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Mortality and predation in ecosystem models: is it important how these are expressed?

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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 more popular more needs to be known about the effects of model formulation on model behaviour and performance. The impact of the form of the grazing response function 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 that close the modelled food web.

When using biogeochemical ecosystem models in shallow marine ecosystems, the most dynamic and sophisticated functional responses describing grazing require more parameters and validation than the simpler Holling disk equation, but usually still lead to the same general conclusions about the 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 necessary if they are not the focus of the study. A quadratic mortality term applied to intermediate predators (such as piscivores) is sufficient to achieve plausible model behaviour. It should be noted, however, 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.

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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; Hollowed et al., 2000; Sainsbury et al., 2000). These models, whether primarily biogeochemical or ecological, have the potential to improve marine ecosystem management, 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

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et al., 2000). Within ecology in general, the issue of the effect of the formulation of biological processes on model performance has received a good deal of attention (DeAngelis et al., 1975; May, 1976; Hassell, 1978; Begon and Mortimer, 1986; McNair, 1986; Berryman, 1992; Ginzburg and Akçakaya, 1992; Legaspi et al., 1996; Myerscough et al., 1996; Varriale and Gomes, 1998). In eutrophication models the topic has also begun to be thoroughly analysed (Fransz et al., 1991; Edwards and Brindley, 1999; Murray and Parslow, 1999; Edwards and Yool, 2000; Gao et al., 2000; Tett and Wilson, 2000; Lima et al., 2002). This has not been the case for ecosystem models that encompass whole food webs, however.

Ecosystem models are often quite large and 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. The work of Steele and Henderson (1992, 1995), Murray and Parslow (1999) 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. DeAngelis et al. (1975) argue that as large-scale ecosystem models are so hard to analyse that the formulations used in them must be clearly understood via mathematical analysis (primarily using trophically simple models). Indeed, much of the existing work has been carried out on models with few compartments and linear food chains. Unfortunately, it is not clear that findings from these trophically simple models easily generalise to web-like ecosystem models. Given the increasing use of ecosystem models as management tools it is imperative that an understanding of the sensitivities of ecosystem models to alternative formulations is gained quickly. This means that direct consideration must be given to the performance of ecosystem models using alternative formulations, even if this can currently only be done with limited sophistication.

Over the last quarter of a century both theoretical and applied studies have shown that the form of predation incorporated into models can have a large effect on their performance, as measured by their stability and predictions (May, 1976; Hassell, 1978;

Hassell and Commins, 1978; Begon and Mortimer, 1986; Legović, 1989; Berryman, 1992; Ginzburg and Akçakaya, 1992; Gutierrez, 1992; Steele and Henderson, 1992; Luckyanov et al., 1995; Legaspi et al., 1996; Myerscough et al., 1996; Varriale and Gomes, 1998; Edwards and Brindley, 1999; Gao et al., 2000; Geçek and Legović, 2001; Lima et al., 2002). 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, extra assumptions may be necessary. One important consideration is whether the effect of predators, that are 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, 1999) because the model's behaviour may be more, or less, plausible depending on the form chosen.

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, 1999; Edwards and Yool, 2000). Studies of the performance of water quality models also indicate 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 (Legaspi et al., 1996; 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; Berryman, 1992; Ginzburg and Akçakaya, 1992); (3) unrealistic behaviour at high predator abundance (Abrams, 1993; Legaspi et al., 1996); and (4) a failure to detect appropriate behaviour (e.g. predator switching, the basis for type III responses) in the field, whereas fine scale spatial organisation (foraging arenas) has been detected (Arditi and Saïah, 1992; Walters and Kitchell, 2001). As a result, other responses have been proposed.

A review of all types of functional responses is beyond the scope of this paper, but it can be said that there have been mixed results and 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, which attempt to incorporate foraging arenas and the pressure on an organism to maximise foraging time while minimising predation risk, such as the one included in ECOSIM (Walters et al., 2000), have been found to be useful (Abrams, 1993).

During the development of two biogeochemical ecosystem models, Bay Model 2 (BM2) (Fulton et al., 2003a) and the Integrated Generic Bay Ecosystem Model (IGBEM) (Fulton et al., 2003b), it became clear that the way in which feeding and mortality is modelled can be critical to ecosystem model be-

haviour. For example, using only linear mortality terms for the fish groups in IGBEM (i.e. linear model closure) can result in unstable behaviour under some conditions (Fulton et al., 2003b). This finding spurred a study examining some aspects of the effect of the form of the grazing terms and model closure on the dynamics and performance of an ecosystem model. As BM2 has been found to acceptably represent real shallow marine systems (Fulton et al., 2003a), it was used as the basis for using the “deep–shallow model” approach. This work is presented here and is one part of a wider study that considers the effects of model formulation and structure on ecosystem model behaviour. Discussion of the many facets of model sensitivity investigated in the wider study are beyond the scope of a single paper. Interested readers are, however, referred to the discussion of the level of physiological formulation detail used in models in Fulton et al. (2003a), the effect of spatial resolution on model behaviour detailed in Fulton et al. (2003c), and the impact of trophic resolution on model predictions described by Fulton (2001).

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. The approach employed to do this is a variation on the “deep model–shallow model” comparison, in which a complex simulation model (BM2) that incorporates complex processes thought to occur in nature, acts as an artificial world (or deep “baseline”) against which the performance of other (“shallow”) models are compared. In this case the “shallow” models are not simplifications of the “deep” model, rather they contain alternative grazing and mortality formulations. This approach allows a modeller to begin with a validated model and then modify it to determine the effect of those changes on model behaviour allowing for the identification of parsimonious models. In addition, this approach separates those parts of the model formulation issues concerned with model structure from those of the accuracy and precision of sample data, as it deals with perfect knowledge. The research discussed here considers only the effect of model formulation on

behaviour and makes no attempt to consider effects of data uncertainty.

It is important to note that in the work discussed here the models are not being used as a simulated replica of any one system. For convenience, the physics of a particular Australian bay (Port Phillip Bay, Melbourne) are utilised, but overall the simulated system is a hypothetical one that has the general ecological structure and dynamics typical of most temperate bays. As BM2 employs standard biogeochemical and ecological modelling structures and as it has been found to realistically reproduce the behaviour of real shallow marine ecosystems (Fulton, 2001), the results from this study should generalise to other ecosystem models applied to marine bays.

2.1. Model structure

BM2 is a biogeochemical ecosystem model constructed as part of a wider study on the effects of model structure on performance. A detailed description of the formulation of BM2 is beyond the scope of this paper, but such a description can be found in Fulton et al. (2003a). Instead, a brief overview of the model is given below and a summary of the major assumptions of the model is given in Table 1 and the food web used is shown in Fig. 1.

BM2 is built at the level of trophic guilds and follows the nitrogen and silicon pools of 21 living groups (pelagic and benthic) and a number of detrital and nutrient pools (Table 2). The very basic form of the equations are given in Table 3, though individual terms may be more detailed in some groups to reflect particular phenomena, such as mixotropy or oxygen dependence. The fish groups represent the most extreme modification of this general form, as the formulations for those groups include an age structure and track the condition of average individuals and the number of such individuals rather than simply following the biomass pool in the model cell. Nevertheless, the equations given in Table 3 should convey the general level of the model formulation.

An 8-box form of this model is used to investigate the alternative grazing and mortality forms considered here. This spatial resolution provides a balance between computational requirements and potential impacts of trophic self-simplification due to system homogeneity and refuge losses (Fulton et al., 2003c).

There are some effects of self-simplification in the 8-box compared with the complete 59-box spatial configuration usually used with BM2 (Fig. 2), but they are small and so the benefits of much shorter processing times outweigh potential costs in this case.

2.2. Grazing functions

Six alternative grazing functions are trialed (Table 4). The forms 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; Ebenhöh et al., 1995; Walters et al., 2000). The forms 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, is quite strong, although such a simplifying assumption is necessary for evaluating the behaviour of a modelled web that is large and complex. Future studies may benefit from considering the effects of differing functional responses across the trophic levels.

2.3. Mortality schemes

Four mortality (trophic closure) schemes are also trialed. Unlike the grazing terms, the various schemes for trophic closure do not all represent completely different formulations. The natural mortality term used in the model for group X has the following general form:

$$M_X = X(m_{\text{lin},X} + m_{\text{quad},X}X + (1 - r_{O_2})m_{O_2,X} + m_{\text{special},X} + m_{\text{top},X}) \quad (1)$$

where $m_{\text{lin},X}$ is the coefficient of linear (or “basal”) mortality, $m_{\text{quad},X}$ is the coefficient of quadratic mortality (representing predation due to groups not explicitly represented in the modelled web), $m_{O_2,X}$ is the coefficient of oxygen-dependent mortality (only non-zero for benthic consumers) and $m_{\text{special},X}$ is the coefficient of special (group-dependent) mortality. This rate of “special” mortality is only non-zero

Table 1

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

Feature	BM2
General features	
Numerical integration scheme	Simple forward difference method
Biological time step	Adaptive ^a
Overall time step (physics and biology)	Daily ^b
Vertical structure	Single water column, epibenthic and sediment layer in each box
Biomass units	mg N/m ^c
Input forcing	Nutrients and physics on interannual, seasonal and tidal frequencies
Level of biological detail	Functional group (defined based on organism size and feeding guild)
Process related	
Bioturbation and bioirrigation	Yes
Consumption formulation	Logistic (Holling-type II)
Formulation detail	General equations: only growth, mortality and excretion explicit
Light limitation	Optimal irradiance fixed
Mixotrophy	Dinoflagellates
Nutrient limitation	External nutrients determine uptake
Nutrient ratio	Redfield
Oxygen limitation of demersal fauna	Yes
Sediment burial	No
Sediment chemistry	Dynamic, with sediment bacteria
Shading of primary producers	Yes
Spatial structure	Flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	Yes
Transport model used for hydrodynamics flows ^c	Yes
Model closure	
Top predators represented by static loss terms	Yes
Linear mortality terms	Yes
Quadratic mortality terms	Yes
Fish and fisheries related	
Age structured fish	Nine age classes
Fishery discards	Target species only
Invertebrate fisheries	Yes
Stock-recruit relationship	
Stock structure	Constant recruitment External: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock

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

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

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

for the macroalgae, seagrass and vertebrates. The macroalgae and seagrass suffer extra mortality due to mechanical bottom stress and fouling by epiphytes, respectively, while the vertebrates may suffer from death due to starvation if conditions are poor. The final term of Eq. (1) was adopted from ERSEM (Bryant et al., 1995) to represent the impact of seabirds and

other top predators on fish groups and is given by:

$$m_{\text{top},X} = m_{\text{seabird},X} + m_{\text{shark},X} \quad (2)$$

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 the groups explicitly listed above. In

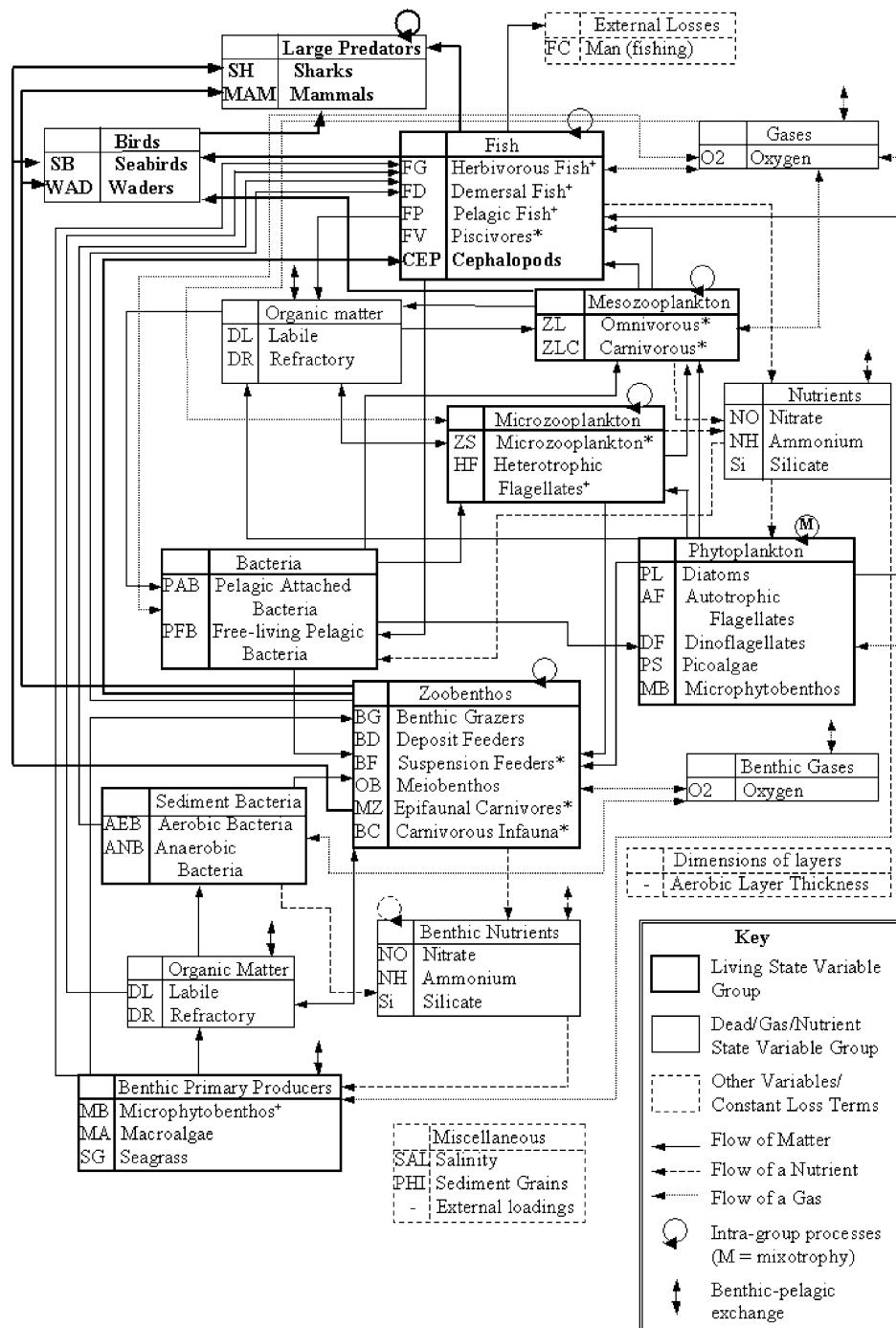


Fig. 1. Biological and physical interactions between the components used in Bay Model 2 (BM2). The flows (arrows) in bold are the linkages associated with the top predators (names in bold) that are not normally included explicitly in the web. Groups marked with asterisk (*) have both quadratic and linear mortality terms, as do those groups marked with plus sign (+). The latter have very small (<0.000001) quadratic mortality coefficients in the “standard” run.

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

Component	Code name	Fig. 3 category
Diatoms ^a	PL	Phytoplankton
Autotrophic flagellates	AF	Phytoplankton
Picophytoplankton	PS	Phytoplankton
Dinoflagellates	DF	Phytoplankton
Free-living pelagic bacteria	PFB	Bacteria
Pelagic attached bacteria	PAB	Bacteria
Heterotrophic flagellates	HF	Zooplankton
Microzooplankton	ZS	Zooplankton
Large omnivorous zooplankton	ZL	Zooplankton
Large carnivorous zooplankton	ZLC	Zooplankton
Planktivorous fish	FP	Fish
Piscivorous fish	FV	Fish
Demersal fish	FD	Fish
Demersal herbivorous fish	FG	Fish
Macroalgae	MA	Macrophyte
Seagrass	SG	Macrophyte
Microphytobenthos ^a	MB	Microphytobenthos
Macrozoobenthos (epifaunal carnivores)	MZ	Epifauna
Benthic (epifaunal) grazers	BG	Epifauna
Benthic suspension feeders	BF	Epifauna
Infaunal carnivores	BC	Infauna
Benthic deposit feeders	BD	Infauna
Meiobenthos	OB	Infauna
Aerobic bacteria	AEB	Bacteria
Anaerobic bacteria	ANB	Bacteria
Cephalopods ^b	CEP	—
Seabirds ^b	SB	—
Wading birds ^b	WAD	—
Sharks ^b	SH	—
Marine mammals ^b	MAM	—
Labile detritus	DL	—
Refractory detritus ^a	DR	—
DON	DON	—
Ammonia	NH	—
Nitrate	NO	—
Dissolved silicate	Si	—
Dissolved oxygen	O2	—

^a Also have an Si internal pool.

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

the “standard” run, every group in BM2 has a non-zero coefficient for linear mortality, but only the following groups have a non-zero coefficient for quadratic mortality: heterotrophic flagellates, microzooplankton, large omnivorous zooplankton, large carnivorous zooplankton, microphytobenthos, planktivorous fish,

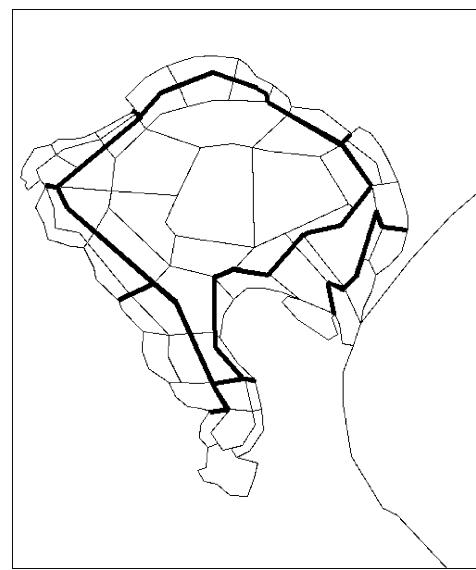


Fig. 2. Spatial structure implemented for Bay Model 2 (BM2). The 8-box configuration marked in bold is the standard structure used for the runs discussed in this paper, while the 59-box structure is the default for BM2.

piscivorous fish, demersal fish, demersal herbivorous fish, macrozoobenthos (epifaunal carnivores), benthic suspension feeders, and infaunal carnivores. In the “no-linear” scheme, the coefficient for the linear mortality term is set to zero, while in the “no-quadratic” scheme the coefficient for the quadratic mortality term is set to zero.

The final form of model closure considered (“top”) considers the explicit and dynamic representation of mortality due to predation from groups high in the trophic web, such as waders, seabirds, sharks and marine mammals. To do this, the modelled foodweb was extended to include more of the higher functional groups (e.g. sharks) omitted from the “standard” version of BM2 (these additional groups are in bold type in Fig. 1). This was done by duplicating the general form of the model structures used to represent the fish groups and then adjusting diets and parameter values to those representative of waders, seabirds, large sharks and marine mammals (in particular seals). In addition, all of the $m_{top,X}$ coefficients and any of the coefficients of quadratic mortality representing predation by these groups on the other model components were set to zero.

Table 3
Basic form of the equations used in Bay Model 2 (BM2)

Rate of change of X for	General formulation	Definitions
Primary producers	$\frac{dX}{dt} = r_{IRR}r_{NUT}r_{SP}XI_X - M_X - \sum_Y G_{Y,X}$	$G_{Y,X}$ = grazing on X by predator Y ; I_X = maximum growth rate of X^a ; M_X = natural mortality of X ; r_{IRR} = limitation due to light levels; r_{NUT} = limitation due to nutrient levels; r_{SP} = limitation due to available space (if benthic)
Invertebrate consumers	$\frac{dX}{dt} = r_{SPROX} \sum_Z G_{X,Z}e_Z - M_X - F_X - \sum_Y G_{Y,X}$	e_Z = assimilation efficiency of X when feeding on Z ; F_X = losses from X due to fishing; $G_{X,Z}$ = grazing on prey Z by X
Fish (S for structural pool of the average individual, R for reserve and N for number of individuals in the age class)	$\frac{dX_S}{dt} = d_X \sum_Z G_{X,Z}e_Z$ $\frac{dX_R}{dt} = (1 - d_X) \sum_Z G_{X,Z}e_Z$ $\frac{dX_N}{dt} = I_X - E_X - M_X - F_X - \sum_Y G_{Y,X}$	d_X = proportion of total growth allocated to structural growth; E_X = emigration by X ; I_X = immigration by X
Bacteria	$\frac{dX}{dt} = \max(1, (1 - J_X)^3)XI_X - M_X - \sum_Y G_{Y,X}$	J_X = substrate, oxygen- and temperature-dependent growth adjustment factor for X
Detritus	$\frac{dX}{dt} = \sum_Y W_Y o_Y - \sum_Y G_{Y,X}$	o_Y = proportion of waste produced that is that type of detritus; W_Y = waste produced by Y (via excretion or mortality)
Nutrient	$\frac{dX}{dt} = \sum_Y W_Y o_Y - \sum_Z U_{Z,X} + C_X$	o_Y = proportion of waste produced that is that type of nutrient; $U_{Z,X}$ = uptake of X by primary producer or bacteria Z ; C_X = production of the nutrient by chemical process, such as mineralisation (may be a negative term for processes such as the nitrification of ammonia)
Oxygen	$\frac{dX}{dt} = \lambda_{ON} \left(\sum_Z r_{IRR}r_{NUT}r_{SP}ZI_Z - \sum_Y W_Y o_{NH} - C_{DON} \right)$	λ_{ON} = redfield ration of oxygen to nitrogen (set to 16 here); Z = primary producer; o_{NH} = proportion of waste produced by Y that is ammonia (i.e. excretion); C_{DON} = dissolved organic nitrogen lost due to remineralisation

To conserve space, each term is defined the first time it is used and the detailed formulation of individual terms not modified in this study is not provided (they can be found in Fulton et al., 2003a), but details of the grazing terms are given in Table 4.

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

Table 4
Alternative forms of the grazing term ($G_{X,Y}$) per consumer considered

Name	Equation ^a	Definitions	Source
Standard (type II)	$G_{X,Y} = \frac{X p_{X,Y} Y c_X}{1 + (c_X/l_X) (\sum_Z e_{X,Z} p_{X,Z} Z)}$	c_X = maximum clearance rate of predator X^b ; $e_{X,Z}$ = assimilation efficiency of predator X on prey Z ; l_X = maximum growth rate of predator X^b ; $p_{X,Y}$ = availability of prey Y to predator X ; Y = biomass of prey Y	Murray and Parslow (1997)
Type I	$G_{X,Y} = X \cdot \min \left(c_X p_{X,Y} Y, \frac{c_X}{l_X} \right)$	c_X = maximum clearance rate of predator X^b ; l_X = maximum growth rate of predator X^b ; $p_{X,Y}$ = availability of prey Y to predator X ; Y = biomass of prey Y	Murray and Parslow (1997)
Type III	$G_{X,Y} = \frac{X (p_{X,Y})^2 c_X}{1 + (c_X/l_X) (\sum_Z e_{X,Z} (p_{X,Z} Z)^2)}$	c_X = maximum clearance rate of predator X^b ; $e_{X,Z}$ = assimilation efficiency of predator X on prey Z ; l_X = maximum growth rate of predator X^b ; $p_{X,Y}$ = availability of prey Y to predator X ; Y = biomass of prey Y	Murray and Parslow (1997)
Ecosim-like	$G_{X,Y} = \frac{X v_X T_X p_{X,Y} Y T_Y}{[(h_X T_X p_{X,Y} (1 + T_Y))/1 + v_X \sum_Z Z T_Z] + v_X X T_X},$ where $T_X = \min \left(t_X, T_X^{\text{prev}} \left(1 - a_X + \frac{a_X Q_X}{\sum_Z G_{X,Z}^{\text{prev}}} \right) \right)$ and $Q_X = \sum_Z G_{X,Z}^{\text{prev}} \frac{(T_X^{\text{prev}} / T_X^{\text{older}}) - 1 + a_X}{a_X}$	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)
Bounded	$G_{X,Y} = \frac{X p_{X,Y} Y c_X l_X (p_{X,Y}^2 Y^2 / p_Y Y + k_X^l)}{k_X^u + \sum_Z (p_{X,Z}^2 Z^2) / (p_{X,Z} Z + k_X^l)}$	c_X = maximum clearance rate of predator X^b ; k_X^l = lower prey biomass threshold for feeding by predator X ; k_X^u = half saturation coefficient for feeding by predator X ; l_X = maximum growth rate of predator X^b ; $p_{X,Y}$ = 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	$G_{X,Y} = \frac{X p_{X,Y} Y V_X}{(1 + H_X V_X \sum_Z p_{X,Z} Z)},$ where V_{XX} and H_{XX} are constants for non-finfish, but are size dependent for finfish such that $V_X = v_{a,X} X_S^{v_{b,X}}$ and $H_X = h_{a,X} X_S^{-h_{b,X}}$	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)

^a Additional crowding and oxygen limitation factors are not shown as they were only relevant in some groups.

^b Temperature dependent. The standard Q_{10} temperature correction formula was used to adjust these rates, with a reference temperature of 15 °C and a Q_{10} coefficient of 2.

Table 5

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	Mortality terms for top predators as of the standard run, only grazing terms differ between runs
Bounded	Uses the equation for the bounded functional response formulation in Table 2
Dynamic	Uses the equation for the dynamic search and handling functional response formulation in Table 2
Ecosim-based	Uses the equation for the ecosim-like functional response formulation in Table 2
Type I	Uses the equation for the type I functional response formulation in Table 2
Type III	Uses the equation for the type III functional response formulation in Table 2
Model closure runs	Grazing terms as of the standard run, only mortality terms for the top predators differ between runs
No-linear	Linear mortality term is set to zero for the top predators
No-quadratic	Quadratic mortality term is set to zero for the top predators
Top	Marine mammals, seabirds, wading birds and cephalopods are explicitly included in the model

2.4. Definition of the “standard” and alternative runs

For convenience each model run is given an identifying name (Table 5), 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 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 forms of 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.

2.5. Parameter tuning

The original form of BM2 is calibrated by tuning the temperature-dependent maximum growth and mortality rates for all groups and the maximum clearance rates of the consumer groups (Fulton et al., 2003a). 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 (Fulton et al., 2003a). The additional groups added for the final mortality scheme are also calibrated in this same way.

To ensure that (as far as possible) the same simulated system is being considered in each case, and any differences are down to dynamical differences between the formulations, limited re-tuning is allowed in each case investigated here. That is in the runs using the alternative grazing, or mortality, formulations all parameters are held at the same value as in the standard run, except for those parameters directly involved in the alternative formulation. The tuning of the growth, or mortality, parameters was then done to minimise the sum of squared differences between the average biomass per group over the entire bay predicted using the alternative formulations and those output by the “standard” run. These parameter settings were then retained unchanged for the scenarios with changing forcing conditions.

2.6. Basal and changing forcing conditions

All runs covered a 10-year simulated period (this is in addition to an initial equilibration period required to remove the chance of confounding due to transient dynamics produced by initial conditions) and had a frequency of recorded output of 14 days. The same light and hydrodynamic transport vectors are also used in all runs.

First sensitivity of the model to the different grazing and mortality terms is examined for “baseline”

conditions—this represents a level of nutrient inputs and fishing pressure typical of moderately impacted temperate marine bays (Fulton et al., 2003a). The examination is then repeated under various forcing conditions to gauge how the model's predictions regarding the effect of changing environmental conditions differed between runs using different forms. The changes in environmental conditions are achieved by increasing the nutrient load or fishing pressure used in the “baseline” run by fivefold (“ $N \times 5$ ” and “ $F \times 5$ ”, 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 (Fulton et al., 2003a). They also represent the range of conditions experienced by some of the most intensively exploited and impacted shallow marine systems around the world (Fulton et al., 2003b). By considering the results across such a wide range of conditions, it is possible to draw some potentially general conclusions.

2.7. Comparing the runs

Several measures are used to compare the various runs. These include the baywide average biomass per group, relative spatial distributions (% area agreement between spatial distributions predicted by the “standard” and alternative runs), the form of the temporal dynamics of each group (assessed using cross-correlations and cross-spectral analysis, as of Chatfield, 1989), and overall levels of pelagic, benthic and bacterial production and consumption.

As the predicted value of the model comparison measures may differ between the various runs under “baseline” conditions, simply repeating these comparisons 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 also differ under changing forcing conditions. 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 give a good indication of the effects of the various formulations on the model output and behaviour. However, since the temporal analyses and the results for production and consumption reinforce the results based on biomass and the relative spatial distributions, and do not impart any new insights, they are not presented here.

3. Results

3.1. Sensitivity to grazing terms

The relative differences between the average (or median) biomasses in the alternative runs (Table 6) 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). 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). The tendency for groups with higher turnover rates to be more heavily impacted by a change in the grazing term is illustrated in Fig. 3, where the infauna and bacteria (in particular) dominate the relative proportional differences between the “standard” run and those using alternative grazing terms.

There is spatial conformity between the runs for many of the modelled groups, as indicated by the number of groups with predicted relative spatial patterns that match those given by the “standard” run (Table 6) for 88% or more of the modelled area. Nevertheless, 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

Table 6

Summary statistics for the proportional difference between the biomass predicted in the “standard” (std) run and those runs using alternative grazing terms

Run	Minimum (group)	Mean (median)	Maximum (group)	Mean (median) with no infauna or bacteria	Groups differ from “std” by <50%	Groups with spatial match of 100/88/50/<50%
Type I	<0.01 (BC, BG, FD, MZ)	0.12 (0.06)	0.91 (OB)	0.09 (0.08)	24	22/3/-/–
Type III	<0.01 (BG, FD, MZ)	20.80 (0.27)	507.95 (OB)	0.51 (0.17)	19	14/8/1/2
Ecosim-like	0.01 (AF)	13.81 (0.50)	220.73 (OB)	0.87 (0.35)	13	9/6/7/3
Bounded	0.07 (FD)	15.34 (0.86)	261.18 (OB)	1.03 (0.49)	11	9/4/7/5
Dynamic	<0.01 (FD)	3.87 (0.32)	53.43 (ANB)	0.82 (0.19)	17	11/5/7/2

Note that there are 25 groups in the these runs and that the group(s) that recorded the minimum or maximum difference is noted. Codes for the components are as of Table 2 and codes for the runs are as of Table 5.

but three zooplankton groups, where there are some minor differences. The other runs show more differences in their spatial distributions, primarily within those groups with faster dynamics. The run employing the “bounded” grazing term shows the greatest degree of spatial divergence from the “standard” run. The “bounded” grazing term tends to lead to predictions of evenly distributed populations where the use of other grazing terms produces stronger spatial structuring with local peaks in density (e.g. heterotrophic flagel-

lates, Fig. 4). It is noteworthy that the groups that show the least spatial conformity between the “standard” and alternative runs are those groups with fast turnover rates (such as bacteria, plankton or infauna).

With changing nutrient loads and fishing pressure (Table 7), 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. When nutrients increase, the run employing

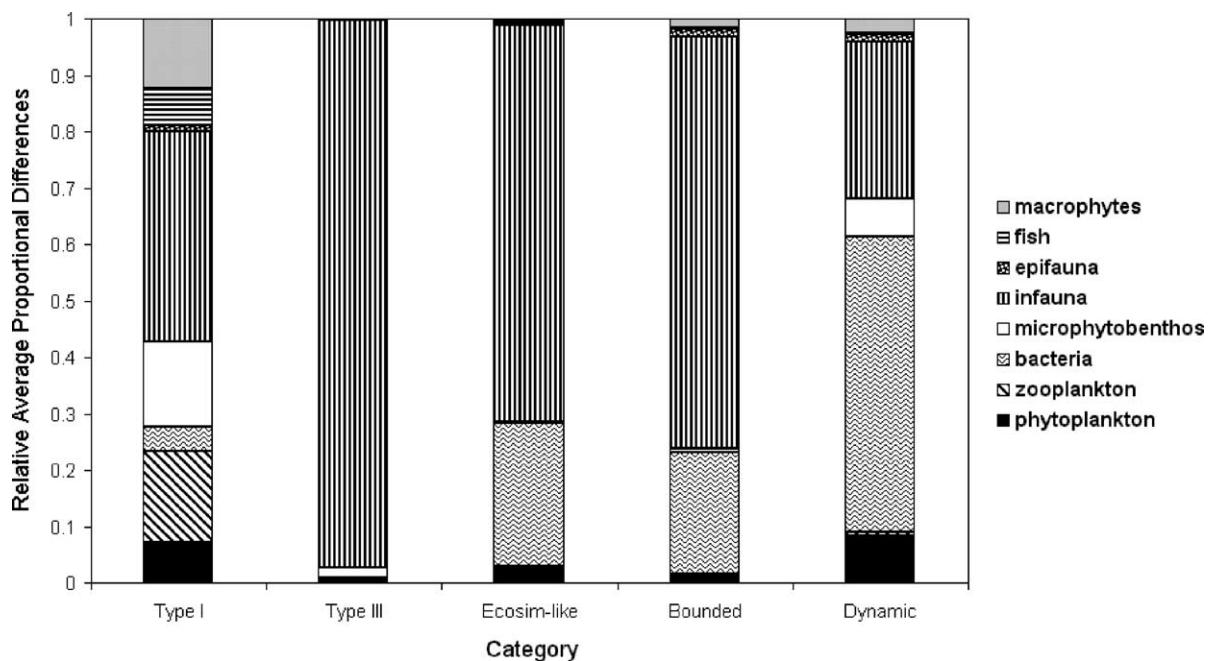


Fig. 3. Average proportional difference between the biomass predicted in the “standard” run and those runs using alternative grazing terms for each category of model groups (see Table 2 for category definitions).

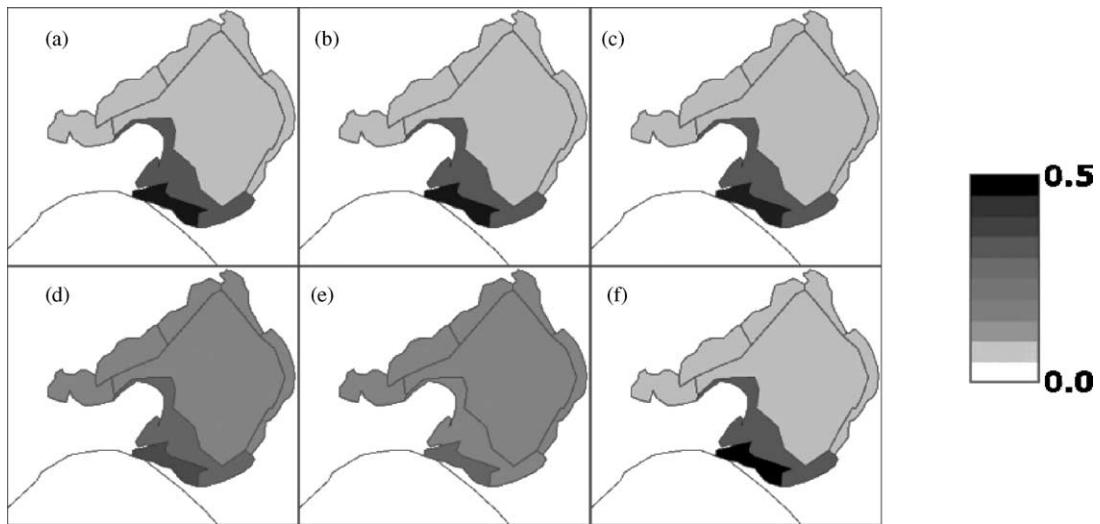


Fig. 4. Proportion of the total average biomass of heterotrophic flagellates in each box for each run with alternative grazing terms: (a) standard (type II), (b) type I, (c) type III, (d) ecosim-like, (e) bounded and (f) dynamic.

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. The differences in the trends in biomass in the various runs are not just in size; for a small number of groups the predicted direction of change is also different. For example, with an increase in nutrient loading, the predicted change in biomass for the picoplankton, in the run employing “ecosim-like” grazing terms, is not only about three 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 decrease).

With a change in forcing conditions in the runs using the alternative grazing terms, there is an increase in the number of groups with spatial patterns that do not conform with those of the “standard” run under the same change in forcing conditions (Table 7). The most notable 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 88% or more of the modelled area. In contrast, when nutrient loading increases fivefold, the number of groups in the run using “type I” grazing terms that show this degree of spatial conformity drops to only 17 of the 25 groups. Generally, with a change in forcing conditions, the groups with fast turnover rates are consistently the most heavily affected by the use of an alternative grazing term (with regard to overall average biomass, spatial and temporal conformity). However, the effects are not restricted to these groups, with more of the groups with slower dynamics diverging from the “standard” run, particularly in those runs using complex grazing terms (i.e. “ecosim-like”, “bounded” and “dynamic”).

3.2. Sensitivity to the form of mortality used in model closure

The relative difference between the baywide mean (or median) 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 8). Generally,

Table 7

Summary statistics for the proportional difference between the size of the trend in “average biomass under changing conditions/average biomass under “baseline” conditions” predicted in the “standard” (std) run and those runs using alternative grazing terms when nutrient load or fishing pressure has increased fivefold

Conditions	Run	Minimum (group)	Mean (median)	Maximum (group)	Mean (median) with no infauna or bacteria	Groups differ from “std” by <50%	Groups where trend is opposite direction to “std”	Groups with spatial match of 100/88/50/<50%
Nutrients × 5	Type I	<0.01 (BG, FD, MZ, PFB, ZLC)	0.93 (0.05)	10.52 (MB)	0.67 (0.04)	19	AEB	15/2/4/4
	Type III	<0.01 (DF, MZ, PFB)	0.42 (0.20)	1.00 (FD, FG, FP, FV, OB)	0.43 (0.17)	16	MB	11/7/5/2
	Ecosim-like	0.01 (DF)	2.52 (0.60)	24.47 (FD)	3.01 (0.61)	11	AEB, ANB, BF, FD, MA, PS, ZLC, ZS	7/4/10/4
	Bounded	0.01 (DF)	0.96 (0.70)	5.61 (AEB)	0.82 (0.74)	12	AEB, BF, MB, PL, PS, ZS	6/5/10/4
	Dynamic	<0.01 (FD)	0.65 (0.32)	3.85 (ZS)	0.65 (0.33)	16	AF, BF, MB, MZ, PS, ZS	9/6/6/4
Fishing × 5	Type I	0.01 (FP, PFB)	150.23 (0.18)	3739.49 (BD)	0.43 (0.16)	17	AEB, ANB, BD, BF, MB, OB, ZS	15/6/2/2
	Type III	<0.01 (FD, PFB)	75.77 (0.25)	1887.85 (BD)	0.24 (0.23)	21	BD	15/3/2/5
	Ecosim-like	0.01 (DF)	133.03 (0.31)	3312.18 (BD)	0.58 (0.22)	14	BG, HF, MB, MZ, PFB, PS	8/5/8/4
	Bounded	<0.01 (AF)	133.25 (0.22)	3321.52 (BD)	0.38 (0.16)	16	MB	8/4/9/4
	Dynamic	0.01 (DF, PFB)	142.38 (0.45)	3543.97 (BD)	0.69 (0.28)	13	—	10/7/6/2

Note that there are 25 groups in these runs and that the group(s) that recorded the minimum or maximum difference is noted. Codes for the components are as of Table 2 and codes for the runs are as of Table 5.

Table 8

Summary statistics for the proportional difference between the biomass predicted in the “standard” (std) run and those runs using alternative forms of model closure

Run	Minimum (group)	Mean (median)	Maximum (group)	Mean (median) with no infauna or bacteria	Groups differ from “std” by <50%	Groups with spatial match of 100/88/50/<50%
Top	<0.01 (AF, BC, BF, BG, DF, FD, FG, FP, HF, MZ, PFB, ZL)	0.10 (0.01)	1.11 (OB)	0.02 (0.01)	23	24/−1/−
No-linear	<0.01 (FD, FP)	0.69 (0.34)	3.55 (OB)	0.43 (0.23)	13	10/9/5/1
No-quadratic	<0.01 (FD, FP, PFB)	0.39 (0.16)	2.45 (OB)	0.29 (0.07)	19	15/6/3/1

Note that only the 25 groups found in all runs are referred to here and that the group(s) that recorded the minimum or maximum difference is noted. Codes for the components are as of Table 2 and codes for the runs are as of Table 5.

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 that differed substantially from the estimate in the “standard” run. The infauna, bacteria, microphytobenthos and macrophytes show the greatest differences between the “standard” run and those using alternative model closure. The largest difference is for benthic deposit feeders in the run with the “no-linear” model closure, which differ from the “standard” run by more than threefold.

While there are some dissimilarities among 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 the “no-linear” run. In this run only 40% of the groups have relative distributions which match the “standard” run and 24% of the groups (all with high turnover rates) 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 8). The spatial conformity of the run with “no-quadratic” model closure is better, with the relative distributions of a majority (84%) of the groups matching the distributions predicted by the “standard” run for 88% or more of the modelled area. 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 of the runs using alternative grazing terms. In the runs using “ecosim-like”, “bounded” or “dynamic” grazing terms, 36–48% of the relative distributions differ by more than 12% of the modelled area from the distribution predicted by the “standard” run (Table 6).

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 diverges slightly more from the “standard” run than the others (Table 9). When nutrient loading is increased, the run using “no-quadratic” model closure diverges from the “standard” run much more than either of the other two alternatives. An increase in nutrient loads or fishing pressure can cause the predicted trends for the sediment infauna (macro- or microscopic) to be orders of magnitude larger in runs using alternative model closure than for the “standard” run, under the same conditions. For example, when fishing pressure increases fivefold the change in biomass for the benthic deposit feeders is more than 3000 times that of the “standard” run in all the runs using alternative forms of model closure. Once again there are a few cases where the differences in the trends go beyond differences in magnitude. The only groups for which the predicted trend

Table 9

Summary statistics for the proportional difference between the size of the trend in “average biomass under changing conditions/average biomass under ‘baseline’ conditions” predicted in the “standard” (std) run and those runs using alternative forms of model closure when nutrient load or fishing pressure has increased fivefold

Conditions	Run	Minimum (group)	Mean (median)	Maximum (group)	Mean (median) with no infauna or bacteria	Groups differ from “std” by <50%	Groups where trend is opposite direction to “std”	Groups with spatial match of 100/88/50/<50%
Nutrients × 5	Top	<0.01 (AEB, ANB, BC, BF, BG, DF, FD, FG, FP, FV, MB, MZ, PFB)	1.28 (<0.01)	31.23 (OB)	0.02 (0.01)	24	–	23/1/1/–
	No-linear	<0.01 (DF, FD, MZ)	0.32 (0.17)	1.00 (OB)	0.19 (0.12)	18	MB, OB	9/7/8/1
	No-quadratic	<0.01 (BG, FD, MZ)	2.13 (0.06)	38.02 (AEB)	0.17 (0.06)	18	AEB, ANB, BF	15/3/5/2
Fishing × 5	Top	<0.01 (AF, FG, PFB)	137.95 (0.05)	3442.71 (BD)	0.15 (0.03)	19	–	18/3/4/–
	No-linear	<0.01 (FP, FV, ZL)	133.62 (0.09)	3333.79 (BD)	0.18 (0.05)	19	–	10/6/7/2
	No-quadratic	<0.01 (FD, FP, PFB)	143.73 (0.08)	3587.31 (BD)	0.18 (0.05)	20	–	13/4/6/2

Note that only the 25 groups found in all runs are referred to here and that the group(s) that recorded the minimum or maximum difference is noted. Codes for the components are as of Table 2 and codes for the runs are as of Table 5.

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 9).

Generally, for the runs using “no-linear” model closure or explicit top predators (“top”), spatial conformity with the patterns predicted by the “standard” run are as close under changing forcing as under “baseline” conditions. This is not the case for either of the runs using “no-quadratic” mortality when forcing conditions change. When nutrient loads or fishing pressure increase, 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 (Table 9). More generally, under changing forcing conditions, any differences in the spatial patterns observed in the runs employing alternative forms of model closure are stronger than under “baseline” conditions. While this means that more of the groups with slower dynamics are affected by a change in model formulation under altered conditions, the groups with high turnover rates remain the most strongly impacted by the use of alternative forms of model closure.

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. This does not agree with the findings of Steele and Henderson (1992) or Murray and Parslow (1999), however. 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. While it is possible that the prevailing physical conditions represented in each model may have contributed to their results it is unlikely to be the primary reason. While many of the plankton models that have been used to consider the effects of the grazing and mortality terms on model performance lack a benthic component and have been applied in purely pelagic systems (Steele and Henderson, 1992; Edwards and Brindley, 1999; Edwards and Yool, 2000), the work of Murray and Parslow (1999) was set in a shallow marine bay

(the same bay used as a basis for the hypothetical system considered here) and did incorporate at least part of the benthic ecosystem. Consequently, it is more likely that the differences between the finding of previous studies and this one is a reflection of the web used here, which incorporates many more consumers in a more highly interconnected web than the simple linear food chains considered previously.

It can be argued that generalities cannot be drawn from the consideration of variants of a single ecosystem model. While there is truth in this, and future work considering other models can only further our understanding, the work presented here is a useful first step. As the ecosystem model used in this study is an extension of biogeochemical model structures used routinely in water quality and marine ecological modelling, and as it is used in a simulation framework to consider the results for a hypothetical system with behaviours typical of real shallow marine systems (Fulton et al., 2003a), the findings should extend beyond theoretical undertakings and be typical of how such models perform at the ecosystem level.

4.1. 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 destabilising 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 (Fig. 5). This finding is similar to that of previous model studies (Legaspi et al., 1996; Gao et al., 2000; Tett and Wilson, 2000) and has also been found under experimental (Wiedenmann and Smith, 1993) and field conditions (Carpenter et al., 1994). This is why evaluating models over a range of conditions is cru-

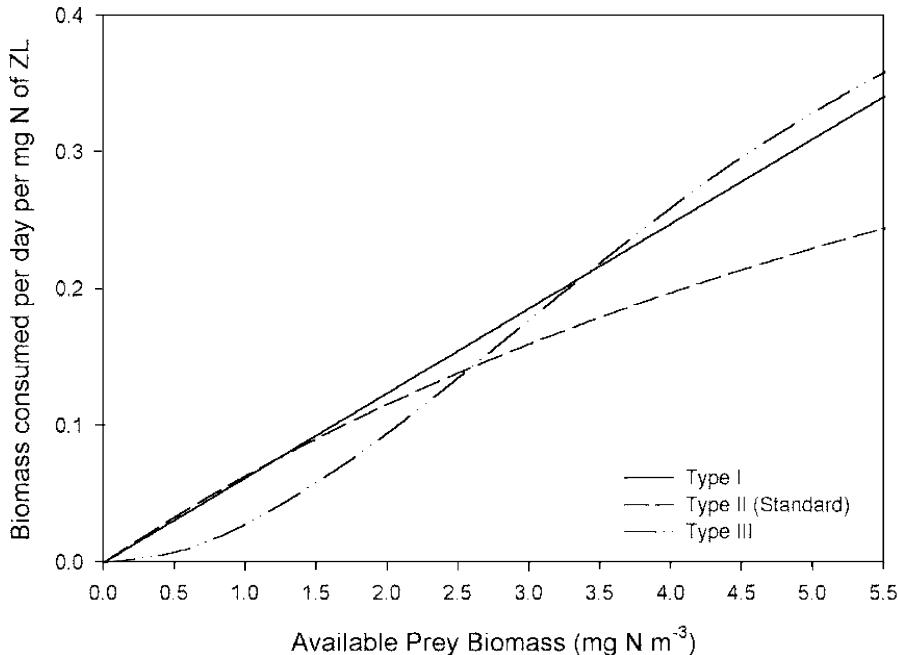


Fig. 5. The “type I”, “type II” (the response used in the standard run) and “type III” functional responses for the large omnivorous zooplankton (ZL). The range of prey biomasses shown covers the typical levels of available prey biomass, although the available biomass can jump to much higher levels (two-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

cial because, as highlighted by Walters (1986) and Carpenter et al. (1994), substantial contrast in the state variables is required to discriminate between alternative models. This is particularly true when considering the effect of grazing terms, as model sensitivity to these (usually saturation-based) terms varies strongly if prey become much more (or less) abundant than average (Slobodkin, 1992). This is illustrated here by the finding that it is only under increasing nutrient loads and/or fishing pressures that the differences in the curves substantially influence overall model behaviour as the biomasses become very large or small (depending on the prey groups in question). Notably, in this case, even under these more extreme conditions there is little to 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 here). In the mixed case, however, where the same functional response is not applied to all groups, selective use of a type III curve may prove to be beneficial for those groups whose behaviour in the field matches the underlying assumptions.

The simple “Holling-type” functional responses are still 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), heterogeneity (Arditi and Saiah, 1992; Berryman, 1992), 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 forms 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 are 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. The performance of the benthic deposit feeding group is substantially improved, however, particularly when nutrient loading increases. The behaviour of this group is a weakness of the standard form of BM2 (Fulton et al., 2003a), which seems to be corrected if the additional checks inherent in the more complex functional responses are added. By itself, 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, that is, to how many feedbacks, thresholds and inflection 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. Despite these considerations, given the high number of parameters biogeochemical models can require and given 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 discussion about model formulation.

One recommendation that can be made here is that there is a clear need for research aimed at determining

empirically the nature of functional responses in real systems. 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. This is particularly true for groups with rapid rates of turnover, which are often poorly known, as they are most responsive to changing conditions and the most sensitive to the model formulations used.

4.2. Model closure

Plankton modellers recognise 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 models (Steele and Henderson, 1992; Edwards and Brindley, 1999; Murray and Parslow, 1999; Edwards and Yool, 2000), it remains an important feature of the model. 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, 1999; Edwards and Yool, 2000) have concentrated on the steady-state stability status achieved when using different closure terms. The present paper has concentrated on the overall effects on model dynamics. Despite these differences, comparison of conclusions from the different studies 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) also recommend it. Edwards and Brindley (1999) and Edwards and Yool (2000), how-

ever, caution that the use of both mortality terms requires the estimation of two (rather than one) poorly known parameters, 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. Caution is required, however, as 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.

Fieldwork undertaken to elucidate the form of functional responses in real systems will also be helpful with regard to the issue of model closure, since it has been suggested that the use of quadratic closure may be an artificial solution to the issue of model stability (C. Walters, personal communication). For the predators implicitly represented by the quadratic closure terms to respond this quickly they would probably have to employ type III switching between prey items. However, prey switching of this form has rarely been detected in field data (Walters and Kitchell, 2001). In contrast, fine scale spatial organisation (e.g. schooling) is more easily detected. Foraging arena functional responses, like the one used in ECOSIM, are based on the assumption that trophic interactions at these fine spatial scales can limit interaction rates. While spatial organisation in marine systems clearly arises, the effect of this structure on interaction rates is not well elucidated empirically. Therefore, any data to indicate the validity of type III functional responses or “foraging arena” (“ecosim-like”) functional responses will also be an important contribution to solving the vexed issue of model closure.

One final concern about model closure is whether the top predators must be included explicitly. A comparative analysis of the application of BM2, IGBEM and ECOSIM 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 (Fulton, 2001). 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 cause 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. In terms of model behaviour, quadratic model closure appears to be acceptable regardless of the size of the web being considered.

5. Conclusions

Ecosystem models are one tool that has been advocated for ecosystem management (Walters et al., 1997; Sainsbury et al., 2000). The impact of formulation decisions on their behaviour therefore needs to be considered carefully to ensure that they facilitate improvements in management. 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. 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, trialed here (Bryant et al., 1995; Walters et al., 2000; Abrams and Ginzburg, 2000). Given the extra detail and increased information required to parameterise and validate these formulations, however, 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 because the simple ap-

plication 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, warrants efforts to determine empirically the form of functional responses in real systems. Along with the topology and the form of the trophic web that defines the framework of the model, the grazing terms deserve particularly careful consideration during the conceptualisation and development of ecosystem models.

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References

- Abrams, P.A., 1993. Why predation rate should not be proportional to predator density. *Ecology* 74, 726–733.
- Abrams, P.A., 1994. The fallacies of “ratio-dependent” predation. *Ecology* 75, 1842–1850.
- Abrams, P.A., Ginzburg, L.R., 2000. The nature of predation: prey dependent, ratio dependent or neither? *TREE* 15, 337–341.
- Ardit, R., Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326.
- Ardit, R., Saïah, H., 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* 73, 1544–1551.
- Baretta, J.W., Ebenhöh, W., Ruardij, P., 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Neth. J. Sea Res.* 33, 233–246.
- Begon, M., Mortimer, M., 1986. Population Ecology: A Unified Study of Animals and Plants. Blackwell Science Publications, London, Melbourne, Boston.
- Berryman, A.A., 1992. The origins and evolution of predator-prey theory. *Ecology* 73, 1530–1535.
- Broström, G., 1998. A note on the C/N and C/P ratio of the biological production of the Nordic seas. *Tellus* 50B, 93–109.
- Bryant, A.D., Heath, M.R., Broekhuizen, N., Ollason, J.G., Gurney, W.S.C., Greenstreet, S.P.R., 1995. Modelling the predation, growth and population dynamics of fish within a spatially-resolved shelf-sea ecosystem model. *Neth. J. Sea Res.* 33, 407–421.
- Büssenschütt, M., Pahl-Wostl, C., 2000. A discrete, allometric approach to the modelling of ecosystem dynamics. *Ecol. Model.* 126, 33–48.
- Carpenter, S.R., Cottingham, K.L., Stow, C.A., 1994. Fitting predator-prey models to time series with observation errors. *Ecology* 75, 1254–1264.
- Chatfield, C., 1989. The Analysis of Time Series: An Introduction, 4th ed. Chapman and Hall, London, Tokyo, Melbourne, Madras.
- Christensen, V., Walters, C.J., Pauly, D., 2000. ECOPATH with ECOSIM: A User’s Guide. October ed. Fisheries Centre, University of British Columbia, Vancouver, Canada, and International Centre for Living Aquatic Resources Management, Penang, Malaysia.
- DeAngelis, D.L., Goldstein, R.A., O’Neill, R.V., 1975. A model for trophic interaction. *Ecology* 56, 881–892.
- Ebenhöh, W., Kohlmeier, C., Radford, P.J., 1995. The benthic biological submodel in the European Regional Seas Ecosystem Model. *Neth. J. Sea Res.* 33, 423–452.
- Edwards, A.M., Brindley, J., 1999. Zooplankton mortality and the dynamical behaviour of plankton population models. *Bull. Math. Biol.* 61, 303–339.
- Edwards, A.M., Yool, A., 2000. The role of higher predation in plankton population models. *J. Plankton Res.* 22, 1085–1112.
- Fransz, H.G., Mommaerts, J.P., Radach, G., 1991. Ecological modelling of the North Sea. *Neth. J. Sea Res.* 28, 67–140.
- Frost, B.W., 1975. A threshold feeding behaviour in *Calanus pacificus*. *Limnol. Oceanogr.* 20, 263–266.
- Fulton, E.A., 2001. The effects of model structure and complexity on the behaviour and performance of marine ecosystem models. Ph.D. thesis, School of Zoology, University of Tasmania, Hobart, Tasmania.
- Fulton, E.A., Parslow, J.S., Smith, A.D.M., Johnson, C.R., in press. Biogeochemical Marine Ecosystem Models. II. The effect of physiological detail on model performance. *Ecol. Model.*
- Fulton, E.A., Smith, A.D.M., Johnson, C.R., in press. Biogeochemical Marine Ecosystem Models. I. A model of Marine Bay Ecosystems. *Ecol. Model.*
- Fulton, E.A., Smith, A.D.M., Johnson, C.R., in press. Effects of spatial resolution on the performance and interpretation of marine ecosystem models. *Ecol. Model.*
- Gao, H., Wei, H., Sun, W., Zhai, X., 2000. Functions used in biological models and their influences on simulations. *Ind. J. Mar. Sci.* 29, 230–237.
- Geček, S., Legović, T., 2001. Nutrients and grazing in modeling the deep chlorophyll maximum. *Ecol. Model.* 138, 143–152.
- Ginzburg, L.R., Akçakaya, H.R., 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* 73, 1536–1543.
- Gleeson, S.K., 1994. Density dependence is better than ratio dependence. *Ecology* 75, 1834–1835.
- Gutierrez, A.P., 1992. Physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm. *Ecology* 73, 1552–1563.

- Hairstone, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control and competition. *Am. Nat.* 94, 421–425.
- Hassell, M.P., 1978. The Dynamics of Arthropod Predator–Prey Systems. Monographs in Population Biology, vol. 13. Princeton University Press, Princeton.
- Hassell, M.P., Commins, H.N., 1978. Sigmoid functional responses and population stability. *Theor. Popul. Biol.* 14, 62–67.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Holling, C.S., 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48, 1–86.
- Hollowed, A.B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., Rice, J.C., 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J. Mar. Res.* 57, 707–719.
- Jørgensen, S.E., 1994. Fundamentals of Ecological Modelling, 2nd ed. Developments in Environmental Modelling 19. Elsevier, Amsterdam, London, New York.
- Legaspi, B.C., Carruthers, R.I., Morales-Ramos, J.A., 1996. Functional response as a component of dynamic simulation models in biological control: the *Catolaccus*-boll weevil system. *Ecol. Model.* 89, 43–57.
- Legović, T., 1989. Predation in food webs. *Ecol. Model.* 48, 267–276.
- Lima, I.D., Olson, D.B., Doney, S.C., 2002. Intrinsic dynamics and stability properties of size-structured pelagic ecosystem models. *J. Plankton Res.* 24, 533–556.
- Luckyanov, N.K., Cropper Jr., W.P., Harwell, M.A., 1995. State analysis of ecological models: model reactions to parameter change. *Ecol. Model.* 82, 99–104.
- Matson, P., Berryman, A.A., 1992. Special feature: ratio-dependent predator–prey theory. *Ecology* 73, 1529–1566.
- May, R.M., 1976. Theoretical Ecology. WB Saunders, Philadelphia.
- McGillicuddy, D.J., McCarthy, J.J., Robinson, A.R., 1995. Coupled physical and biological modelling of the spring bloom in the North Atlantic (I): model formulation and one dimensional bloom processes. *Deep Sea Res.* 42, 1313–1357.
- McNair, J.N., 1986. The effects of refuges on predator–prey interactions: a reconsideration. *Theor. Popul. Biol.* 29, 38–63.
- Murray, A., Parslow, J., 1997. Port Phillip Bay Integrated Model: Final Report. Technical Report No. 44. Port Phillip Bay Environmental Study. CSIRO, Canberra, Australia.
- Murray, A.G., Parslow, J.S., 1999. The analysis of alternative formulations in a simple model of a coastal ecosystem. *Ecol. Model.* 119, 149–166.
- Myerscough, M.R., Darwen, M.J., Hogarth, W.L., 1996. Stability, persistence and structural stability in a classical predator–prey model. *Ecol. Model.* 89, 31–42.
- Radach, J., Moll, A., 1993. Estimation of the variability of production by simulating annual cycles of phytoplankton in the central North Sea. *Prog. Oceanogr.* 31, 339–419.
- Radford, P.J., 1996. The Modules of the European Regional Seas Ecosystem Model II, 1993–1996. Plymouth Marine Laboratory, Plymouth, UK.
- Sainsbury, K., Punt, A.E., Smith, A.D.M., 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. Mar. Res.* 57, 731–741.
- Sarnelle, O., 1994. Inferring process from pattern: trophic level abundances and imbedded interactions. *Ecology* 75, 1835–1841.
- Slobodkin, L.B., 1992. A summary of the special feature and comments on its theoretical context and importance. *Ecology* 73, 1564–1566.
- Steele, J.H., Henderson, E.W., 1992. The role of predation in plankton models. *J. Plankton Res.* 14, 157–172.
- Steele, J.H., Henderson, E.W., 1995. Predation control of plankton demography. *ICES J. Mar. Res.* 52, 565–573.
- Tett, P., Wilson, H., 2000. From biogeochemical to ecological models of marine microplankton. *J. Mar. Syst.* 25, 431–446.
- Varriale, M.C., Gomes, A.A., 1998. A study of a three species food chain. *Ecol. Model.* 110, 119–133.
- Walters, C., 1986. Adaptive Management of Renewable Resources. MacMillan, New York.
- Walters, C., Kitchell, J.F., 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58, 39–50.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish. Biol. Fish.* 7, 139–172.
- Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in an ecosystem model: ECOSIM II. *Ecosystems* 3, 70–83.
- Wiedenmann, R.N., Smith Jr., J.W., 1993. Functional response of the parasite *Cotesia flavipes* (Hymenoptera: Braconidae) at low densities of the host *Diatraea saccharalis* (Lepidoptera: Pyralidae). *Environ. Entomol.* 22, 849–858.