Ecosystem Approaches to Fisheries in the Southern Benguela
Afr. J. mar. Sci. 26: 219–243
2004

LESSONS LEARNT FROM A COMPARISON OF THREE ECOSYSTEM MODELS FOR PORT PHILLIP BAY, AUSTRALIA

E. A. FULTON and A. D. M. SMITH**

Comparing multiple models applied to the same system can be highly instructive, both with regard to the system of interest and the models. In this case, three ecosystem simulation models (ECOSIM, Bay Model 2 [BM2] and the Integrated Generic Bay Ecosystem Model [IGBEM]) were tuned to data from Port Phillip Bay, Australia. ECOSIM is a dynamic biomass model; the other two are biogeochemical ecosystem models. Scenarios of environmental change (altered nutrient loading) and alternative fisheries management strategies (economically and ecologically motivated policies) are run for each model. A comparison of the predictions made by the models for these runs led to several general conclusions, first that large, shallow and enclosed bays, with many fish groups dependent on spawning stocks from outside the immediate area (e.g. Port Phillip Bay), may react more strongly to eutrophication than to fishing. The second conclusion is that a selected set of indicator groups (in this case, sharks, seagrass and chlorophyll *a*) seems to capture the major ecosystem impacts of alternative management scenarios. This has obvious implications for system monitoring in an adaptive management approach. The third is that multispecies or ecosystem models can identify potential impacts that a series of single-species models cannot (such as non-intuitive changes in biomass when species interactions outweigh fishery-induced pressures). Finally, policies focusing on the protection of species or groups only at higher trophic levels can fail to achieve sensible ecosystem objectives and may push systems into states that are far from pristine. These four findings have important ramifications for sustainable multiple-use management of shallow marine ecosystems.

Key words: Australia, ECOSIM, ecosystem, management, model

Concern over sustainable and responsible management of ecosystems, rather than particular species of interest, has grown over the last century, and particularly within the last decade. This is reflected in the increasing adoption in international treaties and national legislation of policies that take explicit account of such concerns. For example, Australia has adopted a national oceans policy that requires, *inter alia*, development of regional marine plans based upon principles of ecosystem management. Despite this level of interest and activity, the scientific and management tools to underpin such policies are poorly developed. In particular, the tools to predict the impact of alternative uses and management strategies are still under development (Sainsbury *et al.* 2000). In the context of ecosystem management, trophic models may be able to predict the impacts of alternative management strategies (Walters *et al.* 1997, 1999). A range of such models has been developed, but to date there has been little effort to compare and contrast them, or to compare their strengths and weaknesses (Baretta *et al.* 1994, 1996, Fulton 2001).

In this study, the utility of ecosystem models for the assessment of potential management strategies and their likely consequences is explored using three models. ECOSIM is a dynamic biomass simulation model (Christensen *et al.* 2000), whereas Bay Model 2 (BM2; Fulton *et al.* 2004a), and the Integrated Generic Bay Ecosystem Model (IGBEM, Fulton *et al.* 2004b) are biogeochemical models incorporating varying degrees of process detail. Between them, these three models reflect much of the range of detail found in simulation models currently being used to understand and predict the ecosystem effects of fishing and eutrophication. Unfortunately, their respective histories and the varying purposes for which they were developed mean that the models differ in many ways and that there is no systematic variation in assumptions. This can make extraction of organizing principles or conclusions difficult. Nevertheless, there is still value in determining whether the different model forms predict similar outcomes in response to changing conditions and management policies. This information can be instructive with regard to understanding the implications of the formulations used and whether predictions and policy prescriptions are robust across models.

The real world system used as the data source for this model comparison is Port Phillip Bay, adjacent to Melbourne, Australia. It is a shallow and nearly enclosed temperate bay with an area of approximately 1 930 km^2. Most of the bay is <8 m deep, although it reaches 24 m at its deepest points. During the 160 years since European settlement, the bay has come under increasing pressure from nutrient enrichment and fisheries exploitation. More than 3.5 million people live within the catchment area of Port Phillip Bay, and it has become the focal point for many of their

* CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tasmania 7001, Australia. E-mail: beth.fulton@csiro.au

Manuscript received June 2003; accepted February 2004

recreational pursuits. It has been estimated that the annual recreational effort is approximately 670 000 angler hours, which results in the landing of about 470 tons of fish (WBM Oceanics Australia 1997). The bay's commercial finfish fisheries land more than 60 species, with a total annual take of between 700 and 2 000 tons, worth about 3 million Australian dollars (AUD, equivalent to US$1.65 million) wholesale. Most invertebrate species landed are taken only opportunistically from bycatch, but the main targeted invertebrate harvests are cultured mussels (600 tons annually, worth 1.5 million AUD) and wild abalone *Haliotis* spp. (annual landings 50 tons, worth 1 million AUD). Until the late 1990s, scallops *Pecten fumatus* were the most intensively harvested and valuable fishery in Port Phillip Bay, with up to 10 000 tons (shell weight) being landed per year. However, the fishery was highly variable (fluctuating by two orders of magnitude in three years), and the sediment plumes associated with the dredges used in the fishery led to public concern. The scallop fishery was closed in 1997.

The difficulties inherent in interpreting and managing the consequences of human actions on marine systems have meant that the sources of the most significant anthropogenic impacts (fishing and nutrient discharge) have traditionally been dealt with separately. This is not just the case for Australian bays and nearshore waters, but is common worldwide. There is increasing evidence, however, that primary productivity and fisheries are more tightly linked than previously thought (Houde and Rutherford 1993, Nielsen and Richardson 1996). With this in mind, the three models are tuned to reflect the conditions in Port Phillip Bay, then compared across a range of levels of fishing pressures and nutrient inputs.

METHODS

Model descriptions

A brief description of the general form of each model is given below, but space precludes an extended discussion of each of their features, structures and assumptions. To allow for informed comparison, the essential details of the models and how they vary are listed in Table I.

ECOSIM

This is a simulation model of the spatially aggregated dynamics of ecosystem components. The components are either aggregate biomass pools or split pools, where adults and juveniles are represented separately. The split pools are dealt with using delay-difference equations, whereas the biomass growth equations used for the aggregate pools are derived from the ECOPATH master equation (for further details of the formulations see Walters *et al*. 1997). Essentially, the growth in biomass of a component is determined by its feeding and immigration, and losses to predation, natural mortality, emigration and fishing. One of the most important aspects of the formulation is the dependence of the consumption (feeding) rates on a foraging-arena concept, where only part of the pool of a prey species is vulnerable to predation at a given time. Transfer rates between the vulnerable and invulnerable parts of the pools determine the form of control of the trophic interactions ("top-down" or "bottom-up", Christensen *et al.* 2000). Such transfer rates are often referred to as "vulnerabilities", but to avoid confusion with the term vulnerability as used in fisheries science, the ECOSIM vulnerabilities are referred hereafter as "refuge parameters". As the settings used for the refuge parameters in an ECOSIM model can be crucial (Christensen *et al.* 2000), alternative sets were tested (see Fulton and Smith 2002). There is very little information available to guide the selection of appropriate values for the refuge parameters for different prey species. Therefore, it was decided that the parameter settings that give stable equilibria (no inherent rate of increase or decline) under *status quo* fishing mortalities (*F*s) would be used in the ECOSIM model to be compared with BM2 and IGBEM (these parameter settings are listed in Table II), but that the outcome of the fisheries policy optimization in ECOSIM would be checked across a wide range of refuge parameter settings.

Key initial parameter values for ECOSIM are inherited from the mass-balance ECOPATH model specified for the same system. The ECOPATH model (and therefore the ECOSIM model) used here contains one phytoplankton group, two zooplankton groups, nine benthic invertebrate groups, three benthic primary producers, 16 fish groups (some of which are species split into juvenile and adult groups), marine mammals, birds and detritus. Whereas the level of aggregation of species in the ECOPATH model does not match that in BM2 and IGBEM, the formulation chosen is more typical of what is usually found in ECOPATH models. The identity of the various groups and the value and source of the input parameters for the ECOPATH model are given in Table II, a schematic diagram of the system in Figure 1, and specific information on the model development is available in Fulton and Smith (2002). When creating the ECOSIM model from this ECOPATH model, a mediation effect

Table I: Comparison of the underlying structure and assumptions of the three ecosystem models, ECOSIM, IGBEM and BM2. The standard set-ups used for the runs in this study are given

Feature	Model		
	ECOSIM	BM2	IGBEM
		General features	
Biomass units	tons km^{-2} (wet weight)	mg N m^{-3} (dry weight)	mg m^{-3} of C, N, P, Si (dry weight)
Input forcing	Yes (of primary producers), interannual	Yes (of nutrients and physics), interannual, seasonal, tidal	Yes (of nutrients and physics), interannual, seasonal, tidal
Level of group detail	Variable (age-group of species up to entire trophic levels)	Functional group	Functional group
		Formulation related	
Consumption formulation	Forage arena	Type II*	Mixed (Type II, Type III)
Formulation detail	Simple (expansion of ECOPATH master equation)	General (growth, mortality, excretion explicit)	Physiological (assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality all explicit)
Light limitation	No	Optimal irradiance fixed	Phytoplankton can adapt to changes in ambient light levels
Mixotrophy	No (no mixed consumers-producers defined in the ECOPATH model)	Yes (dinoflagellates)*	No
Nutrient limitation	No	Yes (external)	Yes (internal)
Nutrient ratio	–	Redfield	Internal nutrient ratio
Oxygen limitation	No	Yes	Yes
Sediment burial	No	No	Yes*
Sediment chemistry	No	Yes (dynamic, with sediment bacteria)	Yes (empirical, sediment bacteria are a tracer only)
Shading of primary producers	No	Yes	Yes
Spatial structure	No explicit spatial structure (ECOSPACE model not considered here)	Explicit (8 and 59 box versions)*	Explicit (8 and 59 box versions)*
Temperature dependence	No	Yes	Yes
		Model closure	
Status of birds	Dynamic	Static loss term on fish only	Static loss term on fish only
Status of marine mammals	Dynamic	Static loss term on fish only	Static loss term on fish only
Status of sharks	Dynamic	Static loss term on fish only	Static loss term on fish only
		Fish and fisheries related	
Age-structured fish	Yes (juvenile + adult)	Yes (9 age-classes)	Yes (9 age-classes)
Fishery discards	Target and bycatch species	Target species only*	Target species only
Invertebrate fisheries	Yes	Yes	No ("fix" implemented by adjusting the mortality terms of the groups concerned)
Stock-recruit relationship	Dynamic	Constant recruitment	Constant recruitment
Stock structure	Self-seeding (entire stock in the bay)	External (reproductive stock outside the bay produces the recruits, oldest age-classes migrate out of the bay to join this stock)	External (reproductive stock outside the bay produces the recruits, oldest age-classes migrate out of the bay to join this stock)

* Feature where alternative may be implemented

is added, to reflect the critical importance of seagrass meadows (dominated by *Zostera muelleri*, *Heterozostera tasmanica* and *Posidonia australis*) to juvenile King George whiting *Sillaginodes punctata.* This does not have a deleterious impact on model stability and behaviour (Fulton and Smith 2002).

Since this work was completed, a revised version of ECOSIM has been made available that includes an option allowing for nutrient limitation of primary production. The results reported here do not use this option, but are compatible with results generated by the default (no limitation) settings of this new version of ECOSIM.

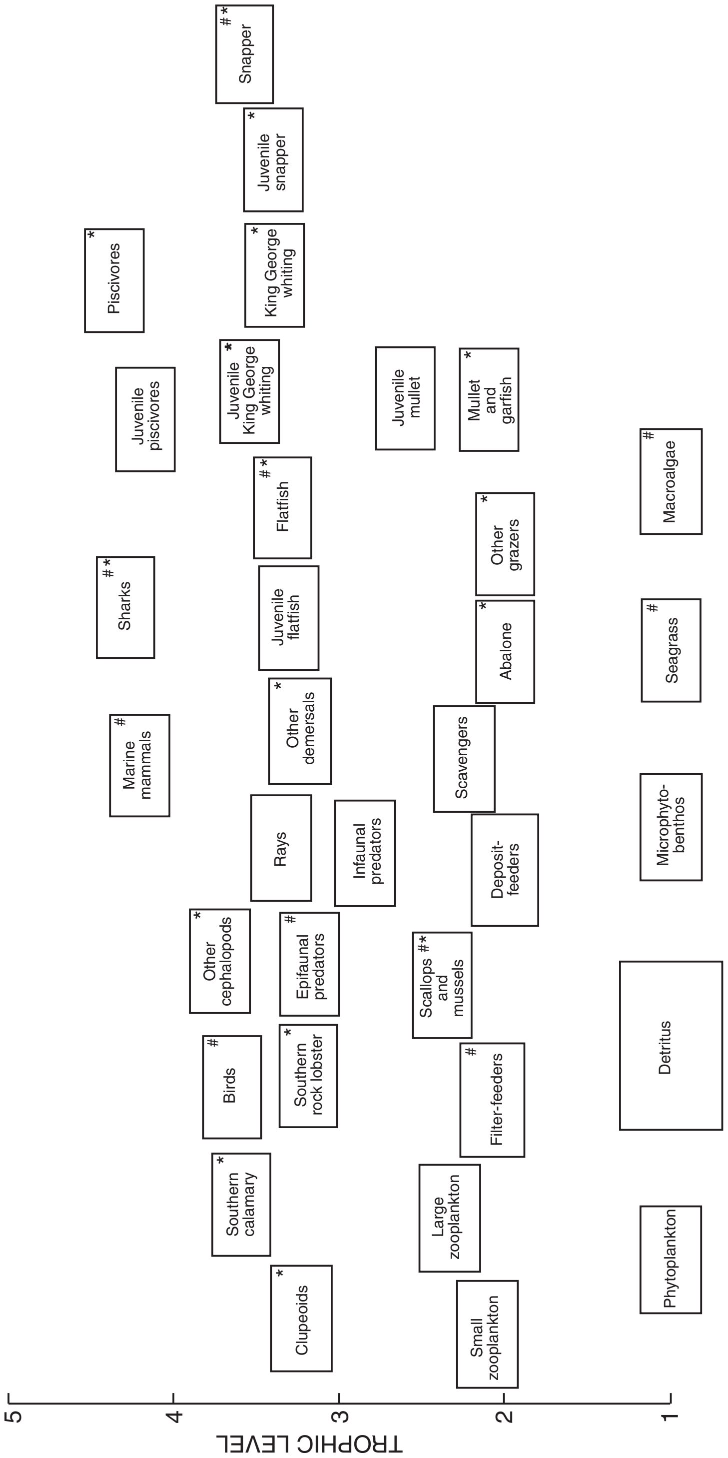

Fig. 1: Schematic diagram of the Port Phillip Bay ECOPATH model, showing the constituent groups and their relative trophic positions. Groups marked with an asterisk are landed by fisheries included in the model, whereas groups marked with a hash are species that are taken and discarded

Table II: The basic input parameters for the final balanced form of the Port Phillip Bay ECOPATH model (after Table 1 of Fulton and Smith 2002). Juvenile fish groups represent those <3 years old

Group name	Biomass (B, tons km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Catch (tons km^{-2} year^{-1})	Discards (tons km^{-2} year^{-1})	Refuge parameters	Reference
Phytoplankton	7.617	250	–	0	0	–	Murray and Parslow (1997)
Small zooplankton (zooflagellates and small copepods)	6.477	36.8	59.781	0	0	0.5	Beattie et al. (1996) Holloway and Jenkins (1993)
Large zooplankton	9.974	23.8	38.609	0	0	0.5	Beattie et al. (1996, Q/B, B) Holloway and Jenkins (1993, P/B)
Deposit-feeders	69.948	4.8	66.7	0	0	0.5	Poore (1992) Wilson *et al*. (1993)
Scallops and mussels	4.922	3.1	10.9	0.862	0.25	0.48	Kailola *et al*. (1993) Poore (1992) Wilson *et al*. (1993)
Filter-feeders	73.511	2.8	11.8	0	0.025	0.5	Poore (1992) Wilson *et al*. (1993)
Infaunal predators (burrowing worms and other predatory infauna)	13.575	5.4	58.4	0	0	0.5	As for filter-feeders
Epifaunal predators (custaceans, gastropods and starfish)	2.363	2.9	21.9	0	0.026	0.5	As for filter-feeders
Southern rock lobster	0.068	0.73	12.41	0.003	0	0.8	MAFRI (1996) Wilson *et al*. (1993)
Abalone	0.699	0.73	12.41	0.048	0	0.45	MAFRI (1996) Poore (1992) Wilson *et al*. (1993)
Other grazers	2.249	0.88	11.68	0	0	0.5	MAFRI (1996) Kailola *et al*. (1993) Poore (1992) Wilson *et al*. (1993)
Scavengers	9.326	6.86	55.48	0	0	0.5	Poore (1992) Wilson *et al*. (1993)
Microphytobenthos	18.135	44	–	0	0	–	Murray and Parslow (1997)
Seagrass	2.591	24	–	0	0.01	–	As for microphytobenthos
Macroalgae	25.907	20	–	0	0.01	–	As for microphytobenthos
Clupeoids (sardine, anchovy and sprat)	2.85	1.15	30.15	0.812	0	0.45	MAFRI (1996) Hall (1992) Parry *et al*. (1995)
Juvenile snapper	0.469	0.548	2.737	0.012	0	0.6	Officer and Parry (1996) Parry *et al*. (1995) Gunthorpe *et al*. (1997)
Snapper	0.376	0.493	2.737	0.033	0.001	0.5	As for juvenile snapper
Juvenile flatfish	2.319	0.821	2.737	0.004	0.001	0.5	As for juvenile snapper
Flatfish	2.285	0.411	2.737	0.143	0.011	0.5	As for juvenile snapper
Juvenile King George whiting	0.142	0.821	2.737	0.06	0	0.8	As for juvenile snapper
King George whiting	0.117	0.548	2.737	0.001	0	0.8	As for juvenile snapper
Juvenile piscivores	0.567	0.821	2.737	0	0	0.4	As for juvenile snapper
Piscivores	0.288	0.411	2.737	0.001	0	0.4	As for juvenile snapper
Juvenile mullet	0.526	0.411	2.737	0	0	0.5	As for juvenile snapper
Mullet and garfish	0.383	0.329	2.737	0.053	0	0.5	As for juvenile snapper
Other demersals	4.899	0.548	2.737	0.041	0	0.5	As for juvenile snapper

(continued)

(Table II: continued)

Group name	Biomass (B, tons km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Catch (tons km^{-2} year^{-1})	Discards (tons km^{-2} year^{-1})	Refuge parameters	Reference
Southern calamary	0.319	1.825	18.25	0.05	0	0.5	Officer and Parry (1996) Parry *et al.* (1995) Gunthorpe *et al.* (1997) Lee (1994)
Other cephalopods (octopus)	0.415	1.369	9.125	0	0	0.5	As for southern calamary
Rays	6.166	0.234	1.56	0	0	0.5	Officer and Parry (1996) Parry *et al.* (1995) Gunthorpe *et al.* (1997) Schmid *et al.* (1990)
Sharks	0.148	0.234	1.56	0.002	0.001	0.5	As for rays
Birds (shorebirds)	1.018	0.07	1.69	0	0	0.5	Briggs *et al.* (1987) PICES (1998)
Marine mammals (dolphins and seals)	0.02	0.09	19.88	0	0	0.9	Dolphin Research Institute (2000)
Detritus	14 766.84	–	–	0	0	–	Nicholson *et al.* (1996) Harris *et al.* (1996)

THE NUTRIENT MODELS

BM2 and IGBEM are biogeochemical marine ecosystem models. They track nutrient flow through seven primary producer groups (three benthic, four planktonic), four zooplankton groups, three infaunal groups, three epifaunal groups and four fish groups (Fig. 2). Because they deal with nutrient pools rather than total biomasses, they are also referred to as nutrient models.

Unlike ECOSIM, the models do not deal separately with any individual species, and the highest trophic levels are only represented by static loss terms rather than by dynamic pools. In contrast, the actual handling of the various trophic levels in the nutrient models is similar to ECOSIM. The top trophic levels are represented by age-structured populations, with explicit recruitment and food intake allocated to growth and reproduction, whereas aggregate pools are used for the lower trophic levels. Similarly, the basic set of processes considered in BM2 and IGBEM match those in ECOSIM (consumption, migration, predation, natural mortality and fishing). It is the underlying formulations that differ markedly between the models.

The equations used in IGBEM are based on the transfer of carbon, nitrogen, phosphorus and silica. In addition, the equations are highly physiologically detailed. Internal nutrient ratios determine final uptake rates, and finely resolved processes (e.g. basal, activity and stress respiration) are all represented explicitly (see Table I and Fulton *et al.* (2004b) for further details). Modelling details at this level is at the upper end of, but not beyond, what is employed in ecosystem models currently in use (e.g Shallow Sea Ecological Model [SSEM], Sekine *et al.* 1991; the European Regional Seas Ecosystem Model II [ERSEM II], Baretta-Bekker and Baretta 1997; and the Across Trophic Level System Simulation [ATLSS], DeAngelis *et al.* 1998).

BM2 employs much less process detail. In contrast to IGBEM, processes such as excretion and respiration are not modelled explicitly in BM2, but are subsumed into generalized assimilation and waste production equations (see Table I and Fulton *et al.* (2004a) for details). Further, BM2 only models the nitrogen component, and relies on Redfield ratios, rather than internal nutrient ratios, to determine the form of nutrient dependent activities. This level of detail is more representative of the most commonly used eutrophication and water column trophic models (Fransz *et al.* 1991).

Unlike ECOSIM, the nutrient models are spatially explicit. The spatial geometry used in this study is a set of 59 polygons (boxes or cells), which parallel the geographical form of Port Phillip Bay. The size of each polygon reflects the speed with which physical variables change within that part of the bay (Fig. 3). The biological network is replicated in each cell, with

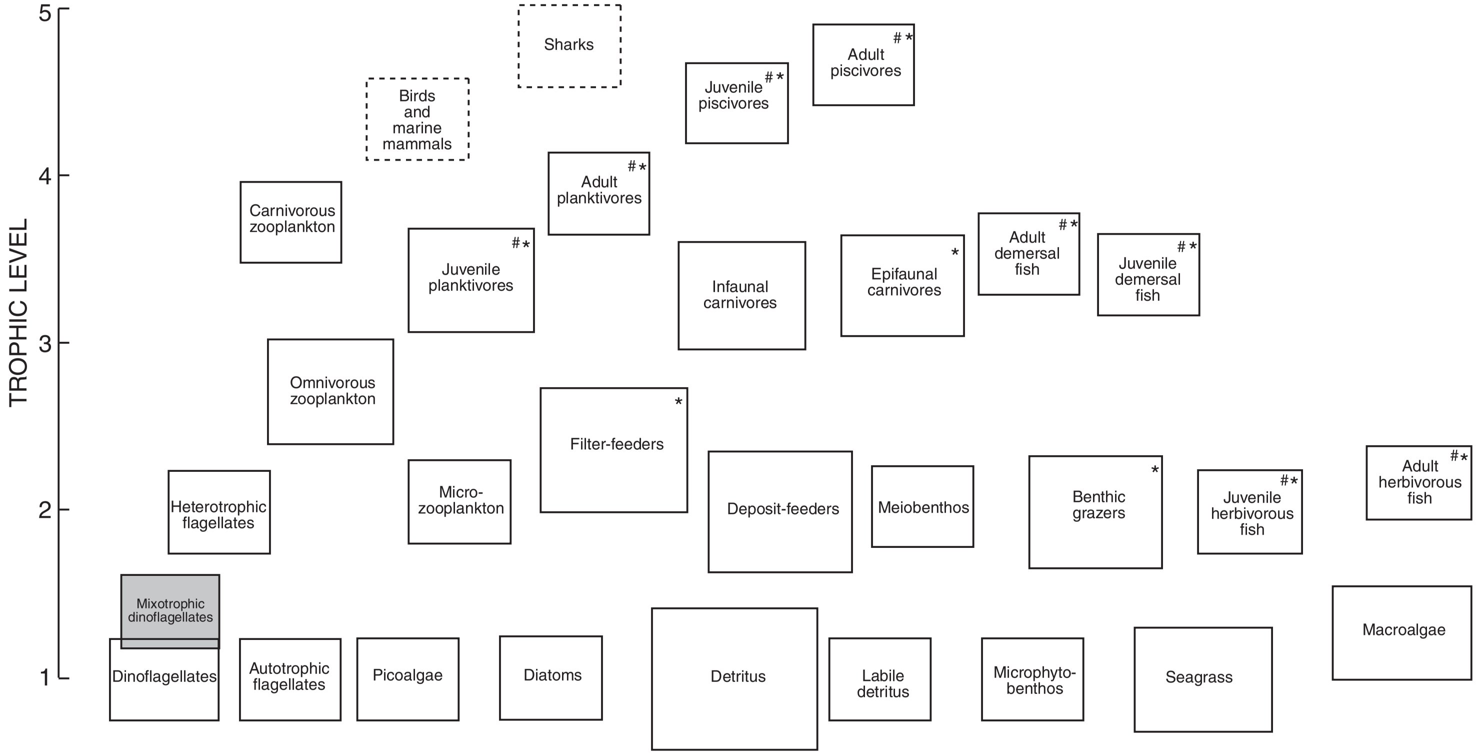

Fig. 2: Schematic diagram showing the groups in BM2 and IGBEM and their relative trophic positions. The bacterial groups are omitted from the diagram and the model comparisons because no equivalent group exists in the ECOPATH model. The grey box indicates the position of the dinoflagellates when mixotrophy was allowed in BM2. The dashed boxes indicate the position of the static predator groups implemented for the nutrient model runs used here. Groups marked with a hash are fished explicitly in IGBEM and those marked with an asterisk are fished in BM2

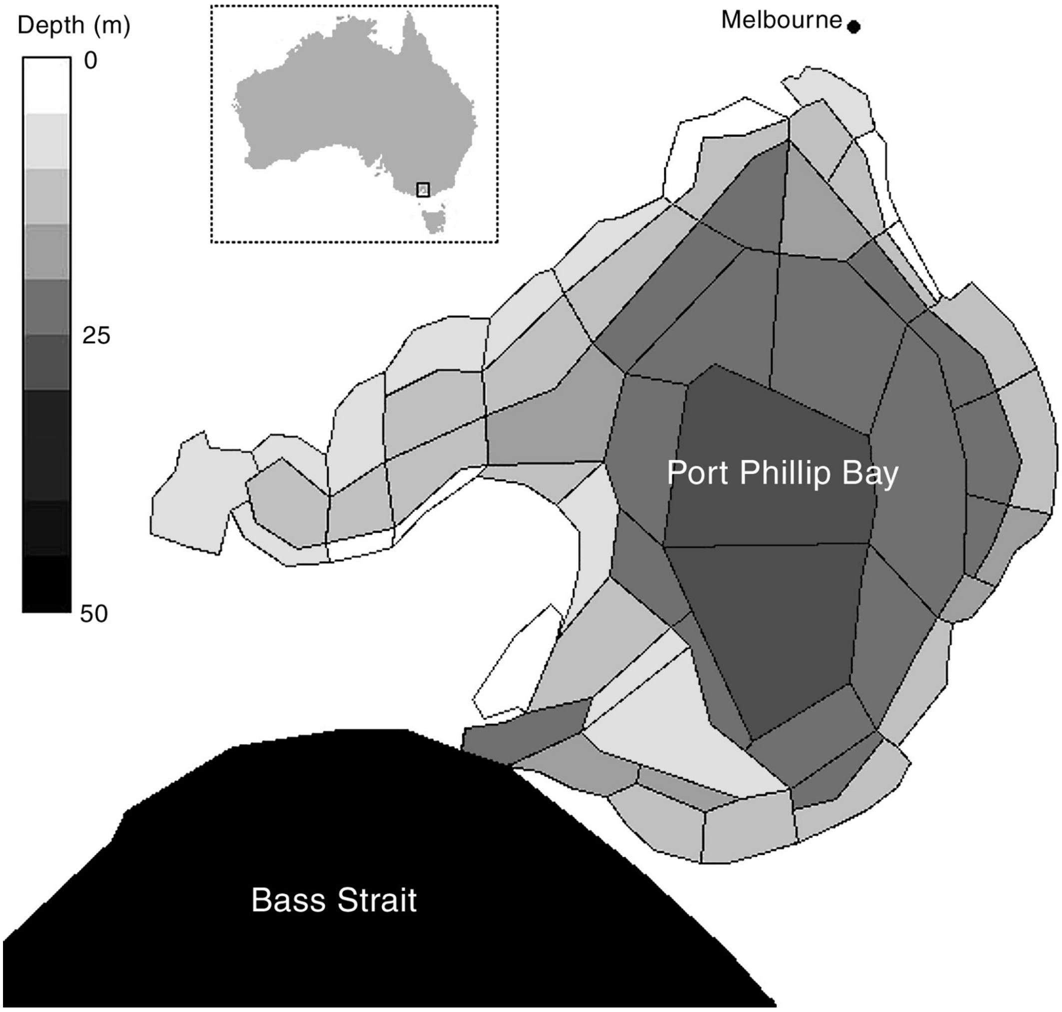

Fig. 3: Depth map of Port Phillip Bay, Melbourne, Australia. The inset map of Australia indicates the location of Port Phillip Bay. The polygons marked on the large map are those of the standard 59-box geometry used for BM2 and IGBEM

movement between cells dealt with explicitly (for the migration of higher trophic levels), or by a simple transport model (for advective transfer).

MODELLED HARVESTING METHODS

In all, eight harvesting methods are modelled. These are purse-seine, scallop dredge, haul-seine, longline, mesh-net, dive and pot fisheries, and culture of mussels (details are summarized in Table III). There is not enough information to specify a separate recreational fishery, so recreational catches are aggregated with those for the commercial fishery using the same gear. ECOSIM and BM2 include all eight harvesting methods, but IGBEM does not contain any of the invertebrate fisheries. To try and account for the fisheries not explicitly included in IGBEM, the mortality rate of the target groups are increased.

IMPORTANT MODEL DIFFERENCES

To give a better idea of the degree of variation in process

Table III: Summary of fisheries information used explicitly in the Port Phillip Bay ECOPATH model (after Table 2 of Fulton and Smith 2002). The landings information was also used in the tuning of the nutrient models. Groups fished in the nutrient models are shown in Figure 2

Fishery	Target species	Bycatch species	Landings (tons km^{-2} year^{-1})	Discards (tons km^{-2} year^{-1})	Value (AUD)
Purse-seine	Clupeoids		0.812	0	1 500 000
Scallop dredge	Scallops	Scallops Filter-feeders Epifaunal predators Seagrass Macroalgae Flatfish	0.551	0.3205	8 000 000
Haul-seine	Juvenile and adult King George whiting Mullet and garfish Southern calamary Other cephalopods	Snapper	0.1639	0.001	930 000
Longline	Juvenile and adult snapper Sharks	Juvenile and adult flatfish	0.041	0.012	500 000
Mesh nets	Juvenile and adult snapper Juvenile and adult flatfish Piscivores Other demersals Sharks	Marine mammals	0.1945	0.00001	780 000
Dive	Abalone Other grazers	Epifaunal predators	0.0483	0.0005	1 175 000
Aquaculture	Mussels		0.311	0	1 500 000
Pot	Southern rock lobster		0.003	0	125 000

detail between the three models, the formulation for phytoplankton production is given in Table IV. This example is a fair representation of the difference in formulation detail for the lower trophic levels. However, as noted above, at the highest levels, where split pools (juvenile and adults) are included in ECOSIM, the differences between the models are smaller. The variation in process detail between the models is one of the motivating forces for the comparison of the models and their predictions. Nevertheless, there are a number of major differences in underlying model assumptions when comparing the models and their dynamics:

(i) the consumption formulations (a forage arena approach is used in ECOSIM, but Holling Type functional responses are used in the other two models);
(ii) the lack of bycatch in the standard versions of IGBEM and BM2;
(iii) the omission of invertebrate fisheries from IGBEM;
(iv) the absence of explicit spatial structure in ECOSIM;
(v) the static (implicit) representation of birds, marine mammals and sharks in BM2 and IGBEM (where they are represented by mortality terms on fish rather than dynamic pools); and
(vi) the stock structure of the fish groups with its inherent implications for the form of the stock-recruit relationship used (ECOSIM assumes a closed stock, whereas the nutrient models receive a constant supply of recruits from an external stock).

These assumptions have the potential to cause differences in model outcome. The assumptions relating to bycatch, invertebrate fisheries, static top predator populations and the form of the stock structure and recruitment relationship are likely to affect the higher trophic levels (fish in particular). More generally, consumption (predation) and spatial structure have been major research topics in theoretical ecology for a large part of the past century, and have significant effects in other ecological model studies. For example, it has been shown for predator-prey and competition models that different forms of the consumption term, or the addition of spatial structure, can lead to very different sets of population behaviour and species interactions (Hassell and May 1973, Holmes *et al.* 1994). In some ways, it is unfortunate that so many factors vary at once between the three models being considered here. However, only the ECOPATH with ECOSIM (EwE) model presented was built explicitly for Port Phillip Bay. The other two models were built as part of a more general and theoretical study of ecosystem

Table IV: Process detail involved in the phytoplankton production for each model

ECOSIM[1]	BM2	IGBEM
$= \frac{r \cdot B}{1 + B \cdot h}$, where B = biomass of the phytoplankton, r = the maximum *P/B* ratio that can be realised (at low B), r / h = the maximum net primary production when the biomass is not limiting to production (at high B).	$= \mu \,.\, \delta_{irr} \,.\, \delta_N \,.\, B$, where B = biomass (mg N m^{-3}) of the phytoplankton group (4 types), μ = maximum temperature-dependent growth rate, $= \frac{DIN}{K_N + DIN}$ δ_N = nutrient limitation factor. and DIN = ammonia + nitrate unless also limited by silica (Si), then $= \min\left(\frac{DIN}{k_N + DIN}, \frac{Si}{k_{Si} + Si} \right)$, κ_{XX} = the half saturation constant for the uptake of the nutrient XX δ_{irr} = light limitation factor $= \min\left(\frac{IRR}{\kappa_{irr}}, 1 \right)$ IRR = light κ_{irr} = is the half saturation constant for the uptake of light	$= \mu \,.\, \delta_{irr} \,.\, \delta_{Nut} \,.\, B_C$, where B_C = biomass (mg C m^{-3}) of the phytoplankton group (4 types)[2], μ = maximum temperature-dependent growth rate, δ_{Nut} = nutrient limitation factor. $= \min(\delta_N, \delta_p)$ $\delta_N = \min\left(1, \max\left(0, \frac{B_C - \beta_{CNlow}}{\beta_{CN\,int} - \beta_{CNlow}} \right) \right)$ $\delta_p = \min\left(1, \max\left(0, \frac{B_C - \beta_{CPlow}}{\beta_{CP\,int} - \beta_{CPlow}} \right) \right)$ β_{CXXlow} = minimum permissible nutrient ratio of *C:XX* for the cell β_{CXXlow} = standard internal nutrient ratio of *C:XX* for the cell unless also limited by silica (Si) then $= \min\left(\min(\delta_N, \delta_P), \min\left(1, \frac{Si}{2 \cdot k_{Si}} \right) \right)$ δ_{irr} = light limitation factor $= \min\left(1, \frac{IRR}{k_{irr\_adjusted}} \right)$ IRR = Light κ_{irr} = the half saturation constant for the uptake light adjusted for acclimation to new ambient light conditions

1. Since the work discussed in this paper was completed, a new version of ECOSIM has been released, which links primary production to free nutrient concentration during each simulation through assumed Michaelis-Menten uptake relationships. The actual formulation used is similar to the one given here, though it has been modified to include a nutrient-based Michaelis constant and a potential (user defined) sensitivity to changes in nutrient levels
2. There are also N and P pools of the biomass explicit in IGBEM and the production in these is based on the internal nutrient ratio and the production for the B_C pool

models (Fulton 2001, 2003), then tuned to data from the bay to allow for the comparisons considered here.

Model calibration

Data from the Port Phillip Bay Environmental Study (PPBES), primarily for the period 1994–1995, were used to calibrate IGBEM and BM2 to achieve a satisfactory representation of the biological conditions in the bay (in mg N m^{-3}). In a few instances it was necessary to draw values from the general literature or to use data from other years to fill in gaps, but this was kept to a minimum.

These datasets were also used to construct an ECOPATH model, converting from mg N m^{-3} to tons km^{-2} wet weight under the assumption that nitrogen makes up 1% of an organism's wet weight. The standard method of balancing ECOPATH was employed; the most uncertain of the input parameters (diet compositions, biomasses, production/biomass ratios [*P/B*] and consumption/biomass ratios [*Q/B*]) were adjusted until all of the ecotrophic efficiencies were <1, and the gross food-conversion efficiencies were within sensible bounds for each group. However, an additional restriction was imposed on this process. All parameter values were also required to remain within the ranges given in the PPBES technical reports.

To try and avoid confounding the model comparison with differences attributable to the influence of inputs rather than model structure, the environmental conditions (e.g. temperature) and forcing used in the nutrient models were taken from data for the period 1994–1995 and looped repeatedly through time in each run. This meant that any difference in the long-term behaviour of the models was not a result of the background environmental settings or the forcing functions.

In hindsight, however, a potentially confounding issue was overlooked. This potential problem arose from the fact that the nutrient models (IGBEM and BM2) were calibrated, whereas the ECOPATH model underwent balancing. The nutrient models were calibrated by setting their parameters (e.g. growth and mortality rates) based on the species composition of Port Phillip Bay, and making minor adjustments to those values so that the predicted biomass levels were reasonable reflections of those reported in the PPBES technical reports. Whereas the biomasses from the technical reports were also used in the ECOPATH model, some undergo substantial changes during balancing. Consequently, the biomass values in the final version of the ECOPATH model no longer matched those used to calibrate the nutrient models. Although not important for all groups in the model, it became obvious that tuning the biogeochemical models to reduce the differences introduced by balancing the ECOPATH model would have been beneficial in some cases; these will be identified later.

Comparison of the three models

Comparisons of the three models and the potential management strategies were undertaken in a multistep process. "Base cases" were compared first. This allowed for differences in the models when there was no change in external forcing conditions to be understood before the management strategies were applied.

The form of the outputs of the three models meant that some conversions were necessary before comparisons could be made. IGBEM and BM2 are spatially explicit models with seasonal forcing, but ECOSIM is not. Therefore, spatial and temporal averaging across the model area was required before the values from ECOSIM and the nutrient models could be compared (details below). The biomass units used in the nutrient models and ECOSIM also differed, so all biomasses were converted to tons km^{-2} to facilitate comparison.

Comparison of the "base case" results

The "base case" run for the nutrient models was a 20-year simulation under current (*status quo*) fisheries pressure and nutrient loading. The outputs from the final four years of these runs were averaged across the bay and compared with the values given in the balanced ECOPATH model. This run length is sufficient for the influence of initial conditions on the final averages to be negligible (Fulton *et al.* 2004a, b).

There was uncertainty associated with the values produced by all three models. However, a model comparison is easier if there is an identifiable baseline for comparison; the easiest way of doing this was to designate one of the three models as that baseline. The work presented here was also done in the context of a larger evaluation of ECOSIM as a tool for considering the effect of fisheries policy. Therefore, it was decided that the ECOPATH values are as good a baseline as any, and the nutrient models were measured against them. Ideally, all three models should be compared with an independent dataset for the bay, but this was not possible at the time.

Fishing policy analysis

The ECOSIM software contains a fisheries optimization module, so fishing mortality rates that meet economic, social and ecological objectives can be formally identified (Walters *et al.* 2002). This optimization module contains both open and closed loop policy analysis, allowing for consideration of the importance of feedback on management strategies.

The optimization's objective function is the weighted sum of an economic, a social and two ecological components. The ecological components are to do with ecosystem structure and the need for mandatory stock rebuilding. Within the social and ecological components, further weights can be specified for each group or gear type. For the social component, the employment value of each fishery (or gear type) can be given. For the ecological components, the weights reflect the perceived value of each group to the ecosystem structure, as well as the importance of stock rebuilding for that group. The weights used to specify the objective function are also known as the criteria.

FISHING POLICIES WITH NO CHANGE IN NUTRIENT LOADING

The ECOSIM fisheries optimization module is used here to suggest optimal fisheries policies for the models of Port Phillip Bay. The *F*s forming these policies were applied (trialled) in 40-year runs of all three models to see if the predicted effects of the policies matched across the models. Within ECOSIM, the impacts of the policies were evaluated by considering biomass trends through time, the overall average total catch and value of the fisheries for the entire period, and the annual total catch, total value and total biomass of the system at the beginning and end of each run.

Table V: Criteria (weights) used to define the ecological components of the objective function used in the ECOSIM policy analysis routine when all species are represented in the ecologically motivated management strategy

Group	Mandated relative biomass	Relative weight
Phytoplankton	1	0
Small zooplankton	1.5	0
Large zooplankton	1.5	0
Deposit-feeders	1.5	0.2
Scallops and mussels	5	0.4
Filter-feeders	1	0.4
Infaunal predators	1	0.2
Epifaunal predators	2	0.4
Southern rock lobster	5	1.4
Abalone	3	1.4
Other grazers	1.5	1.2
Scavengers	1	0.2
Microphytobenthos	1	0
Seagrass	1	0
Macroalgae	1	0
Clupeoids	2	0.8
Juvenile snapper	1	1.8
Snapper	4	2
Juvenile flatfish	1	1.2
Flatfish	2	2.4
Juvenile King George whiting	1	1.2
King George whiting	5	1.8
Juvenile piscivores	1	1.2
Piscivores	3	2.4
Juvenile mullet	1	2.4
Mullet and garfish	2	3
Other demersals	2	1.8
Southern calamary	2	0.6
Other cephalopods	1.5	0.8
Rays	1	4.2
Sharks	2	4.2
Birds	3	14.2
Marine mammals	4	11.2

When comparing the results across the three models, comparisons were made by considering the relative change in biomass at the end of the run (biomass under new policy/"base case" biomass) for each model. The values from the nutrient models were spatially averaged.

The criteria used in the policy optimization match those in Fulton and Smith (2002). Briefly, the social criteria used were set at 1 for all fisheries except the dive fishery (0.2) and the longline and pot fisheries (both 0.5). Two weightings were considered for each ecological component. For the structural component, the first gave little importance to the biomasses of noncharismatic groups and groups not of recreational interest (so only seagrass, snapper *Pagrus auratus*, King George whiting, sharks, birds and marine mammals received biomass growth ratings >1 with an importance criteria of >0 (details in Fulton and Smith 2002). The second set of criteria used for the structural component was more complex. This set (values given in Table V) was not related to the perceived value of the group to humans (commercially, recreationally or aesthetically), but was related to the trophic level of the group. For the mandatory rebuilding component, the first set of criteria did not require the rebuilding of any stocks, whereas the second set did (see Table V for the weightings used).

FISHING POLICIES WITH A CHANGE IN NUTRIENT LOADING

To check for interactions or synergies arising from multiple human pressures on a system, the optimization and trialing process was repeated where there was a long-term change in nutrient loading. Over the course of the 40-year runs, the nutrient loading slowly increased (or decreased) five-fold. This magnitude of change in nutrients was used because it is known to cause substantial shifts in the predicted ecosystem state in BM2 and IGBEM (Fulton *et al.* 2004a,b). The change in loading was implemented in ECOSIM by taking the nutrient input files used to force IGBEM and BM2 and using them to force the phytoplankton and macrophyte groups in the ECOSIM model.

Because the nutrients (and thus the productivity) undergo large changes with time, a single *F* applied for the entire period is unlikely to be particularly informative (Fulton 2001). Therefore, one policy was found for the first 20 years and a second for the final 20 years of the simulation. The second policy did not begin until there had been an obvious change in productivity and system conditions in response to the change in nutrient loading. These two-step policies are also referred to as split policies.

The methods outlined above for considering the impact of the fisheries policies when there is no change in nutrients were also used for these split policies. The biomass trajectories from the end of the first part of the split policy to the end of the second could also be considered for each model. In this case, they did not provide any extra insight and are not discussed further here.

RESULTS

Comparison of the "base case" results

COMPARISON OF BIOMASSES – ECOPATH vs IGBEM

The IGBEM ecosystem is fairly close to that captured by the ECOPATH model. Only eight groups in IGBEM

Table VI: Comparison of the "base case" group data for the three models. The values are given as the relative size of the biomass (*B*), production/biomass (*P/B*) and consumption/biomass (*Q/B*) values output by IGBEM and BM2 in relation to those in ECOPATH (value for model *x* / value in ECOPATH). The values are given only for those groups shared by all three models. To allow for this comparison, the plankton groups in the nutrient models are aggregated to the levels of ECOPATH; the benthic invertebrate groups in ECOPATH are aggregated to the level of trophic groups; the demersal fish of the nutrient models are equated with the flatfish in ECOPATH; and the herbivorous fish are equated with the mullets

Group	IGBEM			BM2		
	B (tons km^{-2})	*P/B* (year^{-1})	*Q/B* (year^{-1})	*B* (tons km^{-2})	*P/B* (year^{-1})	*Q/B* (year^{-1})
Phytoplankton	1.09	1.42	–	1.21	1.12	–
Small zooplankton	1.37	0.70	0.69	1.40	0.68	0.67
Large zooplankton	1.14	1.03	1.02	0.77	1.09	1.24
Deposit-feeders	0.80	2.12	0.80	1.20	1.89	0.59
Filter-feeders	0.96	0.42	0.27	0.96	1.05	1.16
Infaunal predators	1.38	1.98	0.54	1.11	2.13	0.39
Epifaunal predators	2.92	1.13	0.55	0.64	1.08	0.57
Benthic grazers	2.49	0.27	0.08	0.85	2.34	0.70
Microphytobenthos	0.10	1.10	–	0.13	1.00	–
Seagrass	4.10	1.00	–	2.23	0.17	–
Macroalgae	2.01	0.25	–	1.01	0.74	–
Clupeoids	1.92	1.92	0.27	1.66	1.90	0.25
Juvenile flatfish	1.05	1.26	1.03	1.56	1.49	1.20
Flatfish	0.80	0.92	0.43	1.17	1.01	0.68
Juvenile piscivores	2.22	1.40	0.91	0.29	0.75	1.42
Piscivores	1.24	0.41	0.37	1.16	0.80	0.73
Juvenile mullet 0.64	3.50	1.15	0.92	2.90	1.05	
Mullet	0.40	1.42	0.49	2.32	1.67	0.85
Detritus	0.30	–	–	1.34	–	–

have biomasses that differ by more than a factor of two from the ECOPATH values (Table VI). The biomass of detritus is a factor of three lower in IGBEM, whereas the benthic grazer and epifaunal predator groups are nearly three times larger than the corresponding groups in ECOPATH. This reflects IGBEM's apparent tendency to emphasize a trophic web based on primary production over a detritus-based web.

The estimate for detritus given in ECOPATH is closer to real world estimates for Port Phillip Bay, and the low levels predicted by IGBEM are the result of a combination of factors in that model: the point-source detrital input is about two-thirds of what it should be, the assimilation by the detritus-feeders is too efficient and detrital burial is too fast (Fulton *et al.* 2004b). The estimate for microphytobenthos in ECOPATH is also much closer to the true value than that given by IGBEM. This is probably the result of the competitive exclusion of this group by the large macrophyte groups in IGBEM and uncertainty over the true extent of feeding on this group by infauna, which has made parameterization of those grazing processes quite difficult (Fulton 2001). In contrast, the biomass estimates for the benthic invertebrate groups in the PPBES reports are too uncertain to be sure which model is closest to reality. It would be possible to tune the benthic invertebrate groups in IGBEM to more closely match more of the biomasses given in ECOPATH. However, such a move would not be justified, given the uncertainty in the biomass estimates, and noting that the tuning would entail moving a number of the clearance, growth and mortality parameters for these groups beyond the biological limits currently recorded in the literature.

One case where the process specification in IGBEM may not be appropriate is the use of static mortality terms to represent predation by sharks, birds and marine mammals. These parameters are tuned on the basis of intermediate to older age-classes and total longevity of the fish groups. The potential problems with this can be seen most clearly for piscivores. Whereas this mix of age-specific and general pressures on the fish groups serve to represent the dynamics of the intermediate age-classes of the piscivorous fish group well, it does not perform as well for the younger and older age-classes. As a result, the biomass of juvenile piscivores in IGBEM is more than double that of the ECOPATH model.

The spatial structure in IGBEM, rather than parameterization uncertainty or process mis-specification, leads to the difference in the estimates for the macrophyte groups (seagrass and macroalgae) between IGBEM and ECOPATH. The spatial structure allows for a roughly five-year cycle of barren formation and recovery as nutrient availability interacts with the density of benthic grazers. In turn, additional mortality resulting from the starvation of mullet *Aldrichetta forsteri* in IGBEM during those periods when the macrophytes are in a "barren" state leads the adult mullet biomass in IGBEM to be 2.5× lower than in ECOPATH. A macrophyte barren cycle of this form has not been recorded for Port Phillip Bay and may be a model artefact, though such cycles are not uncommon in temperate marine systems (Hagen 1995, Leinaas and Christie 1996, Silvertsen 1997).

COMPARISON OF BIOMASSES – ECOPATH vs BM2

Table VI shows that biomass values in the BM2 and ECOPATH models are closer than the above comparison (only the microphytobenthos, seagrass, juvenile piscivore and mullet biomasses show more than a twofold difference). Microphytobenthos is again only a tenth of that in the ECOPATH model, whereas seagrass is nearly three times higher in BM2 than in ECOPATH. The explanation for these results is the same as that identified above for IGBEM, i.e. the absence of spatial structure in ECOPATH. It is worth noting that the "macrophyte-barren" cycle in BM2 has a shorter period and is not of the same amplitude nor as spatially widespread as that in IGBEM (Fulton *et al.* 2004a). The result is a smaller impact on other groups.

For fish, it is noteworthy that the same groups stand out as in ECOPATH for both IGBEM and BM2, but that the direction of difference is reversed between the two nutrient models. The feeding and migration regimes in BM2 allow the dynamic predators to target the juvenile piscivores more effectively (which compensates for the static top predators) and the altered form of the barren cycle means that adult mullet escape starvation.

COMPARISON OF *P/B* AND *Q/B* RATIOS PREDICTED BY THE THREE MODELS

P/B ratios produced by the nutrient models are generally within a factor of two of those in the ECOPATH model. In IGBEM, the *P/B* ratios for the benthic deposit-feeders and juvenile mullet were more than twice as high as those in ECOPATH, whereas those for filter-feeders, benthic grazers, macroalgae and piscivores are less than half. It may be that, with so many explicit processes to be parameterized in IGBEM, their cumulative effect can result in inappropriate levels of productivity. In BM2, it is likely that the general form of the equations and the specific conversion efficiencies used for groups on diets of low nutritional value (in particular infaunal predators, benthic grazers and juvenile mullet) result in *P/B*s for these consumers being too high. Resetting the efficiencies of these groups to lower levels could correct this problem. The spatial dynamics and the macrophyte-barren cycle may explain the anomalously low *P/B* ratios given for macroalgae in IGBEM and for seagrass in BM2.

The values of the *Q/B* ratios produced by the nutrient models are in several cases much lower than those in ECOPATH. This suggests that overall the assimilative processes in the nutrient models may be too efficient, at least for some groups.

SUMMARY OF CONCLUSIONS FOR "BASE CASE" RESULTS

A number of general conclusions can be drawn from the comparisons above. Whereas the spatial structure of the nutrient models allows for the expression of some more complex model behaviour, the models can also be more susceptible to uncertainty over parameterization. In general, however, the behaviour of the low to middle trophic groups in the nutrient models is probably more realistic than that in ECOPATH, but the higher trophic groups respond more sensibly in ECOPATH than the nutrient models. This is probably another consequence of their respective focus and development histories.

Fishing policy analysis

For ease of understanding, the ECOSIM optimizations when nutrient levels are held steady will be presented first, before the outcomes for the nutrient models. This two-step presentation will then be repeated for the optimization and policy application, when nutrient levels change during the period of the simulation.

ECOSIM WITH NO CHANGE IN NUTRIENTS

The results of the ECOSIM policy analyses under constant environmental conditions are given in Table VII. In summary, over the entire range of objective function weightings tested, only three basic system configurations are produced, corresponding to an economically based strategy, an ecologically based strategy, and a compromise between the two. These outcomes also persist, with very little change, across a range of refuge parameter settings used to test the sensitivity of the ECOSIM model and the optimization process.

"ECONOMIC" STRATEGY

The "economic" strategy exhibited increases in *F*s, relative to current (*status quo*) levels, for all but the haul-seine and pot fisheries. The mesh-net fishery

Table VII: Results of the policy analyses under constant environmental conditions. The *F*s given are those found by the ECOSIM open-loop analysis and the summary statistics are for the ECOSIM output under the suggested *F*s (with a *status quo* entry included for comparative value). The "overall average total catch" and "total value" indicate the cumulative totals over the entire run. The "ratio end/start values" are the ratios of the annual total catch, economic value and biomass at the beginning and end of the run

Parameter	Strategy				
	Status quo	Economic	Ecological (no mandated rebuilding)	Ecological (mandated rebuilding)	Compromise
Weighting					
Economic	–	1	0.0001	0.0001	0.5
Social	–	0.0001	0.0001	0.0001	0.5
Mandated rebuilding	–	0.0	0.0	10	1
Ecosystem	–	0.0001	1	1	1
Estimated relative Fs					
Purse-seine	1	1.9	0.9	0.4	1.7
Scallop dredge	1	2.0	0.2	0.2	3.0
Haul-seine	1	0.5	0.005	0.02	0.2
Longline	1	1.2	0.04	0.06	0.5
Mesh-nets	1	20.1	0.3	0.2	1.1
Dive	1	1.3	2.6	0.4	1.2
Pot	1	0.75	0.5	0.2	0.6
Aquaculture (omitted from search)	1	1	1	1	1
Overall average					
Total catch (tons km^{-2})	880	1 420	570	376	1 161
Total value (million AUD)	1.2	1.9	0.7	0.5	1.4
Ratio end/start values					
Total catch	1	0.56	0.97	1.15	0.76
Total value	1	0.77	0.4	1.46	0.89
Total biomass	1	0.79	1.05	1.1	0.91
Relative change in biomass					
Large zooplankton	1	1.1	0.95	0.9	1.1
Scallops and mussels	1	0.7	1.2	1.2	0.7
Epifaunal predators	1	1.4	1.0	0.9	1.0
Southern rock lobster	1	1.35	2.0	3.0	1.4
Abalone	1	0.8	<0.01	1.5	0.9
Seagrass	1	0.95	1.1	0.9	0.95
Clupeoids	1	0.9	1.3	1.1	0.9
Snapper	1	0.9	1.1	1.2	1.4
Flatfish	1	<0.01	1.0	1.1	0.8
Other cephalopods	1	0.75	0.8	0.9	0.6
Rays	1	0.95	1.1	1.1	0.9
Sharks	1	<0.01	2.0	1.9	1.5
Marine mammals	1	0.75	1.5	1.4	1.2

undergoes the most extreme change as the optimization increases its *F* to 20 times current levels (Table VII). As a consequence of these increased *F*s, there is a general decline in the biomasses of the target and major bycatch groups. Among the invertebrates there is a moderate decline in the biomass of the high-value species abalone and scallops. The effect is more severe for the vertebrates, where the sharks and flatfish are effectively extirpated (Table VII), and bycatch groups, such as marine mammals (Table VII) and the large piscivorous finfish (Table VIII), decline by at least 25% of their *status quo* levels. By reducing these predatory groups, their higher-value prey species (e.g. southern rock lobster *Jasus edwardsii*) can flourish, which improve the economic performance to about 1.5 times *status quo* levels. In spite of this overall increase in total catch and value across the run, the annual catch and value drop by nearly a quarter and biomass drops by almost 50% from the beginning to the end of the simulation. This decline in annual indicators is be-

Table VIII: The relative change in biomasses (biomass under new policy/"base case" biomass) for each of the three models under the ecological and economically based strategies. The lumping and association of groups noted for Table VI also apply here and sharks are given for ECOSIM

Group	Economic strategy			Ecological strategy		
	ECOSIM	BM2	IGBEM	ECOSIM	BM2	IGBEM
Phytoplankton	1	2	2	1	1	1.5
Small zooplankton	1	1	3	1	0.9	4
Large zooplankton	1	4	1.2	1	1.2	0.9
Deposit-feeders	1	5	2	1	0.75	0.75
Filter-feeders	0.5	0.01	1.5	1.2	1.2	2
Infaunal predators	1	1	1.5	1	1	1.5
Epifaunal predators	1.5	0.1	1.5	1.7	3	1.5
Benthic grazers	0.9	2	0.5	1.5	1.5	0.3
Microphytobenthos	1	2	1	1	1	1
Seagrass	1	1	1	0.75	1.1	20
Macroalgae	1	1	2	1	1	3
Clupeoids	0.8	0.5	0.5	1	1	1
Flatfish	0.1	0.01	0.02	1.5	3	1.5
Piscivores	0.5	0.75	0.75	0.75	5	2
Mullet	1.5	2	1.2	2	2.5	2
Sharks	0.05	–	–	2	–	–
Detritus	1	0.5	2	1	1.5	1.5

cause of the wide-spread depletion of so many groups.

These results for an "economic" strategy show little sensitivity to changes in the refuge parameters. The only appreciable change in the optimal policy under economic criteria is when all the refuge parameters are set in excess of 0.7. Under these settings, the optimal "economic" policy more closely resembles the standard "ecological" strategy described below.

"ECOLOGICAL" STRATEGY

A variety of weightings for the ecological components of the objective function all produce generally similar results, with lower *F*s for the majority, if not all, the fisheries (Table VII). The one fishery that is sensitive to the ecological weights is the dive fishery for abalone. When mandatory population rebuilding is given little or no weight, the *F* for the abalone fishery increased substantially. This is probably attributable to competition between the abalone and mullet (a fish identified as a group to be rebuilt), and abalone's very high market price (which is large enough still to affect the objective function, despite the small economic weight used). This results in the abalone biomass being depressed towards commercial extinction and the annual total value falling by more than half from the beginning to the end of the run. In contrast, when mandatory population rebuilding and maintenance are given some weight, the *F* for the dive fishery falls with those for the other fisheries. This indicates how critical the ecological criteria can be to the results obtained for certain species. If ecological concern is focused only on the charismatic or favoured recreational species, then other components of the ecosystem continue to be quite intensively exploited. When ecological criteria emphasize some level of conservation for all groups, a much more balanced system results. However, this balance comes at the expense of the landed catch. When there is mandatory rebuilding, the overall total catch and total value are about two-thirds of the values when there is no such restoration. Further, these values under mandatory rebuilding only equate to about one-quarter of the total catch and one-third of the total value achieved under the economic objective. The low *F*s in this rebuilding case allow the target groups to grow steadily though, and the annual total catch, value and biomass to rise from the beginning to the end of the period. Even with low exploitation, the value of the pot fishery more than doubles, increasing the average total value of all fisheries.

The "ecological" strategy is more heavily impacted by changes in the refuge parameters. The greatest variation in behaviour is shown by high-value groups such as cephalopods and snapper. Nevertheless, there is little qualitative change in the predictions. The most significant variations are at low refuge parameter settings ($v = 0.2$), where a more "even" ecosystem (one not so heavily skewed towards the charismatic species) results, regardless of the explicit ecological criteria selected.

"COMPROMISE" STRATEGY

There is no smooth transition from ecologically to economically based optimizations. Rather, as the weightings are gradually changed from economically to ecologically dominated, the "economic" strategy given above persists as the optimal outcome until the point where the economic:ecological weight equals 0.71:1. At this weighting, a flip-point exists, where the optimal outcome returned is either the "economic" or "compromise" strategy, depending on the initial starting point of the search routine.

The "compromise" strategy (Table VII) closely resembles the "economic" strategy and is apparently heavily influenced by the economic contribution to the objective function. This is evident not only from the pattern of biomass change, but also from the majority of *F* settings, the overall total catch and value of the run, and from the changes in total annual catch, value and biomass from the beginning to the end of the run (Table VII). However, the ecological contribution is still present and shows up in the values of the predatory species. These species suffer excessive depletion under the "economic" strategy, but not under the compromise strategy. The biomass of the snapper, shark and marine mammal groups reverse the pattern of change seen under the "economic" strategy and increase rather than decrease, whereas the flatfish are not depleted to the point of extinction.

As the objective function weightings are moved still further towards those used to define the "ecological" strategy, this "compromise" strategy is the only outcome returned until the point where the economic: ecological weight equals 0.5:1. From this point on, as the economic weighting is reduced still further, the optimal strategy is the "ecological" strategy.

"OPTIMAL" POLICIES IMPLEMENTED IN NUTRIENT MODELS, WITH NO CHANGE IN NUTRIENTS

When the ecologically orientated fisheries policy is applied in the nutrient models, there is good qualitative agreement between the three models with regard to the biomass trajectories of the various groups (Table VIII). There are some differences between IGBEM and the other two models, because IGBEM does not allow for the fishing of invertebrates. The attempt to mimic fishing mortality in these groups using general background (natural) mortality did not succeed. The majority of the differences seen between IGBEM and the other two models in this case are on account of this failure and its flow-on effects. The more important divergence between the ECOSIM and nutrient model predictions is in the piscivorous groups. The nutrient models predicted that the piscivorous fish would increase, whereas ECOSIM suggests that the group would decline marginally. This difference is almost certainly attributable to the fact that the highest trophic levels (sharks, birds and marine mammals) are only static, not dynamic, components of IGBEM and BM2. In ECOSIM, these groups are dynamic, and impact the piscivorous group accordingly.

When the economically driven set of *F*s is applied in IGBEM and BM2, there is again wide qualitative agreement between the model predictions. All models show similar impacts of the proposed fishing mortalities on fish groups, but there are differences for invertebrate groups. IGBEM predicts an increase in filter-feeders, whereas the other models do not. More importantly, BM2 predicts a collapse in the population of filter-feeders, leading to a considerable drop in the epifaunal predators (despite the drop in *F* for the pot fishery), which in turn releases the benthic grazers, allowing the biomass of that group to grow (despite the increase in *F* for the dive fishery). Therefore, through foodweb interactions, two of the three harvested invertebrate groups respond counter to what would be expected from a simple consideration of the change in *F* of the fisheries targeting them. Another important difference between the models is in the detritus, where there is no concurrence between any of the models – ECOSIM predicts no change, BM2 a twofold drop and IGBEM a twofold increase. This appears to be attributable to the dynamics of the major detritus producers and consumers in each model. The collapse of the flatfish and epibenthic predators in BM2 allows the deposit-feeders in that model to increase fivefold, and this in turn depletes the standing stock of available detritus. In IGBEM, the major producers of detritus (the primary producer groups) all increase, leading to an increase in the amount of detritus. The biomass of deposit-feeders in IGBEM does increase a little, but not to the extent seen in BM2, because the epifaunal carnivores also increase and keep the deposit-feeders in check. Consequently, the detritus in IGBEM remains slightly higher than the *status quo* level. In ECOSIM, there is no change in the biomass of the major producers or consumers of detritus, so the biomass of detritus remains unchanged.

FISHING POLICY ANALYSIS BY ECOSIM, WITH A CHANGE IN NUTRIENTS

With an economically orientated objective function, the set of two policies (split policies) chosen under a fall in productivity appears to be reasonable (Table IX). The policy begins by following the path of the "economic" strategy selected when there is no change in nutrients. Once there is a change in productivity, the split policy changes from one resembling the "economic" strategy to the "ecological" one, as the policy optimization attempts to correct for the declines initiated

Table IX: Results of the policy analyses under changing environmental conditions. The *F*s are those found by the ECOSIM open-loop analysis and the summary statistics are for the ECOSIM output under these *F*s. The "overall average total catch" and "total value" indicate the cumulative totals over the entire run. The "ratio end/start values" are the ratios of the annual total catch, economic value and biomass at the beginning and end of the run

Parameter	Nutrients rise		Nutrients decline	
	Split economic	Split ecological	Split economic	Split ecological
		Estimated relative Fs		
Purse-seine	1.1–1.15	1.6–1.1	1.75–1.3	0.1–1.1
Scallop dredge	0.8–1.5	1–1.2	2–0.5	0.08–0.3
Haul-seine	0.8–1.1	0.6–1	0.5–1	0.02–0.02
Longline	1.2–1.3	0.6–1.1	2.5–0.75	0.03–0.06
Mesh nets	1.4–1.1	0.7–1.9	11.9–0.7	0.01–0.3
Dive	1.2–0.7	0.5–1.2	1.2–2.4	0.25–0.6
Pot	1.1–2.1	1.7–1.4	0.9–1.2	0.1–0.1
Aquaculture (omitted from the search)	1–1	1–1	1–1	1–1
		Overall average		
Total catch (tons km^{-2})	4 325	4 028	813	169
Total value (million AUD)	5.5	5.1	1.2	0.4
		Ratio end/start values		
Total catch	6.86	4.77	0.06	0.04
Total value	6.03	4.56	<0.01	<0.01
Total biomass	2.3	2.28	0.73	0.73

by the drop in productivity. For rising nutrient input the response is somewhat different. Depending on the basal food group (phytoplankton or detritus v. macrophyte), some sub-webs increase substantially while others collapse. As a consequence, the objective function surface seems to have become highly complex, and the best result that can be found is to stay fairly close to current *F*s both before and after the change in conditions.

When a split policy is implemented with an ecologically weighted objective function, results under both increasing and decreasing productivity again appear to be reasonable, though some of the details are surprising. When productivity rises over time, the solution parallels the constant "ecological" strategy until the increase in productivity takes effect. After this rise in productivity there is a general rise in *F*s. The *F*s for the longline, dive and pot fisheries reach the levels of those in the "economic" strategy. Under a fall in productivity, the solution once again begins by tracking the "ecological" strategy. Interestingly, even though the absolute *F* values continue to remain low after the conditions change (all but the dive fishery remaining closer to the "ecological" than the "economic" strategy), they do increase in relative terms (rising by between two- and tenfold). It appears that the increase in biomasses that occur under the low *F*s set in the first half of the policy allows for the later increase in the *F*s during the second half of the split-policy.

One clear result emerges from comparing the overall average total catch and value for each of the runs, as well as the ratios of the annual catch, value and biomass at the beginning and end of each run. The effects of the change in productivity all but overwhelm any changes attributable to the fishing strategies implemented. If productivity rises, then all these summary statistics rise too, regardless of the strategy. Similarly, if productivity falls then all the summary statistics fall whether an "economic" or "ecological" strategy is implemented. However, the effects of the policies are not completely subsumed by the effects attributable to changes in nutrients. The "economic" strategies continue to produce total catches and values for the entire period that are appreciably higher then those produced by the "ecological" strategies. The disparities in the values are much more striking for the case where there is a drop in productivity, with the "ecological" total catches only about one-quarter and the total values only about one-third of the "economic" ones.

"OPTIMAL" POLICIES IMPLEMENTED IN NUTRIENT MODELS, WITH A CHANGE IN NUTRIENTS

When the nutrient scenarios and matching split-policy *F*s identified in ECOSIM are applied in BM2 and

Table X: The relative change in end-point biomasses (end biomass under new policies and nutrient change/end biomass in "base case"), for each of the three models under the ecological and economically based strategies when there is a change in environmental conditions

Group	Nutrients rise						Nutrients decline					
	Split economic			Split ecological			Split economic			Split ecological		
	ECOSIM	BM2	IGBEM	ECOSIM	BM2	IGBEM	ECOSIM	BM2	IGBEM	ECOSIM	BM2	IGBEM
Phytoplankton	6	0.2	3	5	1.5	5.5	0.15	1	0.5	0.2	0.8	0.5
Small zooplankton	7	2	2.5	7	2	3	0.1	0.5	0.5	0.1	0.9	0.75
Large zooplankton	8	0.75	1.6	6	1.5	2	0.1	1.5	0.9	0.1	0.8	0.9
Deposit-feeders	4	2	2.5	4	2	2	0.5	0.5	0.75	0.5	0.75	0.75
Filter-feeders	8	1.3	2	8	1.5	2	0.13	1.1	0.75	0.13	0.9	0.9
Infaunal predators	4	1	3	8	1	3	0.2	1	0.75	0.3	1	0.9
Epifaunal predators	10	1.2	2	10	1.2	2	0.1	0.15	0.2	0.1	0.75	0.3
Benthic grazers	0.5	4	0.1	10	0.3	0.1	0.7	3	1.2	2	2	1.3
Microphytobenthos	8	4	0.6	10	100	1	0.1	0.75	2	0.1	1.2	1.1
Seagrass	0.1	0.1	0.3	0.1	0.01	0.2	7	1.4	1.1	10	0.8	1.2
Macroalgae	2	1.5	5	10	1.5	3	0.1	0.2	0.01	0.1	0.01	0.01
Clupeoids	6	1.2	1.2	8	0.5	1	0.1	1.5	0.8	0.1	1	1
Flatfish	4	0.75	0.8	2.5	1.5	0.6	0.1	1.3	1.2	0.1	2	2
Piscivores	3	0.8	1	5	2	0.9	0.1	1.5	0.75	0.1	2	1.5
Mullet	1.5	2	1.5	4	1.1	1.2	5	1	1	10	4	1.5
Sharks	9	–	–	9	–	–	0.05	–	–	1.5	–	–
Detritus	2.5	2	2	3	2	2	0.5	0.9	1.5	0.5	0.13	0.75

IGBEM, the biomass trajectories of the three models largely concur (Table X), at least qualitatively. The ECOSIM biomass results, however, tend to be more extreme. This is true for both the ecologically and economically driven *F*s for both of the nutrient change scenarios. However, there are some differences in the biomasses predicted for a few of the groups that are treated differently in the various models. The dynamics of the fish groups in the nutrient models do not always match those in ECOSIM. Once again, this appears to be on account of the static representation of birds, sharks and marine mammals in IGBEM and BM2, as well as the constant stock-recruitment assumptions used in these models. This combination of formulations buffers fish groups, allowing for faster recoveries from economic exploitation, but also prevents the large increases in biomass when nutrient levels rise to the extent ECOSIM (with its feedback between stock size and recruitment) predicts. The other major difference between the model predictions is in the long-term dynamics of abalone biomass. These differences apparently arise from differences in the dynamics of the macrophyte groups. ECOSIM consistently predicts a much smaller change in these groups with changes in nutrients, which can be traced to a lack of a shading effect by phytoplankton and other suspended material in the ECOSIM model. It is conceivable that a mediation or forcing function could be built into ECOSIM to mimic this, but this was not attempted.

CONCLUSIONS FROM FISHING POLICY ANALYSES

Analysis of the outcome of the fisheries strategies in all three models indicates general qualitative agreement between the models, though specific responses can vary widely. In particular, the nutrient models are more sensitive to changes in *F*; and the default (no nutrient limitation) setting of ECOSIM is more sensitive to changes in nutrients, though this can largely be eliminated by using the nutrient-limitation option in the more recent version of ECOSIM (E. Fulton, unpublished data). The analysis also highlights the fact that all of these trophic models predict unexpected changes in species not directly impacted by fishing. Such effects cannot, of course, be predicted from single-species models.

DISCUSSION

It is now widely accepted that human activity has had a significant impact on biogeochemical cycles at local, regional and global scales (Ver *et al.* 1999). One response to this realization has been the call for an ecosystem perspective in assessing and managing human impacts such as fishing and nutrient discharge. Developing the tools to meet this challenge has proved demanding for scientists. Until recently, limita-

Table XI: Summary of the major conclusions and supporting results from the three ecosystem models considered here. The comment "no conflict" in the bottom panel of the Table indicates that the model agrees with at least one other model for all groups

Summary of conclusions	Major supporting evidence		
	ECOSIM	BM2	IGBEM
Best multispecies example from each model			
Multispecies effects – Changes in biomass and productivity that single species models would not identify as they are due to inter-species interactions	The direct (bycatch) effect of fishing on top predators is compounded by indirect (prey removal) effects	Benthic grazers rise despite an increase in fishing pressure (economic strategy)	An increase in Chl *a* as a result of increased fishing pressure on clupeoids
Ratio nutrient/fishing pressure induced change in biomass for each model			
Sensitivity to nutrients rather than fishing – Changes in nutrients have a much larger, and more widespread, impact than changes in fishing pressure	Approximately 1.5–60	1.5–>1 000	Approximately 1.5–20
Indicator group sets in each model – the pairs of groups where the state of one of the pair (e.g. benthic herbivores) can be characterized by the state of the other member of the pair (e.g. seagrass)			
Choice of indicator groups – The dynamics of groups such as seagrass, sharks and Chl *a* (as a proxy for phytoplankton) consistently characterize the behaviour of many other groups and may summarize wider system responses and changes	Planktonic – Chl *a* Benthic herbivores – seagrass Herbivorous fish – seagrass + sharks Other fish – sharks Harvested groups – sharks Other benthos – Chl *a* Top predators – sharks	Planktonic – Chl *a* Benthic herbivores – seagrass Herbivorous fish – seagrass + piscivores Other fish – piscivores Harvested groups – piscivores Other benthos – Chl *a* + detritus	Planktonic – Chl *a* Benthic herbivores – seagrass Herbivorous fish – seagrass + piscivores Other fish – piscivores Other benthos – Chl *a*
Groups for which the models do not all agree in each scenario			
Robustness to model formulation – Many results showed qualitative agreement across models, but there were a few important differences. These differences usually occurred when one or the other of the nutrient models produced results that differed from results that held across the other two models	Economic *F*: detritus unchanged Ecological *F*: zooplankton unchanged, piscivores and seagrass decline Split economic *F* and N rises: no conflict Split economic *F* and N declines: Mullet rise only in this model Split ecological *F* and N rises: benthic grazers rise Split ecological *F* and N declines: microphytobenthos, clupeiods, flat fish and piscivores decline and seagrass rises	Economic *F*: detritus declines Ecological *F*: small zooplankton decline and large zooplankton rise Split economic *F* and N rises: phytoplankton and large zooplankton decline Split economic *F* and N declines: large zooplankton, clupeoids and piscivores rise Split ecological *F* and N rises: clupeoids decline Split ecological *F* and N declines: no conflict	Economic *F*: detritus rises Ecological *F*: small zooplankton rise and large zooplankton decline Split economic *F* and N rises: no conflict Split economic *F* and N drops: detritus rises and benthic grazers decline Split ecological *F* and N declines: flatfish and piscivores decline Split ecological *F* and N declines: no conflict

tions in knowledge and computing power have constrained attempts to model marine ecosystems. Despite earlier attempts (e.g. Andersen and Ursin 1977) and derived methods (like MSVPA; Sparre 1991), comprehensive marine ecosystem models were not widely available until the past decade, and their utility as predictive tools is still questioned by many. This paper gives some insight into the "robustness" of ecosystem models, by comparing different models developed for the same marine ecosystem, and examining some of their policy implications. Four general conclusions that emerge from these analyses are listed below and summarized in Table XI.

Multispecies effects

One possible value of ecosystem models is in identifying impacts from human activities that other methods would miss. For instance, single-species models cannot predict the potential fall in epifaunal predators and rise in benthic grazers that BM2 predicts would result from the "economic" strategy. This effect arises from a combination of direct and indirect multispecies interactions, and is in direct contradiction to what single-species models would predict, given the drop in the direct harvesting of epifaunal predators and the rise in the targeting of benthic grazers under the suggested policy.

However, model predictions are only of use if they can be shown to be robust to model formulation and parameter uncertainties. If predictions are used to guide management, as they are in management strategy evaluation, then tests should be undertaken to determine the robustness of management options to the predictions and uncertainties associated with them. In cases where there is strong disagreement between models (e.g. the macrophyte barren cycle discussed here), further investigation of the dynamics (both in the model and in reality) would be needed before any confidence could be put in predictions involving those dynamics. In the particular example given above (the impacts of the "economic" strategy in BM2), the questionable dynamic (the macrophyte barren cycle) does not affect the outcome (E. Fulton, unpublished data), but this may not always be the case.

Sensitivity to nutrients rather than fishing

Many finfish species in Port Phillip Bay recruit, at least in part, from external reproductive stocks (Gunthorpe *et al.* 1997). This means that at least some of the effects of fishing within the bay may be limited, as long as the external stocks are healthy. Because a number of the notable differences between the outputs of the nutrient models and those from ECOSIM are attributable to the constant recruitment term in the nutrient models, this suggests that it may play an important role in compensating for changes in *F*. Under intensive fishing, shifts in local population sizes of the target species, their competitors, predators and prey will still occur (e.g. the change in the biomasses of flatfish, epifaunal carnivores, sharks and deposit-feeders in all models under the "economic" strategy). However, in general, impacts of fishing are likely to be greater on species that recruit locally, such as snapper (Coutin 1997, Gunthorpe *et al.* 1997), than on species that recruit principally from outside the Bay, such as King George whiting (Gunthorpe *et al.* 1997, Smith and MacDonald 1997).

One conclusion about impacts in Port Phillip Bay appears to be robust to model uncertainty. Given the enclosed nature of the bay and the stock structure of most of the fished species (few entirely "local" stocks), the bay is more likely to respond strongly to the effects of eutrophication than to those of fishing. For all models, the ecosystem was more sensitive to a change in nutrients than to a change in *F*. The bay's geography (large and shallow, with restricted oceanic access) is such that, if nutrient inputs change significantly, the entire system can be heavily impacted. This applies especially if it reaches the level where nitrogen disposal, by flushing and denitrification, is overwhelmed (Murray and Parslow 1997). This is also true for other models of Port Phillip Bay (Murray and Parslow 1999). In addition, these impacts have the potential to be quite long-lived (Fulton 2001). This is on account of positive feedbacks involving denitrification (Murray and Parslow 1997, 1999), the immense nitrogen reservoir in the bay's sediments; and the apparent dominance of a detritus-based, rather than a more traditionally recognized primary-production-based, foodweb (Harris *et al.* 1996, Fulton 2001). This phenomenon, whereby anthropogenically induced changes in nutrient status dominate the effects of fishing, is not unique to Port Phillip Bay. Worldwide, many semi-enclosed bays have seen nutrient impacts overwhelm or modify the impacts of fishing (Caddy 2000). As that author points out, these nutrient impacts on marine catchment basins make integrated management essential, because fisheries management alone cannot address the problems.

Choice of indicator groups

Across the range of fishing and nutrient pressures imposed upon the ECOSIM model of Port Phillip Bay, only three qualitatively different system states arise, and these system states can be characterized by the status of a few key groups (Fulton and Smith 2002). Given the increasing management interest in identification of indicator species, it is notable that a small group of species is sufficient to characterize these three system states broadly. Using sharks as an indicator group, the three states are characterized as follows:

(i) The biomass of sharks declining to negligible levels. This characterizes a fishing policy heavily influenced by economic objectives or a drop in the system's productivity (nutrient input);
(ii) Sharks persisting at about the current levels of biomass. This characterizes a system free from recent extensive shifts in productivity. It also

arises from a fishing policy that attempts to find a compromise between ecological and economic objectives, although it is not clear that a deliberate strategy of this sort is the cause of the current state of the resources in Port Phillip Bay.

(iii) The biomass of sharks increasing. This reflects a fishing policy guided primarily, or entirely, by ecological objectives or a general rise in the system's productivity (though not to the point where the system is highly eutrophied, because ECOSIM is currently unable to capture the indirect effects of changes in the nutrient- and denitrification-based system dynamics).

The persistence of the three system states across a range of refuge parameter settings, management objectives and environmental scenarios, in conjunction with the lack of response to fishing by many ancillary or lower trophic groups, does seem to result from the nature of the bay as discussed above. It is perhaps not surprising that a bay with as many in-built buffers as Port Phillip Bay has only a few "managed system" states where it is stable, requiring quite large perturbations to push it from one state to another.

Despite the generalization noted above, the sharks alone do not summarize the entire state of the system under all policies and environmental changes. However, a set of indicators comprising chlorophyll *a*, seagrass and sharks captures most of the effects. Changes in these indicators do seem to provide a warning that larger changes in the state of the system may have begun. Chlorophyll *a* is a much stronger indicator of the effects of changes in system productivity than any of the other groups and should be included in a set of indicators for that purpose. In contrast, the biomass of larger fish in ECOSIM, particularly sharks, are good indicators of fishery-based impacts on the system, though they also respond to changes in productivity. Seagrass is included in the list because it is particularly sensitive to changes in nutrient conditions, but it is also impacted by fishing (either through habitat destruction or change in grazing pressure). Therefore, between the three, they give a good indication of the force having the largest effect on the system and what overall state the system is in. It should be noted that this conclusion is limited to a "perfect information" case for a modelled system. When monitoring real systems in the field, a larger set of indicator groups may be more appropriate because they not only indicate change, but may also suggest some explanation of the cause. However, it is encouraging that groups frequently referred to as sensitive to change in nature are those that stand out as indicator species within the models. Chlorophyll *a* (as an easily measurable index of phytoplankton) is already used in monitoring for the effects of eutrophication (Harris *et al.* 1996) and is increasingly the subject of correlative studies with fisheries production (Lima and Castello 1995, Parsons and Chen 1994); whereas the loss of large shark species and the incursions of dogfish *Squalus acanthias*, mark regime shifts in systems such as the Gulf of Alaska (Wright and Hulbert 2000) and the Grand Banks (Fogarty and Murawski 1998); and a loss of seagrass has been noted in many studies of impacted estuaries (Nienhuis 1983, Walker and McComb 1992). Identifying species, or groups, which are persistently reported as sensitive to changes in ambient environmental conditions and anthropogenic activities may be a first step to finding a set of useful indicators.

Robustness to model formulation

In spite of the qualitative agreement between the models at the broadest level, and the consistent form of the policy solutions found by ECOSIM, the differences in detail within and between the models also serve as a warning. For example, some of the policy conclusions from ECOSIM are sensitive to the refuge parameters used. This underlines the requirement for analysis of parameter sensitivity regardless of the complexity of ecosystem models. Because completely inclusive, systematic sensitivity analyses are not yet possible for such models, a good understanding of likely key parameters is essential (Fulton 2001).

The results from this study also serve to underline the broader sensitivity to model formulation and approach. Formulation of multiple models, or at least multiple formulations of crucial mechanisms and processes, can identify groups that are sensitive to key assumptions. Substantial differences in some key groups have been demonstrated in this study in all three models examined. For example, with the "economic" strategy and no change in nutrients, the interaction of the impact of fishing and the foodweb dynamics in the three models leads to three different patterns of change in the detritus. Given the long-term storage of nutrients in the form of detritus in Port Phillip Bay, such a range of outcomes is a crucial result. While different models may agree qualitatively at the overall system level, management objectives are often concerned with particular groups and species, and conclusions about impacts on these can vary widely between model formulations (e.g. abalone).

However, the assumption that conclusions that match across models are robust should be regarded with caution. Such an assumption is sound with regard to the assumptions that differ between models. Unfortunately, it cannot guard against the situation where the models share similarities in ecosystem structure or representation, and do not allow for processes that result in fundamental change to that structure. This is potentially one of the greatest problems facing "ecosystem" models. Where should the line be drawn, beyond which it is declared that model uncertainties and lack of knowledge of processes are too great to dare to use process-based models to extrapolate system state at the level of the entire system? This is a question that remains to be answered. One solution may be the use of monitoring programmes. For instance, data from the literature show that the biogeochemical models employed here do a reasonable job of capturing the effects of mild to moderate eutrophication, but they may well fail under conditions of extreme eutrophication (Fulton *et al.* 2004a).

CONCLUSIONS

Three further general points arising from this study need be made.

First, care needs to be taken in specifying objective functions for policy analysis. Clearly and not surprisingly, emphasis on economic objectives alone can result in systems that are very different from pristine. Perhaps more importantly, even where ecological criteria are included in the objective function, emphasis on particular groups can also result in systems that are far from pristine. The results in this paper suggest that focusing attention on the conservation of higher trophic groups does not produce a balanced system. A system populated only by those sub-webs featuring marine mammals is no more inherently balanced and representative than a system where they do not feature at all. Balanced objectives are not only required across sectors of human interest (e.g. economic and ecological), but also across the trophic groups that make up the systems being impacted.

Second, this study draws attention to an ongoing need to identify reliable means of synthesizing the often complex and voluminous information produced by ecosystem models. A wide range of output indices is used in this study, and none alone captures the key differences across policy options and forcing scenarios. Nevertheless, a small set of key indices that can be intuitively and quickly grasped will be needed to communicate results to policy- and decision-makers.

Third, whereas ecosystem models are emerging as key tools for investigating options for managing marine ecosystems, there is still much to learn about them. In this context, comparisons of predictions across alternative model formulations for the same system can be informative. The results from this study suggest that, although some conclusions may be robust to model uncertainty, others clearly are not. Whereas the use of ecosystem models for investigating management of marine systems has increased substantially in the last few years, there are as yet very few instances of multiple implementations for the same system. This study suggests that this comparative approach may lead to better understanding of key processes and assumptions in the use of these tools for ecosystem management.

ACKNOWLEDGEMENTS

We are indebted to John Parslow for numerous discussions about Port Phillip Bay and its dynamics, and useful suggestions about alternative model specifications. We also acknowledge the helpful suggestions made on earlier drafts of this paper by John Parslow, Xi He and two anonymous reviewers. The CSIRO Division of Marine Research provided financial support for this work.

LITERATURE CITED

ANDERSEN, K. P. and E. URSIN 1977 — A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddr Danm. Fisk. og Havunders.* **7**: 319–435.

BARETTA, J. W., BARETTA-BEKKER, J. G. and P. RUARDIJ 1996 — From EMS to ERSEM, towards generic coastal ecosystem models. *Aquabiol.* **104**: 197–209 (translated from Japanese).

BARETTA, J. W., RUARDIJ, P., VESTED, H. J. and J. G. BARETTA-BEKKER 1994 — Eutrophication modelling of the North Sea: two different approaches. *Ecol. Model.* **75/76**: 471–483.

BARETTA-BEKKER, J. G. and J. W. BARETTA (Eds) 1997 — Special Issue: European Regional Seas Ecosystem Model II. *J. Sea Res.* **38**: 169–436.

BEATTIE, G., REDDEN, A. and R. ROYLE 1996 — *Micro-zooplankton Grazing on Phytoplankton in Port Phillip Bay.* Technical Report **31**. Port Phillip Bay Environmental Study. CSIRO Canberra, Australia: 39 pp.

BRIGGS, K. T., TYLER, W. B., LEWIS, D. B. and D. R. CARLSON 1987 — Bird communities at sea off California: 1975–1983. *Stud. Avian Biol.* **11**. 74 pp.

CADDY, J. F. 2000 — Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. *ICES J. mar. Sci.* **57**: 628–640.

CHRISTENSEN, V., WALTERS, C. J. and D. PAULY 2000 — *ECOPATH with ECOSIM: a User's Guide*, October 2000 edition. Fisheries Centre, University of British Columbia, Vancouver, Canada and International Centre for Living Aquatic Resources Management, Penang, Malaysia: 130 pp.

COUTIN, P. (Ed.) 1997 — *Snapper – 1996*. Bay & Inlet Fisheries and Stock Assessment Group. Fisheries Victoria Assessment Report **12**. Fisheries Victoria; East Melbourne: 1–25.

DeANGELIS, D., GROSS, L. J., HUSTON, M. A., WOLFF, W. F., FLEMING, D. M., COMISKEY, E. J. and S. M. SYLVESTER 1998 — Landscape modeling for everglades ecosystem restoration. *Ecosystems* **1**: 64–75.

DOLPHIN RESEARCH INSTITUTE 2000 — Dolphin education project question and answers. Dolphin Research Institute, Frankston, Victoria, Australia: 10 pp.

FOGARTY, M. J. and S. A. MURAWSKI 1998 — Large-scale disturbance and the structure of marine system-fishery impacts on the Georges Bank. *Ecol. Appl.* **8**(1 Suppl S): S6–S22.

FRANSZ, H. G., MOMMAERTS, J. P. and G. RADACH 1991 — Ecological modelling of the North Sea. *Neth. J. Sea Res.* **28**: 67–140.

FULTON, E. A. 2001 — The effects of model structure and complexity on the behaviour and performance of marine ecosystem models. Ph.D. thesis, University of Tasmania, Hobart, Australia: 427 pp.

FULTON, E. A., PARSLOW, J. S., SMITH, A. D. M. and C. R. JOHNSON 2004a — Biogeochemical marine ecosystem models. 2. The effect of physiological detail on model performance. *Ecol. Model.* **173**: 371–406.

FULTON, E. A. and A. D. M. SMITH 2002 — ECOSIM case study: Port Phillip Bay, Australia. In *The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries*. Fisheries Centre Research Reports **10**(2): 83–93.

FULTON, E. A., SMITH, A. D. M. and C. R. JOHNSON 2003 — Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.* **253**: 1–16.

FULTON, E. A., SMITH, A. D. M. and C. R. JOHNSON 2004b — Biogeochemical marine ecosystem models. 1. A model of marine bay ecosystems. *Ecol. Model.* **174**: 267–307.

GUNTHORPE, L., HAMER, P. and S. WALKER 1997 — Bays and inlets scalefish fisheries review. 1. Life cycles and habitat requirements of selected Victorian fish species, including an assessment of the main habitat threatening processes and recommendations for habitat maintenance, rehabilitation and enhancement. Marine and Freshwater Resources Institute, Queenscliff, Victoria, Australia: 87 pp.

HAGEN, N. T. 1995 — Recurrent destructive grazing of successionally immature kelp forests by green sea urchins in Vestfjorden, northern Norway. *Mar. Ecol. Prog. Ser.* **123**: 95–106.

HALL, D. N. (Ed.) 1992 — Port Phillip Bay environmental study: status review. *Tech. Rep*. **9**. Port Phillip Bay Environmental Study.Canberra; CSIRO: 154 pp.

HARRIS, G., BATLEY, G., FOX, D., HALL, D., JERNAKOFF, P., MOLLOY, R., MURRAY, A., NEWELL, B., PARSLOW, J., SKYRING, G. and S. WALKER 1996 — Port Phillip Bay environmental study final report. Canberra; CSIRO: 239 pp.

HASSELL, M. P. and R. M. MAY 1973 — Stability in insect host-parasite models. *J. Anim. Ecol.* **42**: 693–736.

HOLLOWAY, M. and G. JENKINS 1993 — The role of zooplankton in nitrogen and carbon cycling in Port Phillip Bay. *Tech. Rep*. **11**. Port Phillip Bay Environmental Study.Canberra; CSIRO: 36 pp.

HOLMES, E. E., LEWIS, M. A., BANKS, J. E. and R. R. VEIT 1994 — Partial differential equations in ecology – spatial interactions and population dynamics. *Ecology* **75**: 17–29.

HOUDE, E. D. and E. S. RUTHERFORD 1993 — Recent trends in estuarine fisheries – predictions of fish production and yield. *Estuaries* **16**: 161–176.

KAILOLA, P. J., WILLIAMS, M. J., STEWART, P. C., REICHELT, R. E., McNEE, A. and C. GRIEVE 1993 — *Australian Fisheries Resources*. Canberra; Bureau of Resource Sciences and the Fisheries Research and Development Corporation: 422 pp.

LEE, P. G. 1994 — Nutrition of cephalopods: fueling the system. *Mar. Behav. Physiol.* **25**: 35–51.

LEINAAS, H. P. and H. CHRISTIE 1996 — Effects of removing sea urchins (*Strongylocentrotus droebachiensis*) – stability of the barrens state and succession of kelp forest recovery in the East Atlantic. *Oecologia* **105**: 524–536.

LIMA, I. D. and J P CASTELLO 1995 — Distribution and abundance of South-West Atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic processes in the southern Brazilian Shelf. *Fish. Oceanogr.* **4**: 1–16.

MAFRI 1996 — Catch and effort information bulletin 1995. Conservation and Natural Resources, Victorian Fisheries Research Institute, Queenscliff, Victoria, Australia: 4–27.

MURRAY, A. [G.] and J. [S.] PARSLOW 1997 — Port Phillip Bay integrated model: final report. *Tech. Rep*. **44**. Port Phillip Bay Environmental Study.Canberra; CSIRO: 201 pp.

MURRAY, A. G. and J. S. PARSLOW 1999 — Modelling of nutrient impacts in Port Phillip Bay – a semi-enclosed marine Australian ecosystem. *Mar. Freshwat. Res.* **50**: 597–611.

NICHOLSON, G. J., LONGMORE, A. R. and R. A. COWDELL 1996 — Nutrient status of the sediments of Port Phillip Bay. *Tech. Rep*. **26**. Port Phillip Bay Environmental Study. Canberra; CSIRO: 36 pp.

NIELSEN, E. and K. RICHARDSON 1996 — Can changes in the fisheries yield in the Kattegat (1950–1992) be linked to changes in primary production. *ICES J. mar. Sci.* **53**: 988–994.

NIENHUIS, P. H. 1983 — Temporal and spatial patterns of eelgrass (*Zostera marina* L.) in a former estuary of the Netherlands, dominated by human activities. *Mar. Technol. Soc. J.* **17**: 69–77.

OFFICER, R. A. and G. D. PARRY 1996 — Food webs of demersal fish in Port Phillip Bay. *Tech. Rep*. **36**. Port Phillip Bay Environmental Study. Canberra; CSIRO: 27 pp.

PARRY, G. D., HOBDAY, D. K., CURRIE, D. R., OFFICER, R. A. and A. S. GASON 1995 — The distribution, abundance and diets of demersal fish in Port Phillip Bay. *Tech. Rep*. **21**. Port Phillip Bay Environmental Study. Canberra; CSIRO: 74 pp.

PARSONS, T. R. and Y. L. L. CHEN 1994 — Estimates of trophic efficiency, based on the size distribution of phytoplankton and fish in different environments. *Zool. Stud.* **33**: 296–301.

PICES 1998 — Consumption of marine resources by marine birds and mammals in the PICES region. 1998 Report of Working Group 11. Sidney, Canada; PICES: 67–72.

POORE, G. C. B. 1992 — Soft-bottom macrobenthos of Port Phillip Bay: a literature review. *Tech. Rep*. **2**. Port Phillip Bay Environmental Study. Canberra; CSIRO: 26 pp.

SAINSBURY, K., PUNT, A. E. and A. D. M. SMITH 2000 — Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. mar. Sci.* **57**: 731–741.

SCHMID, T. H., MURRU, F. L. and F. McDONALD 1990 — Feeding habits and growth rates of bull (*Carcharhinus leucas* (Valenciennes)), sandbar (*Carcharhinus plumbeus* (Nardo)), sandtiger (*Eugomphodus taurus* (Rafinesque)) and nurse (*Ginglymostoma cirratum* (Bonnaterre)) sharks maintained in captivity. *J. Aquaricult. aquat. Sci*. **5**(4): 100–105.

SEKINE, M., NAKANISHI, H., UKITA, M. and S. MURAKAMI 1991 — A shallow-sea ecological model using an object-oriented programming language. *Ecol. Model.* **57**: 221–236.

SILVERTSEN, K. 1997 — Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. *Can. J. Fish. aquat. Sci.* **54**: 2872–2887.

SMITH, D. C. and C. M. MacDONALD (Eds) 1997 — *King*

George whiting – 1996. Compiled by the Bay & Inlet Fisheries and Stock Assessment Group. Fisheries Victoria Assessment Report. **15**. Fisheries Victoria: East Melbourne: 1–10.

SPARRE, P. 1991 — An introduction to multispecies virtual population analysis. *ICES mar. Sci. Symp.* **193**: 12–21.

VER, L. M. B., MACKENZIE, F. T. and A. LERMAN 1999 — Biogeochemical responses of the carbon cycle to natural and human perturbations: past, present, and future. *Am. J. Sci*. **299**: 762–801.

WALKER, D. I. and A. J. McCOMB 1992 — Seagrass degradation in Australian coastal waters. *Mar. Pollut. Bull*. **25**: 191–195.

WALTERS, C., CHRISTENSEN, V. and D. PAULY 1997 — Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Revs Fish Biol. Fish*. **7**: 139–172.

WALTERS, C., CHRISTENSEN, V. and D. PAULY 2002 — Searching for optimum fishing strategies for fishery development, recovery and sustainability. In *The Use of Ecosystem Models to Investigate Multispecies Management Strategies for Capture Fisheries*. *Fish. Cent. Res. Rep*. **10**: 11–15.

WALTERS, C., PAULY, D. and V. CHRISTENSEN 1999 — ECOSPACE: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems with emphasis on the impacts of marine protected areas. *Ecosystems* **2**: 539–554.

WBM OCEANICS AUSTRALIA 1997 — Bays and inlets scalefish fisheries review: review of scalefish fishing practices in Victoria's bays and inlets. WBM Oceanics Australia, Final Report. State of Victoria, Fisheries Co-management Council: 106 pp.

WILSON, R. S., COHEN, B. F. and G. C. B. POORE 1993 — The role of suspension-feeding and deposit-feeding benthic macroinvertebrates in nutrient cycling in Port Phillip Bay. *Tech. Rep*. **10**. Port Phillip Bay Environmental Study. Canberra; CSIRO: 39 pp.

WRIGHT, B. A. and L. HULBERT 2000 — Shark abundance increases in the Gulf of Alaska. *PICES Press*. **8**: 16–22.