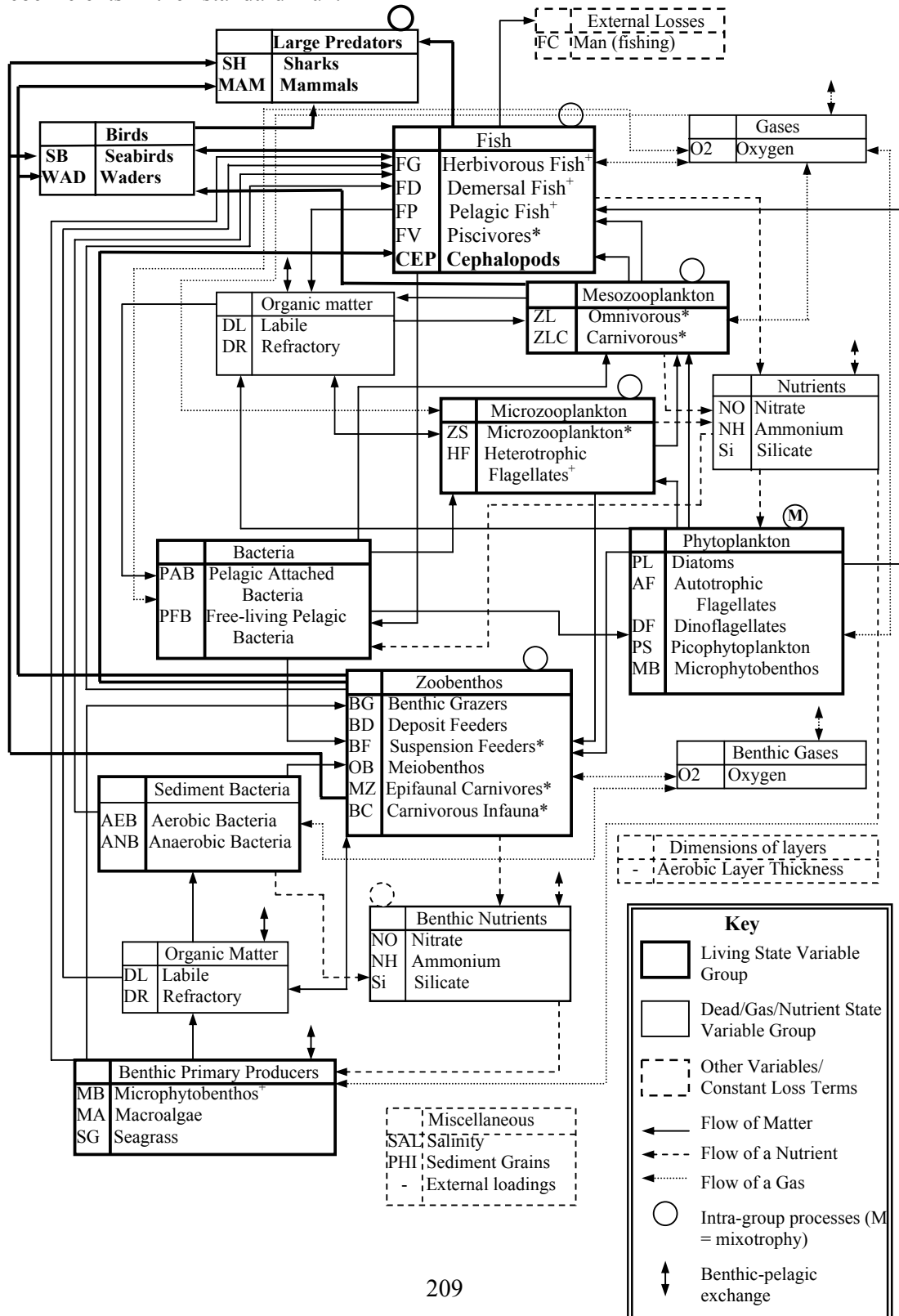
Table 6.1: Biologically associated components present in Bay Model 2 (BM2).

Component	Codename
Diatoms*	PL
Autotrophic flagellates	AF
Picophytoplankton	PS
Dinoflagellates	DF
Free-living pelagic bacteria	PFB
Pelagic attached bacteria	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 suspension feeders	BF
Infaunal carnivores	BC
Benthic deposit feeders	BD
Meiobenthos	OB
Aerobic bacteria	AEB
Anaerobic bacteria	ANB
Cephalopods ⁺	CEP
Seabirds ⁺	SB
Wading birds ⁺	WAD
Sharks ⁺	SH
Marine mammals ⁺	MAM
Labile detritus	DL
Refractory detritus*	DR
DON	DON
Ammonia	NH
Nitrate	NO
Dissolved silicate	Si
Dissolved oxygen	O2

* Also have an Si internal pool.

⁺ Not present explicitly in the standard model, but added under one of the alternative model closure schemes.

Figure 6.1: Biological and physical interactions between the components used in Bay Model 2 (BM2). The flows (arrows) in bold are the linkages associated with the top predators (names in bold) that are not normally included explicitly in the web. Groups marked with * have both quadratic and linear mortality terms, as do those groups marked with a ⁺. However, the later have very small (<0.000001) quadratic mortality coefficients in the “standard” run.



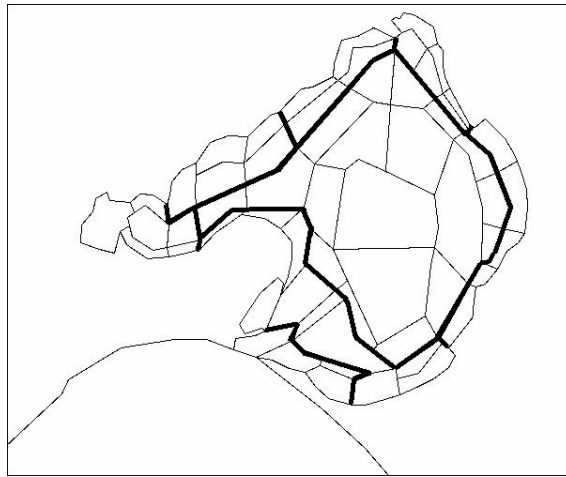


Figure 6.2: Spatial structure implemented for Bay Model 2 (BM2). The 8-box configuration marked in bold is the standard structure used for the runs discussed in this paper, while the 59-box structure is the default for BM2.

6.2.A Grazing functions

Six alternative grazing functions are trialled (Table 6.2). The formulations used are taken from the general ecological literature (Holling 1966, Begon and Mortimer 1986) or represent grazing formulations used in other ecological and ecosystem models (Baretta et al. 1995, Bryant et al. 1995, Ebenhöf et al. 1995, Walters et al. 2000). The formulations chosen cover a wide range of structural assumptions, from simple proportionality in the “type I” grazing term to complex behaviours trading predation risk against food requirements in the “ecosim-based” formulation. In each case the same grazing term is used for all consumers. This assumption that a single functional response is appropriate for all consumers, vertebrate and invertebrate alike, may not be valid. However, as there are no earlier studies to work from and as the modelled web is large and complex, it is considered to be an acceptable first step. Future studies may benefit from considering the effects of differing functional responses across the trophic levels.

6.2.B Mortality schemes

Four mortality (trophic closure) schemes are trialled. Unlike the grazing terms, the various schemes for trophic closure do not all represent completely different formulations. Every group in BM2 has a linear (or “basal”) mortality term and any “special” mortality terms (due to bottom stress, eutrophication or oxygen stress) are applied separately to this “basal” mortality. In addition to these “basal” and “special” mortality terms the groups in each subweb which are predated upon by functional groups not explicitly included in the modelled web also have a quadratic mortality term. These groups (marked in Figure 6.1) are: heterotrophic flagellates, microzooplankton, large omnivorous zooplankton, large carnivorous zooplankton, microphytobenthos, planktivorous fish, piscivorous fish, demersal fish, demersal herbivorous fish, macrozoobenthos (epifaunal carnivores), benthic suspension feeders, and infaunal carnivores. The difference between the “standard”, “no-linear” and “no-quadratic” mortality schemes is in the value given to the coefficients for linear and quadratic mortality applied to these groups. In the “standard” scheme both linear and quadratic mortality have non-zero coefficients. In the “no-linear” scheme the coefficient for the linear mortality term is set to zero and in the “no-quadratic” scheme the coefficient for the quadratic mortality term is set to zero. The final form of model closure considered (“top”) involves extending the web to explicitly include more of the higher functional groups omitted (e.g. sharks) from the “standard” version of BM2 (these additional groups are in bold in Figure 6.1).

6.2.C Definition of the “standard” and alternative runs

For convenience each model run is given an identifying name (Table 6.3), which will be used for the remainder of this paper. The “standard” run is the run using the standard settings of BM2 – the top predators have non-zero linear and quadratic

Table 6.2: Alternative formulations of the grazing term ($G_{X,Y}$) per consumer considered. Additional crowding and oxygen limitation factors are not shown as they were only relevant in some groups.

Name	Equation	Definitions	Source
Standard (type II)	$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot c_X}{1 + \frac{c_X}{I_X} \cdot \left(\sum_{ZZ} e_{X,Z} \cdot p_{X,Z} \cdot Z \right)}$	c_X = maximum clearance rate of predator X* $e_{X,Z}$ = assimilation efficiency of predator X on prey Z I_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey YY to predator X Y = biomass of prey Y	Murray and Parslow 1997
Type I	$G_{X,Y} = \min \left(c_X \cdot p_{X,Y} \cdot Y, \frac{c_X}{I_X} \right)$	c_X = maximum clearance rate of predator X* I_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X Y = biomass of prey Y	Murray and Parslow 1997
Type III	$G_{X,Y} = \frac{(p_{X,Y} \cdot Y)^2 \cdot c_X}{1 + \frac{c_X}{I_X} \cdot \left(\sum_Z e_{X,Z} \cdot (p_{X,Z} \cdot Z)^2 \right)}$	c_X = maximum clearance rate of predator X* $e_{X,Z}$ = assimilation efficiency of predator X on prey Z I_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X Y = biomass of prey Y	Murray and Parslow 1997
Ecosim-like	$G_{XX,YY} = \frac{v_X \cdot T_X \cdot p_{X,Y} \cdot Y \cdot T_Y}{h_X \cdot T_X \cdot p_{X,Y} \cdot (1 + T_Y) + v_X \cdot X \cdot T_X}$ $\text{where } T_X = \min \left(t_X, T_X^{prev} \cdot \left(1 - a_X + \frac{a_X \cdot Q_X}{\sum_Z G_{X,Z}^{prev}} \right) \right)$ $\text{and } Q_X = \sum_Z G_{X,Z}^{prev} \cdot \left(\frac{T_X^{prev}}{T_X^{older}} - 1 + a_X \right) a_X$	a_X = feeding time adjustment factor (how quickly adjustments to relative feeding time occur) h_X = handling time of predator X G_X^{prev} = previous per consumer grazing for predator X $p_{X,Y}$ = availability of prey Y to predator X Q_X = optimal per consumer grazing for predator X v_X = search rate of predator X t_X = maximum relative feeding time allowed for predator X T_X = relative feeding time for predator X T_X^{prev} = previous relative feeding time for predator X T_X^{older} = relative feeding time for predator X from time period before last. T_Y = relative feeding time for predator Y T_Z = relative feeding time for predator Z X = biomass of predator X Y = biomass of prey Y	Christensen et al. 2000.

Table 6.2: Continued

Name	Equation	Definitions	Source
Bounded	$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot c_X \cdot I_X \cdot \left(\frac{p_{X,Y}^2 \cdot Y^2}{p_Y \cdot Y + k_X^I} \right)}{k_X^u + \sum_Z \frac{p_{X,Z}^2 \cdot Z^2}{p_{X,Z} \cdot Z + k_X^I}}$	c_X = maximum clearance rate of predator X* k_X^I = lower prey biomass threshold for feeding by predator X k_X^u = half saturation coefficient for feeding by predator X I_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X $p_{X,Z}$ = availability of prey Z to predator X Y = biomass of prey Y	Radford 1996
Dynamic search and handling	$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot V_X}{\left(1 + H_X \cdot V_X \cdot \sum_Z p_{X,Z} \cdot Z \right)}$ <p>where V_{XX} and H_{XX} are constants for non-fish, but are size dependent for fish such that</p> $V_X = v_{a,X} \cdot X_S^{v_{b,X}}$ $H_X = h_{a,X} \cdot X_S^{-h_{b,X}}$	H_X = Handling time of predator X (as function of size in finfish, constant in other groups) $h_{a,X}$ = coefficient of handling time for finfish X $h_{b,X}$ = exponent of handling time for finfish X $p_{X,Y}$ = availability of prey Y to predator X $p_{X,Z}$ = availability of prey Z to predator X V_X = search rate of predator X (as function of size in finfish, constant in other groups) $v_{a,X}$ = coefficient of search rate for finfish X $v_{b,X}$ = exponent of search rate for finfish X X_S = structure weight of finfish X Y = biomass of prey Y	Radford 1996

* Temperature dependent. The standard Q_{10} temperature correction formula was used to adjust these rates, with a reference temperature of 15 degrees Celsius and a Q_{10} coefficient of 2.

mortality terms and all consumers use standard (type II) grazing terms. This run is used as the standard to compare against for the runs using alternative grazing terms and the runs using alternative trophic closure. Apart from this common run, consideration of the alternative (non-standard) grazing and mortality terms is done separately. For all the grazing term runs, the standard trophic closure (non-zero linear and quadratic mortality terms for the top predators) is used; and for all the model closure runs the standard grazing term (standard (type II)) is used. Consideration of the effects of different combinations of trophic closure and grazing terms, as well as different grazing terms for different functional groups (rather than one formulation applied to all groups), is left for future study.

6.2.D Parameter tuning

The original form of BM2 was calibrated by tuning the temperature-dependent maximum growth and mortality rates for all groups and the maximum clearance rates of the consumer groups (chapter 2). The final tuned values for these parameters are required to lie within the range of empirical estimates reported in the literature, rather than to match a specific set of observations (chapter 2). Consequently, limited re-tuning is allowed in each case investigated here. For the grazing terms, only those parameters in the grazing formulation are tuned, while for the mortality schemes only the mortality coefficients are modified for those groups present in the standard food web used in BM2. The additional groups added for the final mortality scheme are all calibrated in the same way as for the standard BM2 groups.

6.2.E Changing forcing conditions

The sensitivity of the model to different formulations is examined for “baseline” conditions. The examination is then repeated under various forcing conditions to gauge

Table 6.3: List of the identifying names given to the runs and sets of forcing conditions discussed in this paper.

Run name	Run details
Standard	Top predators have non-zero linear and quadratic mortality terms and all consumers use standard (type II) grazing terms
Grazing term runs	
bounded	Mortality terms for top predators as of the standard run, only grazing terms differ between runs
dynamic	Uses the equation for the Bounded functional response formulation in Table 6.2
ecosim-based	Uses the equation for the Dynamic search and handling functional response formulation in Table 6.2
type I	Uses the equation for the Ecosim-like functional response formulation in Table 6.2
type III	Uses the equation for the Type I functional response formulation in Table 6.2
Model closure runs	
no-linear	Grazing terms as of the standard run, only mortality terms for the top predators differ between runs
no-quadratic	Linear mortality term is set to zero for the top predators
top	Quadratic mortality term is set to zero for the top predators
	Marine mammals, seabirds, wading birds and cephalopods are explicitly included in the model

how the model's predictions regarding the effect of changing environmental conditions differ between runs using different formulations. The "baseline" conditions used the default nutrient forcing files and levels of fishing pressure for BM2 (chapter 2), while a change in environmental conditions is reflected by increasing the nutrient load or fishing pressure used by fivefold ("Nx5" and "Fx5" respectively). This degree of change in forcing conditions has previously been found to cause the standard form of BM2 to predict a change in system state, marked by substantial shifts in the biomass and spatial distribution of many of the modelled groups (chapter 2)

6.2.F Comparing the runs

Several measures are used to compare the various runs. These include the baywide average biomass per group, relative spatial distributions, the form of the temporal dynamics, and overall levels of pelagic, benthic and bacterial production and consumption. The degree of conformity between the relative spatial distributions predicted by the runs is evaluated using the number of boxes for which the relative spatial distribution of a functional group in a run using an alternative formulation differs from the distribution in the "standard" run. In contrast, the match between the temporal dynamics of the predicted time-series in the run using an alternative formulation and the "standard" run is ranked based on the matches between their respective shapes, amplitude, mean and timing. An exact match is given a rank of 1 and an additional 1 is added to this rank for each feature (shape, amplitude, mean or timing) which differs between the two time-series. Thus, a rank of 5 indicates no match in any feature between the time-series.

As the predicted value of the biomass, consumption and production per group may differ between runs under "baseline" conditions, simply repeating the comparison of these values for the runs under altered forcing conditions is not informative. Runs

predicting the same effects of changing forcing conditions may end up with different absolute results, because their “baseline” estimates differ and so the estimates under changing forcing conditions also differ. Thus, under altered conditions the relative change of a measure (average value under changed conditions / average value under “baseline” conditions) is a better choice, as it allows for the assessment of the predicted system changes in each run and it removes any potentially confounding effects caused by different runs predicting different values under “baseline” conditions.

The measures used here give a good indication of the effects of the various formulations on the model output and behaviour. However, since results for production and consumption reinforce the results based on biomass, and do not impart any new insights, they are not presented here.

6.3 Results

6.3.A Sensitivity to Grazing Terms

The relative differences between the average overall biomasses in the alternative runs indicates that under “baseline” conditions the “type I” grazing term produces results that are closest to those of the “standard” run (usually <30% difference). The run using a “bounded” grazing term shows the greatest overall divergence from the results of the “standard” run (with only 44% of the groups having predicted biomasses within 50% of the estimates from the “standard” run). This run is the only run where the majority of groups in the run is not within 50% of that predicted in the “standard” run (Table 6.4). However, even in the runs where the majority of groups are within 50%, there are a few groups (in particular those with high turnover rates) where the difference can be much larger (peaking at 507.95 times larger for meiobenthos in the “type III” run).

Considering the conformity of relative spatial distributions, it is clear that the

spatial distribution of some groups is influenced by the choice of grazing term and as a result there are some differences in spatial distributions between runs. The distributions for the “type I” run matches those of the “standard” run for all but the zooplankton groups, where there are some minor differences (Table 6.5). The other runs show more differences in their spatial distributions, primarily within those groups with faster dynamics (Table 6.5). The run employing the “bounded” grazing term shows the greatest degree of spatial divergence from the “standard” run. The “bounded” grazing term tends to predict evenly distributed populations where other grazing terms suggest stronger spatial structuring with local peaks in density (e.g heterotrophic flagellates, Figure 6.3).

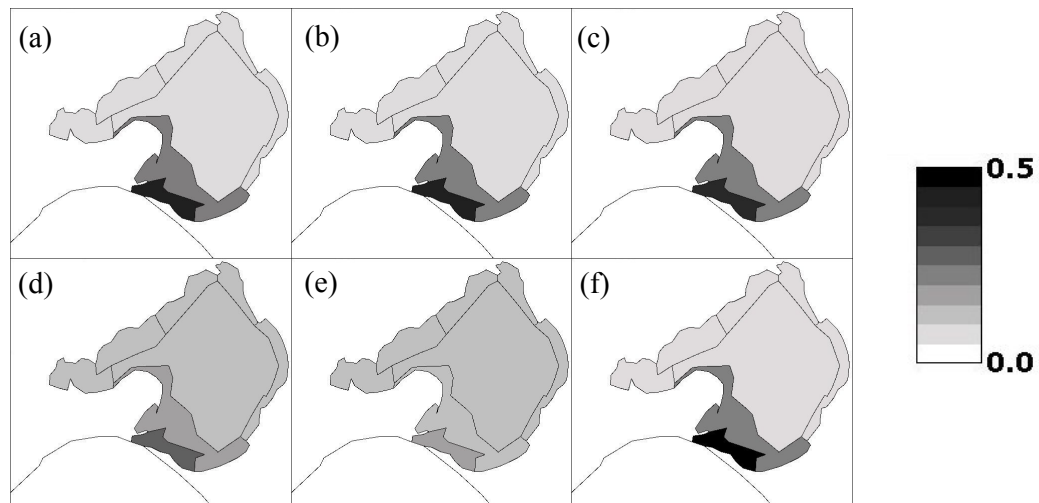
Table 6.4: Proportional difference between the biomass predicted in the “standard” run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	0.06	0.46	1.64	2.09	0.88
AF	0.11	0.08	0.01	0.38	0.07
ANB	0.06	0.46	101.88	93.96	53.43
BC	< 0.01	1.04	0.60	0.08	0.07
BD	0.26	0.45	0.99	0.90	0.37
BF	0.03	0.09	0.25	0.86	0.15
BG	< 0.01	< 0.01	0.25	0.38	0.50
DF	0.05	0.49	0.50	0.50	0.05
FD	< 0.01	< 0.01	0.56	0.07	< 0.01
FG	0.04	0.03	0.71	0.47	0.32
FP	0.06	0.09	0.23	0.21	0.03
FV	0.16	0.80	0.06	0.21	0.08
HF	0.08	0.04	0.64	1.09	0.19
MA	0.19	0.21	0.08	1.00	1.00
MB	0.16	3.12	0.43	0.89	1.84
MZ	< 0.01	< 0.01	0.50	4.03	0.39
OB	0.91	507.95	220.73	261.18	22.98
PAB	0.04	0.16	0.71	1.09	0.81
PFB	0.01	0.27	2.95	5.60	3.42
PL	0.06	0.25	0.17	0.12	0.09
PS	0.08	1.37	9.57	4.94	9.14
SG	0.07	0.33	0.78	2.64	0.33
ZL	0.12	0.30	0.28	0.53	0.31
ZLC	0.28	1.76	0.38	0.07	0.02
ZS	0.19	0.13	0.32	0.17	0.19
Average	0.12	20.80	13.81	15.34	3.87

Table 6.5: Number of boxes for which the relative spatial distributions of the “standard” run differs from that predicted by the runs using an alternative grazing term. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	0	2	3	3	4
AF	0	0	1	7	1
ANB	0	5	2	2	5
BC	0	1	0	0	1
BD	0	0	0	0	0
BF	0	1	4	1	0
BG	0	0	1	3	0
DF	0	7	6	6	0
FD	0	0	0	0	0
FG	0	0	0	0	0
FP	0	0	0	0	0
FV	0	0	0	0	0
HF	0	0	2	7	0
MA	0	0	1	2	2
MB	0	1	1	3	4
MZ	0	0	4	5	2
OB	0	1	0	0	3
PAB	0	0	0	0	0
PFB	0	0	2	2	2
PL	0	1	5	5	5
PS	0	1	2	2	2
SG	0	1	0	1	1
ZL	1	1	1	1	1
ZLC	1	0	6	1	1
ZS	1	0	1	0	0

Figure 6.3: Proportion of the total average biomass of heterotrophic flagellates in each box for each run with alternative grazing formulations: (a) standard (type II), (b) type I, (c) type III, (d) ecosim-like, (e) bounded, and (f) dynamic.



The form of the time series for each group is generally more sensitive to the details of the grazing term than the time average values of the runs or the relative spatial distributions (Table 6.6). Runs with “type III” and “type I” functional responses are the least affected, with 30 – 40% of their component groups showing no difference to use of the “standard” grazing term. Runs using the other grazing functions diverge more from the “standard” model, though not all groups show major changes in their temporal dynamics (Table 6.6).

With changing nutrient loads and fishing pressure, some of the groups in the runs using alternative grazing terms have predicted biomass trends that diverge from the predicted trends in the “standard” run under the same change in forcing conditions (Tables 6.7 and 6.8). When nutrients increase (“Nx5”), the run employing the “ecosim-like” grazing term shows the greatest divergence from the “standard” run under the same conditions. In contrast, the run using “type I” grazing terms is the most different to the “standard” run when fishing pressure increases. The majority of groups in most runs using alternative grazing terms did follow the same general trends as for the “standard” run under the same changing forcing conditions. However, with an increase in fishing pressure, the predicted trend for the benthic deposit feeders in each of the runs using alternative grazing terms is consistently more than 1880 times the size of the trend predicted by the “standard” run (Table 6.8). The differences in the trends in biomass in the various runs are not just in size, but for some groups the predicted direction of change is also different (marked by a * in Table 6.7 and 6.8). For example, with an increase in nutrient loading (Table 6.8), the predicted change in biomass for the picoplankton in the run employing “ecosim-like” grazing terms is not only 2.92 times the magnitude of the trend in the “standard” run with an increasing nutrient load, but it is in the opposite direction (an increase rather than a decline).

Table 6.6: Quality of the match between the predicted time-series for each component in the “standard” run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3. The entries are ranks indicating the degree to which the time-series matched that of the standard run. An exact match of the predicted time-series in the run using an alternative grazing term and the “standard” run has a rank of 1, and an additional 1 is added to this rank for each feature (shape, amplitude, mean or timing) which differs between the two time-series. Thus, a rank of 5 indicates no match in any feature between the time-series.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	1	3	3	3	3
AF	3	5	5	5	5
ANB	1	3	5	5	5
BC	1	1	3	5	5
BD	3	3	5	5	3
BF	3	3	5	5	5
BG	1	1	2	3	1
DF	1	3	3	3	3
FD	1	1	5	5	2
FG	1	1	1	3	1
FP	1	1	1	2	1
FV	1	1	1	1	1
HF	5	5	5	5	5
MA	3	3	5	5	5
MB	5	5	5	5	5
MZ	1	1	5	5	4
OB	3	1	5	5	5
PAB	3	3	3	3	3
PFB	3	3	5	5	5
PL	3	3	5	5	5
PS	3	5	5	5	5
SG	2	3	5	5	4
ZL	3	5	5	5	5
ZLC	3	3	5	5	5
ZS	3	5	5	5	5

Table 6.7: Proportional difference between the change in biomass (average biomass under changing conditions / average biomass under “baseline” conditions) predicted in the “standard” run and those runs using alternative grazing formulations when the nutrient load is increased fivefold. Note that the Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	4.64*	0.26	4.82*	5.61*	0.32
AF	0.04	0.12	0.11	0.85	0.32*
ANB	4.64	0.25	1.87*	1.38	0.12
BC	0.60	0.41	0.42	0.40	0.50
BD	0.15	0.69	0.40	0.40	0.63
BF	0.39	0.08	1.52*	1.43*	1.23*
BG	< 0.01	0.74	0.85	0.70	0.55
DF	0.03	< 0.01	0.01	0.01	0.12
FD	< 0.01	1.00	24.47*	0.36	< 0.01
FG	0.02	1.00	0.79	0.25	0.03
FP	0.01	1.00	0.60	0.16	0.30
FV	0.05	1.00	18.80	0.06	0.05
HF	0.06	0.09	0.08	0.11	0.12
MA	0.25	0.19	0.87*	0.77	0.78
MB	10.52	0.92*	0.57	0.83*	0.86*
MZ	< 0.01	0.00	0.63	0.80	0.35*
OB	0.81	1.00	1.00	1.00	1.00
PAB	0.29	0.06	0.15	0.34	0.09
PFB	< 0.01	< 0.01	0.01	0.20	0.14
PL	0.04	0.09	0.07	1.34*	0.20
PS	0.01	0.14	2.92*	0.96*	3.27*
SG	0.57	0.91	0.38	2.05	0.43
ZL	0.11	0.15	0.31	0.04	0.87
ZLC	< 0.01	0.20	0.34*	0.18	0.16
ZS	0.05	0.10	0.92*	3.79*	3.85*
Average	0.93	0.42	2.52	0.96	0.65

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the “standard” run under the same conditions - for instance, a decline in place of an increase.

Table 6.8: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under “baseline” conditions) predicted in the “standard” run and those runs using alternative grazing formulations when the fishing pressure is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	3.41*	0.40	0.70	0.69	0.68
AF	0.03	0.10	0.14	< 0.01	0.12
ANB	3.44*	0.40	0.73	0.73	0.70
BC	0.52	0.16	0.52	0.52	0.52
BD	3739.49*	1887.85*	3312.18	3321.52	3543.97
BF	0.17*	0.21	0.08	0.07	0.08
BG	1.67	0.31	2.09*	1.64	1.67
DF	0.04	0.01	0.01	0.01	0.01
FD	0.05	< 0.01	2.05	0.11	3.08
FG	0.07	0.03	0.46	0.11	0.98
FP	0.01	0.08	1.60	0.30	1.78
FV	0.18	0.45	0.05	0.64	0.68
HF	0.05	0.13	0.21*	0.18	0.15
MA	0.06	0.30	0.07	0.10	0.10
MB	0.62*	0.51	0.15*	0.22*	0.08
MZ	0.15	0.15	0.22*	0.14	0.16
OB	1.00*	1.00	1.00	1.00	1.00
PAB	0.19	0.06	0.05	0.08	0.09
PFB	0.01	< 0.01	0.07*	0.01	0.01
PL	0.20	0.01	0.10	0.12	0.04
PS	0.11	0.44	0.57*	0.03	0.45
SG	0.32	0.25	0.31	0.31	0.31
ZL	0.28	0.31	0.03	0.44	0.25
ZLC	0.18	0.69	0.64	0.63	0.63
ZS	3.59*	0.34	1.73	1.72	1.85
Average	150.23	75.77	133.03	133.25	142.38

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the “standard” run under the same conditions - for instance, a decline in place of an increase.

In the runs using the alternative grazing terms, there is an increase in the number of groups with spatial and/or temporal patterns which do not conform with those of the “standard” run under the same change in forcing conditions (Tables 6.9 and 6.10). The most noticeable differences are for groups in the “type I” run. Under “baseline” conditions, the relative distributions of all groups in the run with “type I” grazing terms conform with the relative distribution in the “standard” run for 7 or more boxes. In contrast, when nutrient loading increases fivefold (“Nx5”), only 68% of the groups in the run using “type I” grazing terms conform with the relative distribution predicted by the “standard” run, under the same conditions, for 7 or more boxes (Table 6.9). Similarly, with changing forcing conditions, there are an increasing number of groups in the run using “type I” grazing terms that have time-series that differ markedly from the form of the time-series in the “standard” run under the same forcing conditions (Table 6.10).

6.3.B Sensitivity to the form of mortality used in model closure

The relative difference between the baywide mean biomasses of the “standard” run and the runs using alternative forms of model closure indicates that under “baseline” conditions the greatest changes occur when the linear mortality term is set to zero for those groups which have predators not explicitly represented in the modelled web (Table 6.11). Generally, the run (“top”) where the top predators (sharks, mammals and birds) are included explicitly shows the least divergence from the “standard” run, with predicted biomasses usually within 5% of the “standard” run. There is no run using an alternative form of model closure for which the predicted biomasses of the majority of the groups are not within 50% of the estimates in the “standard” run. However, there are still some groups in each run which differed substantially from the estimate in the “standard” run (the largest difference is for benthic deposit feeders in the run with the

“no-linear” model closure, which differ from the “standard” run by 355%).

Table 6.9: Number of boxes for which the relative spatial distributions of the “standard” run differs from that predicted by the runs using an alternative grazing term when forcing conditions are changing. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

Component	Type I		Type III		Ecosim-like		Bounded		Dynamic	
	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5
AEB	5	2	1	7	3	4	3	4	0	1
AF	2	6	6	6	3	5	1	1	6	2
ANB	5	3	1	6	3	4	3	4	1	0
BC	4	1	1	0	1	1	1	1	1	0
BD	0	0	1	0	1	0	1	0	1	1
BF	6	1	4	3	6	5	6	2	6	1
BG	0	0	0	0	1	1	2	2	2	0
DF	0	0	7	7	6	6	6	6	0	0
FD	0	0	0	0	0	0	0	0	0	0
FG	0	0	0	0	0	0	0	0	0	0
FP	0	0	0	0	0	0	0	0	0	0
FV	0	0	0	0	0	0	0	0	0	0
HF	0	0	0	0	6	0	7	7	1	1
MA	0	0	0	0	3	1	2	2	2	2
MB	4	0	2	0	1	2	1	3	1	4
MZ	0	0	0	0	4	4	6	5	1	2
OB	4	1	4	4	4	1	4	1	5	5
PAB	0	0	0	0	0	0	0	0	0	0
PFB	0	0	0	0	2	2	2	2	2	2
PL	5	1	2	1	4	4	2	0	5	1
PS	0	0	1	1	2	2	2	2	2	2
SG	1	1	2	0	2	1	2	2	3	0
ZL	0	0	1	1	0	0	1	0	0	1
ZLC	0	1	1	0	7	2	0	1	0	1
ZS	1	6	0	6	0	6	3	6	4	6

Table 6.10: Quality of the match between the predicted time-series under changing forcing conditions for each component in the “standard” run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

Component	Type I		Type III		Ecosim-like		Bounded		Dynamic	
	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5
AEB	3	3	3	3	3	3	3	3	4	3
AF	5	3	5	5	5	5	5	5	5	5
ANB	3	3	3	3	5	5	5	5	5	5
BC	1	1	1	1	5	3	5	5	5	5
BD	2	3	1	3	5	5	5	5	2	3
BF	5	5	3	5	5	5	5	5	4	5
BG	1	1	1	1	5	5	3	2	5	1
DF	3	3	3	3	3	3	3	3	3	3
FD	1	1	1	1	5	5	3	1	2	5
FG	1	1	1	1	5	1	1	1	1	1
FP	1	4	1	1	5	5	2	4	2	4
FV	1	1	1	1	5	1	1	1	1	1
HF	5	5	5	3	5	3	5	3	5	3
MA	3	3	1	3	5	5	5	5	5	5
MB	4	3	5	5	5	3	5	5	5	5
MZ	1	1	1	1	3	3	5	5	4	3
OB	5	5	5	1	5	5	5	5	5	5
PAB	3	3	1	3	3	3	3	5	3	1
PFB	3	3	3	3	5	5	5	3	5	5
PL	3	3	5	3	5	5	5	5	5	5
PS	3	5	5	5	5	5	5	5	5	5
SG	5	3	3	3	5	5	5	4	5	3
ZL	3	5	5	5	5	5	5	5	5	5
ZLC	3	5	5	5	5	5	5	5	5	5
ZS	3	3	5	5	5	5	5	5	5	3

Table 6.11: Proportional difference between the biomass predicted in the “standard” run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Top	No-linear	No-quadratic
AEB	0.01	0.97	1.00
AF	0.01	0.58	0.01
ANB	0.01	0.97	1.00
BC	< 0.01	2.41	0.66
BD	1.11	3.55	0.44
BF	< 0.01	0.77	0.34
BG	< 0.01	0.12	0.49
DF	< 0.01	0.29	0.16
FD	< 0.01	< 0.01	< 0.01
FG	< 0.01	0.26	0.03
FP	< 0.01	< 0.01	< 0.01
FV	0.04	0.01	0.01
HF	< 0.01	0.60	0.03
MA	0.17	0.96	0.22
MB	0.01	0.74	0.82
MZ	< 0.01	0.18	0.29
OB	1.00	1.00	1.00
PAB	0.02	0.55	0.50
PFB	< 0.01	0.02	< 0.01
PL	0.01	0.15	0.02
PS	0.02	0.34	0.15
SG	0.02	2.54	2.45
ZL	< 0.01	0.03	0.02
ZLC	0.01	0.02	0.03
ZS	0.03	0.19	0.11
Average	0.10	0.69	0.39

While there are some dissimilarities between the relative spatial distributions of the “standard” run and the runs using alternative forms of model closure, these differences are not as large as for some of the runs using alternative grazing functions. The relative spatial distributions of each group, in the run where the top predators are included explicitly (“top”), are identical to those of the “standard” run, except for the meiobenthos where the distribution matches that of the runs using the other alternative forms of model closure. The runs where there is “no-linear” or “no-quadratic” mortality do not show as much spatial conformity (with the “standard” run) as the “top” run. The

run using an alternative model closure scheme that has the poorest spatial conformity with the “standard” run is “no-linear”. In this run only 40% of the groups have relative distributions which match the “standard” run and 24% of the groups have spatial distributions that suggest a more widespread population, or one that is centred in a different part of the bay, to that predicted by the “standard” model run (Table 6.12). The spatial conformity of the run with “no-quadratic” model closure is better, with the relative distributions of a majority of the groups matching the distributions predicted by the “standard” run. The “no-linear” and “no-quadratic” model closure runs do not conform as well with the “standard” run as the “top” run, but they are closer than some

Table 6.12: Number of boxes for which the relative spatial distribution of the “standard” run differs from that predicted by the runs using an alternative forms of model closure. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Top	No-linear	No-quadratic
AEB	0	2	2
AF	0	1	0
ANB	0	2	3
BC	0	1	1
BD	0	0	0
BF	0	5	7
BG	0	1	0
DF	0	4	1
FD	0	0	0
FG	0	0	0
FP	0	0	0
FV	0	0	0
HF	0	2	0
MA	0	0	0
MB	0	1	1
MZ	0	0	0
OB	2	2	2
PAB	0	1	1
PFB	0	0	0
PL	0	1	0
PS	0	1	0
SG	0	1	1
ZL	0	0	0
ZLC	0	0	1
ZS	0	1	0

of the runs using alternative grazing terms. In the runs using “ecosim-like”, “bounded” or “dynamic” grazing terms 36 – 48% of the relative distributions differed by more than 2 boxes from the distribution predicted by the “standard” run (Table 6.5).

The form of the patterns observed in the time-series of each group is dependent on the form of model closure used. The run with explicit top predators included (“top”) shows the least effect of using alternative model closures, while the other two configurations are more heavily impacted (Table 6.13). For each run there are some groups that show the same form of time-series as the “standard” run, and these are mostly the slower growers (fish and benthic groups). However, each of the runs using an alternative form of model closure also has groups whose time-series do not match that of the “standard” run (Table 6.13). In some cases (e.g. for the large carnivorous zooplankton) the differences are only minor, with the same general pattern holding regardless of the form of closure used, but where there are changes in the amplitude or the mean or timing of the pattern (Figure 6.4). In other cases (e.g. the meiobenthos) the change in temporal dynamics is striking (Figure 6.5).

When fishing pressure is increased, there is little difference in the overall performance of the runs using the alternative forms of model closure, though the run employing the “no-quadratic” model closure does diverge slightly more from the “standard” run than the others (Table 6.14). When nutrient loading is increased the run using “no-quadratic” model closure diverges from the “standard” run much more than does either of the other two alternatives (Table 6.15). When nutrient loads or fishing pressure are increased, the predicted trends for the sediment infauna (macro- or microscopic) can be orders of magnitude larger in runs using alternative model closure than for the “standard” run, under the same conditions (Tables 6.14 and 6.15). For example, when fishing pressure increases fivefold the change in biomass for the benthic deposit feeders is more than 3442 times that of the “standard” run in all the runs using

Table 6.13: Quality of the match between the predicted time-series for each component in the “standard” run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	1	3	5
AF	3	5	3
ANB	1	3	5
BC	1	1	5
BD	3	3	5
BF	1	5	5
BG	1	1	1
DF	1	2	1
FD	5	1	1
FG	5	1	1
FP	5	1	1
FV	5	1	1
HF	1	3	2
MA	2	3	3
MB	1	3	3
MZ	1	1	3
OB	5	5	5
PAB	1	3	3
PFB	2	3	3
PL	2	3	2
PS	3	5	2
SG	1	3	3
ZL	2	4	2
ZLC	3	3	2
ZS	3	3	1

Figure 6.4: An example of only minor differences in time-series for alternative forms of model closure. Shown here is the biomass of large carnivorous zooplankton (ZLC) in box 8 (in the centre of the bay) over the same four-year period for runs using the “standard”, “no-linear” and “no-quadratic” forms of model closure.

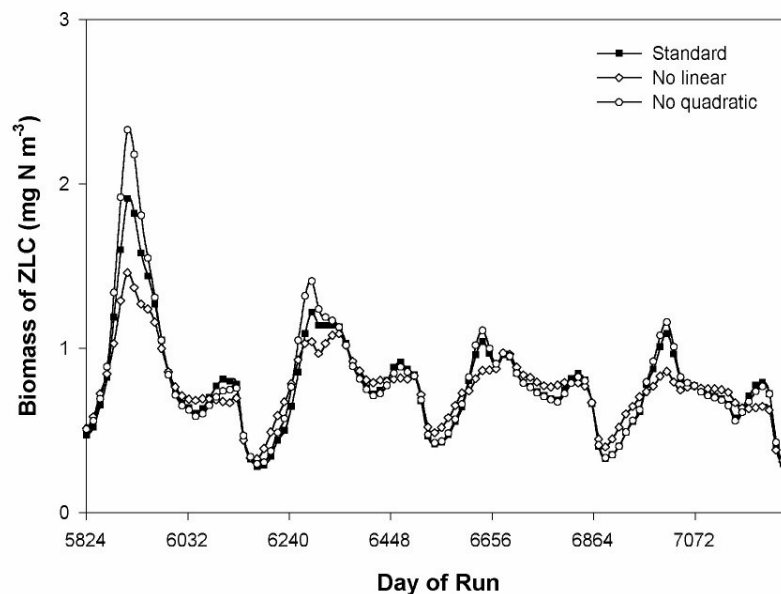


Figure 6.5: An example of major differences in time-series for alternative forms of model closure. Shown here is the biomass of autotrophic flagellates (AF) in box 8 (in the centre of the bay) over the same four-year period for the runs using the “standard” and “no-linear” forms of model closure.

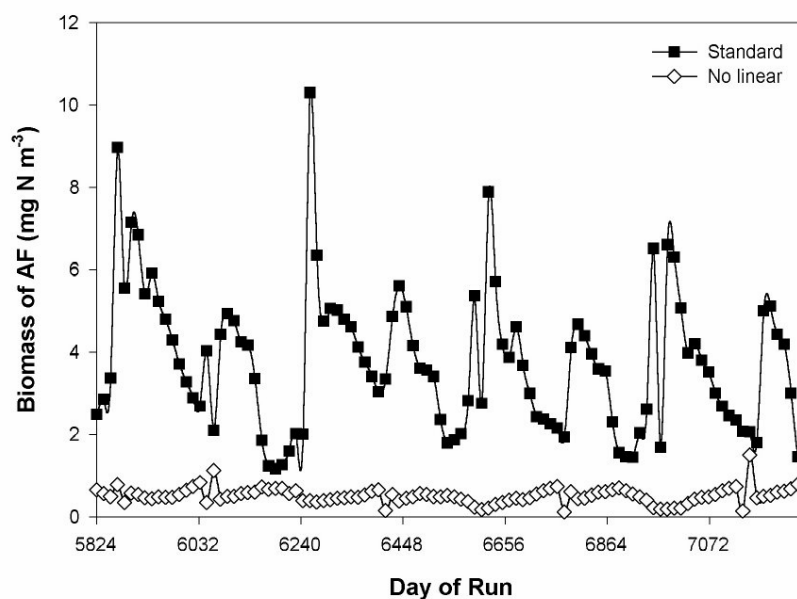


Table 6.14: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under “baseline” conditions) predicted in the “standard” run and those runs using alternative forms of model closure when the fishing pressure is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	0.81	0.87	0.38
AF	< 0.01	0.16	0.03
ANB	0.82	0.88	0.69
BC	0.52	0.52	0.52
BD	3442.71	3333.79	3587.31
BF	0.13	0.05	0.42
BG	1.67	1.69	1.67
DF	0.02	0.01	0.10
FD	0.02	0.01	< 0.01
FG	< 0.01	0.07	0.05
FP	0.02	< 0.01	< 0.01
FV	0.05	< 0.01	0.01
HF	0.02	0.02	0.01
MA	0.14	0.10	0.08
MB	0.06	0.04	0.03
MZ	0.15	0.15	0.15
OB	1.00	1.00	1.00
PAB	0.16	0.09	0.17
PFB	< 0.01	0.01	< 0.01
PL	0.05	0.04	0.07
PS	0.02	0.44	0.13
SG	0.29	0.31	0.31
ZL	0.02	< 0.01	0.06
ZLC	0.02	0.05	0.03
ZS	0.03	0.14	0.02
Average	137.95	133.62	143.73

Table 6.15: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under “baseline” conditions) predicted in the “standard” run and those runs using alternative forms of model closure when the nutrient load is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	< 0.01	0.93	38.02*
AF	0.02	0.16	0.05
ANB	< 0.01	0.98	9.13*
BC	< 0.01	0.77	0.80
BD	0.42	0.51	0.54
BF	< 0.01	0.24	1.49*
BG	< 0.01	0.10	< 0.01
DF	< 0.01	< 0.01	0.20
FD	< 0.01	< 0.01	< 0.01
FG	< 0.01	0.19	0.01
FP	< 0.01	0.02	0.01
FV	< 0.01	0.08	0.06
HF	0.01	0.11	0.06
MA	0.10	0.45	0.21
MB	< 0.01	0.67*	0.65
MZ	< 0.01	< 0.01	< 0.01
OB	31.23	1.00*	1.00
PAB	0.01	0.46	0.49
PFB	< 0.01	0.01	0.01
PL	0.01	0.08	0.02
PS	0.03	0.13	0.05
SG	0.07	0.76	0.01
ZL	0.01	0.20	0.13
ZLC	0.01	0.17	0.13
ZS	0.01	0.05	0.06
Average	1.28	0.32	2.13

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the “standard” run under the same conditions - for instance, a decline in place of an increase.

alternative forms of model closure (Table 6.14). Once again there are a few cases where the differences in the trends go beyond differences in magnitude. However, the only groups for which the predicted trend in biomass is in the opposite direction to the trend in the “standard” run, under the same conditions, are in the runs employing “no-linear” and “no-quadratic” mortality when nutrient loading increases (Table 6.15).

Generally, for the runs using “no-linear” model closure or explicit top predators (“top”), spatial and temporal conformity with the patterns predicted by the “standard” run are as good under changing forcing as under “baseline” conditions (Tables 6.16 and 6.17). This is not the case for either of the runs using “no-quadratic” mortality when forcing conditions change. When nutrient loads or fishing pressure increases there is a reduction in the number of groups for which the patterns predicted by the run with “no-quadratic” mortality match those of the “standard” run (Tables 6.16 and 6.17). More generally, under changing forcing conditions, any differences in the spatial patterns observed in the runs employing alternative forms of model closure are usually stronger than under “baseline” conditions (Table 6.16). Such a consistent result is not evident for the form of the temporal dynamics predicted in each run (Table 6.17).

6.4 Discussion

Given their direct impact throughout the web, rather than just at higher trophic levels, it is not surprising that the effects of alternative grazing terms were larger and more pervasive than those due to using different forms of model closure. However, this does not agree with the findings of Steele and Henderson (1992) or Murray and Parslow (1999b). They found that the form of the model closure was generally far more important in determining model behaviour than internal details, such as the functional responses of consumers. This difference may reflect that the web used in the ecosystem model investigated here incorporates many more consumers in a more highly

Table 6.16: Number of boxes for which the relative spatial distributions of the “standard” run differs from that predicted by the runs using an alternative forms of model closure when forcing conditions are changing. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

Component	Top-predators explicit		No-linear		No-quadratic	
	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5
AEB	0	4	4	4	3	4
AF	0	0	1	1	0	0
ANB	0	4	4	4	7	5
BC	0	1	8	2	8	2
BD	0	0	1	0	1	0
BF	0	1	2	3	4	5
BG	0	0	0	1	0	0
DF	0	0	4	5	1	1
FD	0	0	0	0	0	0
FG	0	0	0	0	0	0
FP	0	0	0	0	0	0
FV	0	0	0	0	0	0
HF	0	0	3	6	0	0
MA	0	0	0	0	0	0
MB	1	0	2	1	2	1
MZ	2	3	0	3	1	4
OB	0	3	4	3	4	3
PAB	0	0	1	1	0	1
PFB	0	0	0	0	0	0
PL	0	0	2	1	0	2
PS	0	0	1	0	0	0
SG	0	1	1	2	2	2
ZL	0	0	0	0	0	0
ZLC	0	0	1	0	0	0
ZS	0	0	1	1	0	1

Table 6.17: Quality of the match between the predicted time-series under changing forcing conditions for each component in the “standard” run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

Component	Top-predators explicit		No-linear		No-quadratic	
	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5
AEB	1	3	5	3	5	5
AF	3	3	5	5	3	3
ANB	1	1	5	5	5	5
BC	1	1	1	1	5	5
BD	1	3	1	3	5	5
BF	1	3	5	5	5	5
BG	1	1	1	1	1	1
DF	1	1	3	1	3	3
FD	5	1	1	1	1	1
FG	5	4	1	1	1	1
FP	5	5	1	3	1	4
FV	5	1	1	1	1	1
HF	1	3	2	3	2	5
MA	1	1	1	3	3	3
MB	1	1	5	5	5	3
MZ	1	1	3	1	3	3
OB	3	5	5	5	5	5
PAB	1	3	3	3	3	3
PFB	1	3	3	5	3	3
PL	1	3	3	3	3	3
PS	3	1	3	3	3	5
SG	2	1	5	3	5	3
ZL	3	2	3	3	3	3
ZLC	3	1	3	1	3	3
ZS	2	3	3	3	3	3

interconnected web than the simple Nutrient-Phytoplankton-Zooplankton chains considered by Steele and Henderson (1992) and Murray and Parslow (1999b).

Functional responses

The sensitivity of model behaviour to the form of the grazing term, especially under changing ecosystem conditions, indicates that careful thought must be given to the choice of grazing term and the associated assumptions and data requirements. For

the simpler “Holling-type” functional responses, the behaviour of the model under “baseline” conditions indicates that the biomasses of the various prey groups are at a level where the potentially destabilizing nature of the simpler functional responses (Begon and Mortimer 1986) is of little importance. There are the occasional exceptions (like meiobenthos when using the “type III” response), but overall there is very little difference in the outcome of the standard, “type I” and “type III” runs under “baseline” conditions. This is because the prey biomasses keep the functional response curves within a section where they are similar to each other (Figure 6.6). This finding is similar to that of previous studies (Gao et al. 2000, Tett and Wilson 2000). It is only under increasing nutrient loads and/or fishing pressures that the differences in the curves influence model behaviour as the biomasses become very large or small (depending on the prey groups in question). Even under these more extreme conditions there is little to

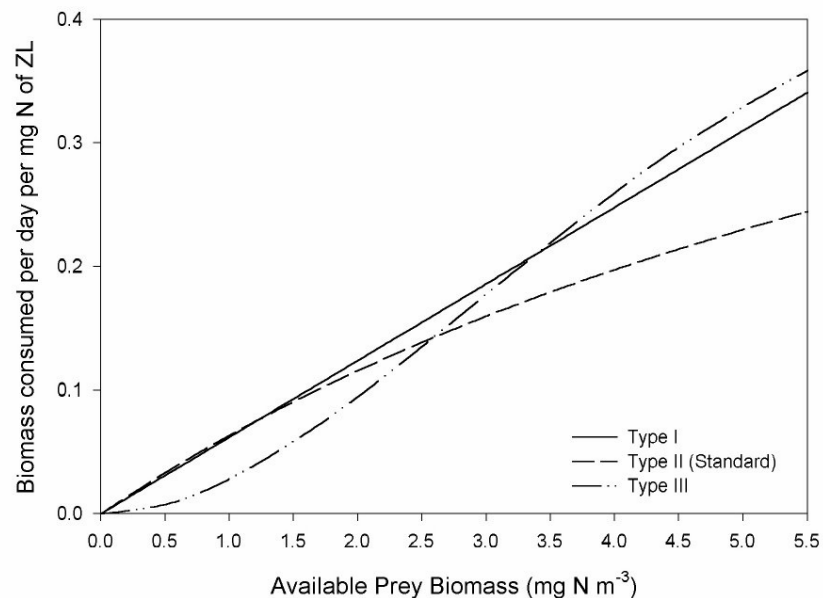


Figure 6.6: The “type I”, “type II” (the response used in the standard run) and “type III” functional responses for the large omnivorous zooplankton (ZL). The range of prey biomasses shown covers the typical levels of available prey biomass, although the available biomass can jump to much higher levels (2 – 5 fold higher) for short periods during bloom events.

recommend the general use of a Type III curve over that of a Type II if coefficients of prey availability feature in the formulations (as they do in this case). However, in the mixed case, where the same functional response is not applied to all groups, selective use of a Type III may prove to be beneficial for those groups whose behaviour in the field matches the formulation's assumptions.

The simple "Holling-type" functional responses are used widely in food chain and ecosystem models (Büssenschütt and Pahl-Wostl 2000), but they are not the only functional responses employed. Other functional responses in use include: the modified disk equation that incorporates thresholds (Radach and Moll 1993, Baretta et al. 1995, Tett and Wilson 2000); the Ivlev formula (McGillicuddy et al. 1995); ratio-dependent functions (Arditi and Ginzburg 1989, Matson and Berryman 1992); and a two-dimensional function of the biomasses of predator and prey (Büssenschütt and Pahl-Wostl 2000). Consideration of the complete list of functional responses is beyond the scope of our work and recent work suggests that ratio-dependent functions may not be suitable for use in general models such as BM2 (Gleeson 1994, Sarnelle 1994, Abrams 1994, Abrams and Ginzburg 2000, Büssenschütt and Pahl-Wostl 2000). Conversely, the arguments regarding the effects of thresholds (Frost 1975, Bryant et al. 1995) and the impacts on behaviour and feeding of groups other than the predator and prey (Abrams and Ginzburg 2000, Walters et al. 2000) are well made. For this reason we examined the effects of using "bounded", "dynamic" and "ecosim-like" functional responses. The effects of using these formulations are often greater than moving from the standard to "type I" or "type III" functional responses. They also tend to have greatest impact on groups that are poorly known or only beginning to attract attention in biogeochemical models (such as infauna, flagellates and bacteria). For many of these groups the behaviour under the more sophisticated functional response is no closer to real biomass dynamics than that achieved with the simpler standard functional response. However,

the performance of the benthic deposit feeding group is substantially improved, particularly when nutrient loading increases. The behaviour of this group is a weakness of the standard form of BM2 (chapter 2), which seems to be corrected if the additional checks inherent in the more complex functional responses are added. By itself however, this is no reason to include high levels of added complexity in functional responses across all groups as a matter of course. While the “type I” functional response is obviously insufficient if the model is to behave realistically as conditions change, careful thought must be given to how much flexibility should be added - to how many feedbacks, thresholds and inflexion points are added – when more sophisticated responses are used. Jørgensen (1994), amongst others, has advocated structurally dynamic models (models where parameters change according to a goal function) as the best way of capturing changes in species with changes in conditions. Without going to that extent, functional responses with the flexibility of the “ecosim-like” response used here, set within a multi-linked web, are also able to reflect the more dynamic changes that may occur within a web as ecosystem conditions change. However, given the high number of parameters biogeochemical models can require and that trends rather than specific quantitative values are usually sufficient for model interpretation and subsequent recommendations, “Holling-type” functional responses may still suffice. As stated above, this topic requires careful thought and should be a key part of any model formulation discussion.

One recommendation that can be made based on the results presented here is that research aimed at empirically determining the nature of functional responses in real systems is clearly needed. It is likely that, unlike the model presented here, in real systems different groups will have different types of functional responses. Furthermore, many bay ecosystems are changing and given the sensitivity of models like BM2 to the form of functional response used, there is a real need to properly establish the nature of

the functional responses in real systems (at least for some groups).

Model closure

Plankton modelers recognize that the form of model closure used requires careful consideration. While it is notable that the form of model closure does not have the dominating effect on the BM2 ecosystem model that it has on simpler plankton models (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000), it was important nevertheless. Detailed bifurcation analysis, such as in Edwards and Brindley (1999), is not possible for a model of this size, so our conclusions must be based on the simulation runs. Previous papers on the subject (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000) have concentrated on the steady-state stability status achieved when using different closure terms, while this paper has concentrated on the overall effects on model dynamics. Despite these differences, comparison of conclusions from the different works is instructive.

The necessity of including responsive top predators (either explicitly or implicitly via a quadratic mortality term) agrees with the general findings of the earlier studies. The change in behaviour of the run employing “no-linear” model closure under “baseline” conditions also gives some support for inclusion of separate natural mortality (linear) and higher predation (quadratic) terms. McGillicuddy et al. (1995), Murray and Parslow (1997) and Broström (1998) have successfully used this division of mortality terms, and the findings of Edwards and Brindley (1999) and Edwards and Yool (2000) do recommend it. However, Edwards and Brindley (1999) and Edwards and Yool (2000) caution that the use of both mortality terms requires the estimation of two (rather than one) poorly known parameter, which may mitigate against its use. Thus, given our results, the argument for the use of both terms is not overwhelming, and use of the

linear term may not be necessary. However, this may not be the case under oligotrophic conditions or extreme overfishing. In both of these cases the biomasses of many groups may be very low, which is precisely the situation in which quadratic mortality alone may yield unrealistic dynamics (Edwards and Brindley 1999). Further work to address this issue is required.

One final concern about model closure is whether or not the top predators must be included explicitly. A comparative analysis of the application of BM2, IGBEM and ECOSIM (Christensen and Pauly 1992, Walters et al. 1997) to Port Phillip Bay suggested that the implicit representation of the top predators (sharks, mammals and birds) in the biogeochemical models may not be capable of capturing some of the dynamics of that part of the web (chapter 7). This suggests that the top predators might need to be included explicitly, but the expansion of BM2 to explicitly represent the top predators did not see any substantial shifts in model behaviour. The clear indication is that unless the top predators are of particular concern in themselves (due to being a large component of the system, a conservation concern, or harvested group), their explicit inclusion in biogeochemical models is not required. Quadratic model closure appears to be acceptable regardless of the size of the web being considered.

6.5 Conclusions

Ecosystem models are one tool that has been advocated for ecosystem management (Walters et al. 1997, Sainsbury et al. 2000). Consequently, the impact of formulation decisions on their behaviour needs to be considered. Predation, in the form of grazing terms and model closure, is a crucial part of ecosystem models that incorporate ecology or biogeochemistry (Edwards and Yool 2000, Tett and Wilson 2000). The work discussed here indicates that, unless the top predators of a system are of particular interest, the additional complexity of their explicit inclusion can be avoided

by the use of a quadratic term for model closure. The use of a quadratic mortality term to close the model allows for realistic predictions across a range of conditions.

The specification of a suitable grazing term is more complex. Whereas linear plankton models have predicted that the grazing term has little real effect on model behaviour, our results for more complex webs indicate otherwise. Thus, careful consideration must be given to this part of the model formulation. There are biologically and mathematically sound arguments for including the more sophisticated dynamics of functional responses such as the “bounded”, “dynamic” and “ecosim-like” responses trialled here (Bryant et al. 1995, Walters et al. 2000, Abrams and Linzburg 2000). However, given the extra detail and increased information required to parameterise and validate these formulations, a simpler “Holling-type” functional response may be sufficient. This is particularly true if preliminary studies or modelling exercises indicate that the “Holling-type” functional responses will lead to the same general conclusions and behaviour as more sophisticated functional responses. Nevertheless, some degree of sophistication is required in the functional response employed as the simple application of a “type I” response is unlikely to be useful under changing ecosystem conditions (e.g. increasing nutrient loads or fishing pressure). It is doubtful that any one functional response will be suitable for all groups, models and environments. The demonstration here, that model behaviour can be sensitive to the form of the grazing terms used, shows that efforts to empirically determine the form of functional responses in real systems are warranted. Along with the topology and the form of the trophic web that defines the framework of the model, the grazing terms are a feature that require particularly careful consideration during the conceptualisation and development of ecosystem models.