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Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model

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Abstract

An investigation into the potential carrying capacity of suspended bivalve culture was undertaken using a linear food web model. The investigation involved configuring the model for the present state using all available information, and then perturbing the food web by introducing the bivalve culture until pre-determined carrying capacity limits were achieved. These carrying capacity trigger levels were defined by the production carrying capacity and the ecological carrying capacity. The production carrying capacity represents the theoretical maximum bivalve culture that could be supported in the embayment. This is defined as when the ecosystem collapses down to a nutrient–phytoplankton–culture–detritus dominated system. This level of culture was found to be a yield of bivalve culture of 310 t km^{-2} $year^{-1}$ averaged across the bays in question. By contrast, the ecological carrying capacity was defined as the level of culture that could be introduced without significantly changing the major energy fluxes or structure of the food web. This limit was found to correspond to a bivalve culture yield of 65 t km^{-2} $year^{-1}$ averaged across the bays. Introducing the large-scale bivalve culture resulted in a decrease in the mean trophic level of the ecosystem, an increase in the total yield, throughput and efficiency, and the bivalves replaced zooplankton as the major grazers in the modelled system.
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1. Introduction

In many cases, the ability to predict carrying capacity is a pre-requisite to establishing or expanding large-scale bivalve culturing operations. For example,

potential investors and resource managers wish to know the development potential and other stake-holders are often interested in the effects of the activities. This demand has lead to an increasing number of investigations of bivalve carrying capacity studies over the last three decades. Furthermore, over the last two decades, the widespread introduction of affordable computers has underpinned the development of complex numerical NPZ (nutrient–phyto-plankton–zooplankton) models that have been used to

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attempt to predict carrying capacity of coastal regions (e.g. Dame and Prins, 1997; Smaal et al., 1997; Bacher et al., 1998; Duarte et al., 2003). However, whilst these models have made significant contributions to our understanding of particularly primary production processes in growing regions, and interactions between the culture and these ecosystems processes, there are still considerable shortfalls in the technology (Herman, 1993). These shortfalls are a result of both the lack of accuracy in estimating the values of the large number of parameters required, but also in the numerical schemes themselves that are generally an eclectic mix of full discrete mechanistic relationships and broad parameterisation of other processes. A further shortfall of these NPZ models is their inability to encompass higher trophic levels in the ecosystem. This means that these models are making implicit assumptions about the role of these higher trophic levels in exerting top-down control over the lower trophic levels. In other words these models cannot account for any possible trophic cascades that may occur.

This latter assumption is reasonable in some cases, the most relevant of which here is when the bivalve culture is close to the theoretical production carrying capacity. As identified by Gibbs (2004), the ultimate production carrying capacity for suspended culture occurs when the bivalve culture replaces the ecological role of zooplankton (the culture may be thought of as tethered zooplankton, J. Steele, personal communication) and in this case, the ecosystem essentially collapses down to a nutrient–phytoplankton–culture–detritus system (Gibbs, 2004). Since zooplankton are now not abundant, the higher trophic levels that are underpinned by zooplankton are also not present. Whilst it is recognized that the system cannot ever practically achieve a state without zooplankton, this serves as the theoretical upper bound for the culture. Hence, modelling the system without these higher trophic levels is a reasonable assumption if the culture dominates the energy fluxes in the food web. However, in many cases anywhere near this theoretical maximum level of culture may be unacceptable to other stakeholders in the marine environment and a more appropriate level of development may be around the ecological carrying capacity; defined here as the level of culture that can be introduced without significantly altering energy fluxes

in the food web, and correspondingly trophic spectra. If this is the desired development target then we really need to consider the entire food web in our analyses. Note that the carrying capacity definitions used here are slightly different than the range of definitions offered previously. For example Carver and Mallet (1990) define carrying capacity as 'the stock density at which production levels are maximised without negatively affecting growth rates'. This definition is generally more useful from an economics or farm management perspective, rather than the resource allocation application pursued here. The term ecological carrying capacity, as originally proposed by Odum (1983), has also often been used more to describe what we define here as the production carrying capacity.

Food web modelling represents an alternative methodology to fully discrete NPZ type models. However, although these models do encompass the entire ecosystem, they have shortfalls in that they generally fail to have the same level of detail of spatial and temporal dynamics that NPZ models typically feature. However, if we follow the philosophy that models are best used in targeted, process-type investigations rather than aspiring to operational type forecasting tools, then food web models can be a useful tool in these types of investigations. Following this approach, here we apply a food web in a very focused manner in order to investigate the production carrying capacity and ecological carrying capacity limits for bivalve shellfish activities in New Zealand. The key to this application is that we are not attempting to replicate or predict specifically how the food web will respond to the introduction of various levels of culture, as this will be impossible to achieve in a defensible manner. By contrast, we predefine boundary ecological states that represent the carrying capacity limits and attempt to determine how much culture can be introduced to achieve these boundary limits.

The area under investigation is the Tasman/Golden Bay system, at the top of the South Island of New Zealand. These bays are semi-enclosed, relatively shallow water embayments of around 4500 km^2 total surface area (Fig. 1). Whilst majority of Golden Bay is shallower than 30 m, water depths in Tasman Bay exceed 60 m in places although the majority of the bay is considerably shallower. Both bays are charac-
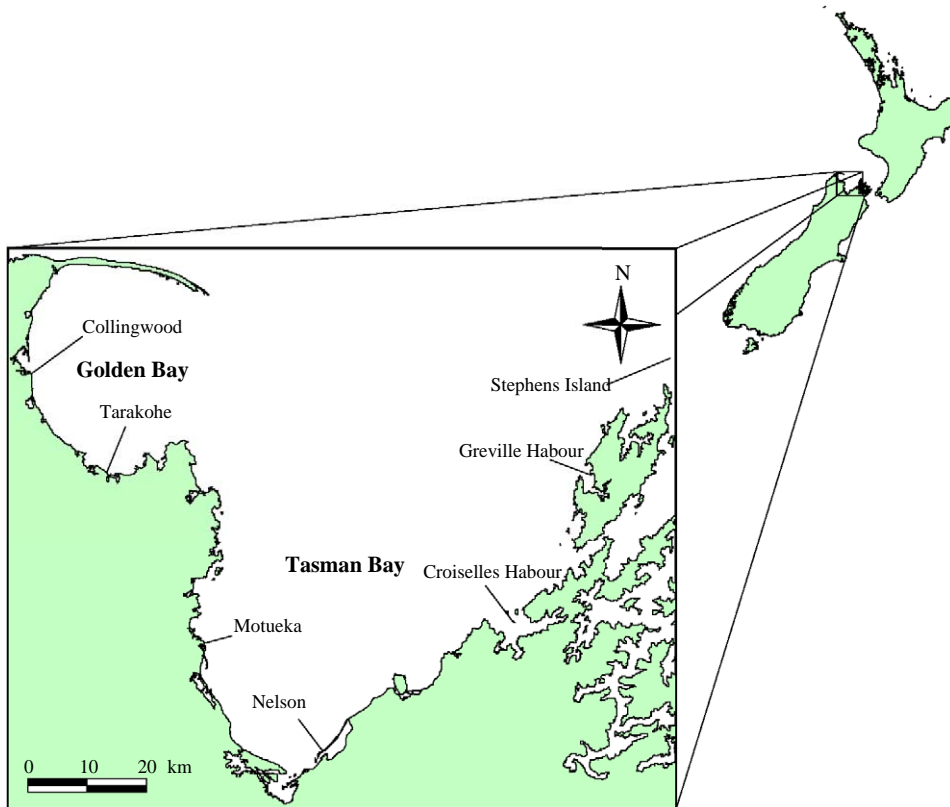
Fig. 1. Map showing Golden and Tasman Bays, northern end of the South Island of New Zealand.

terized by low-gradient bathymetric contours following the coastline and the seabed is relatively homogeneous, consisting mostly of silt/mud, with a patchy distribution of shell fragments. Sediment is mainly introduced through river discharge and the fine-grained nature of the bottom sediment reflects the relatively low wave and current activity in the two bays (Tuckey et al., submitted for publication). Areas of rocky reef habitat featuring macro-algal beds are extremely limited by comparison with the vast soft-sediment habitat in the study region.

Tasman and Golden Bays support important inshore finfish fisheries and a total of around 200 fish species are harvested for commercial, recreational and customary use in the two bays. During the period of 1989/90 to 2001/02 fishing year, average annual catch of these fishes totalled 6000 t (data provided by NZ Ministry of Fisheries). Among these, barracuda were the most caught species, with an average annual catch over 1200 t, which accounted for over 20% of

the total catch. Red cod (*Pseudophycis bachus*), spiny dogfish (*Squalus acanthias*), and mackerel (*Trachurus declivis*), flatfish and kahawai (*Arripis trutta*) are amongst the other landed species, with annual average landings in the range of 300–500 t. Although less than 200 t of snapper are caught annually, snapper are a high-value species (Paul, 2000).

Scallops (*Pecten novaezelandiae*) harvested from the fishery in the Tasman/Golden Bays system have been a New Zealand culinary icon for over four decades. The fishery started in Tasman Bay in 1959 and in Golden Bay in 1967 and catches rose rapidly to peak at approximately 8000 t in 1975. The fishery then crashed to a low level with closed seasons being imposed in 1981 and 1982 (Bradford-Grieve et al., 1994). The dramatic reductions in yields during late 1970s lead to the development an enhanced and rotational fishery. The enhancement programme aims to minimise recruitment variability, and the rotational harvesting allows sub-legal sized animals to remain

unharvested in designated areas. Though effort has been made to carefully manage the fishery, annual catches have fluctuated between 1.3–188.3 t, with an average of 42.1 t over the period 1990–2002 (data provided by NZ Ministry of Fisheries). Previous research has shown that this variability may partly be due to variation in the scallop growth, which is likely to be affected by the quantity and quality of suspended particulate material, especially phytoplankton (Gillespie, 1997). A key initiative in this management restructuring was to form a management company whose stakeholders consist of all the fishers in the fishery. Hence the management company has considerable autonomy over the management of the fishery although management plans must be signed off from the New Zealand Ministry of Fisheries. This approach considerably reduced the effort to levels more appropriate to the stock size and has been hailed as a model way to manage shellfish fisheries.

Tasman and Golden Bay also support other shellfish resources in addition to scallops and these include, cockles (*Austrovensus stutchburyi*), oysters (*Tiostrea chilensis*) and green mussels (*Perna canaliculus*). Total landing of these three species averaged 500 t annually over the last 10 years. Among these, cockles made up 58%, whilst oyster and green mussels constituted 12% and 3%, respectively (data provided by NZ Ministry of Fisheries).

Over the last three decades the Greenshell™ mussel aquaculture industry has grown considerably and up to 60 000 t have typically been harvested annually over the last few years throughout New Zealand. The mussel aquaculture industry developed first in the nearby Marlborough Sounds although has now expanded to a number of other growing areas around New Zealand including the Firth of Thames in the Hauraki Gulf and Stewart Island, south of the South Island. During the 1990s, the mussel industry began to seek new growing areas in the Tasman/ Golden Bay system as a result of the suitable shellfish growing conditions in the bays, and proximity to the heart of the industry in the nearby Marlborough Sounds. However, the marine habitat in this region is presently utilised by a number of users, not the least of which is the scallop fishery. Hence potentially the establishment of the mussel industry may lead to costs to existing fisheries, such as the scallop fishery, and other marine communities. Therefore from a norma-

tive resource management perspective, it is appropriate to investigate these possible interactions. It is important to highlight here that we are not investigating the social or economic aspects of these activities, nor advocating a preference for any particular activity. By contrast we seek to quantify how much mussel culture can be introduced into the system before predefined development milestones are achieved.

2. Methods

The Ecopath (Christensen and Pauly, 1993; Pauly et al., 2000; Christensen et al., 2000) steady state mass balance model was used. Ecopath has previously been used to investigate the structure of marine systems subjected to fishing pressure (Wolff, 1994; Okey and Pauly, 1999; Pauly et al., 2000; Wolff et al., 2000; Bradford-Grieve et al., 2003). The model was configured to the best guess of the present state of the ecosystem and then perturbed to investigate the levels of culture that could be introduced until significant changes to energy fluxes occurred (defined here as the ecological carrying capacity), and to the point where the culture replaces the ecological role of zooplankton (the theoretical production carrying capacity—see Gibbs, 2004 for details).

In this application the total biota in the two bays were grouped into 23 key system components defined from the available information according to the production/biomass ratio (P/B), consumption/biomass ratio (Q/B), catch, biomass, and level of knowledge. The Ecopath model assumes mass balance in that production of any given prey group is equal to the sum of biomass consumed by predators, the yield, and any exports from the system, i.e.

$$B_i(P/B)_i EE_i - \sum_{j=1}^{n} B_j(Q/B)_j DC_{ij} - Y_i - E_i = 0$$

where: B_i and B_j represent the biomass of prey and predators, respectively, $(P/B)_i$ is the production of unit biomass, $(Q/B)_j$ is the consumption per unit biomass by predator j, EE_i is the ecotrophic efficiency, i.e. the fraction of the production that is used in the system, DC_{ij} is the fraction of prey i in the average diet of predator j, Y_i is the harvest and E_i is the export. For each group, the model needs three of

the four basic input parameters: B_i, $(P/B)_i$, $(Q/B)_j$ and EE_i as initial input. In addition, the model requires input of the dietary composition of each group. This can be somewhat problematic as diet compositions often change with age. Where possible, the full range of diet groups was incorporated.

For commercial species, biomass estimates in the study area were acquired either from trawl surveys or from other stock assessment models (e.g. Annala et al., 2000; Gillbert and Phillips, 2002; Stevenson, 2003). Biomass for most of the benthos was estimated from the results of a large number of core/grab samples contained in the Cawthron Institute database. When appropriate estimates could not be obtained, biomass was left for the Ecopath model to estimate by assuming ecotrophic efficiency to be 0.95. The P/B ratio is equivalent to the instantaneous rate of total mortality (Z) commonly used in fisheries

modelling (Allen, 1971), which is the sum of fishing mortality (F) and natural mortality (M). For commercially exploited species, M was often available from New Zealand Ministry of Fisheries Fishery Assessment Reports (Annala et al., 2000). For cases where F was unavailable, total mortality was obtained through dividing catch by biomass. Alternatively, P/B ratio for fish species was also estimated from the equation given by Banse and Mosher (1980):

$$\log(P/B) = \log a + b \log M_s$$

where log $a=0.38$, $b=-0.26$ and M_s is in g wet weight (Haedrich and Merrett, 1992).

For benthos, P/B ratios were estimated based on the habitat type, water depth, bottom water temperature, their individual body mass, taxonomy and feeding type (Brey, 1999 cited by Christensen et al.,

Table 1
Initial input parameters

Group name	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	Catch (t)	Source (or derived from)
Mammals mainly fur seals	0.04[a]	0.22[b]	14.886[b]		[a]Taylor et al. (1995); [b]Own estimate
Birds mainly gannet, seagull	0.02[a]	0.3[a]	74.599[a]		[a]Own estimate
Sharks (school shark, spiny dogfish, rig etc.)		0.8[a]	3.9[b]	0.19	[a]Own estimate; [b]Christensen et al. (2000).
Barracouta	0.35[a]	1.26[b]	4.2[c]	0.281	[a]Stevenson (2003); [b]Own estimate; [c]Based on Christensen et al. (2000).
Red cod	0.005[a]	1.26[b]	4.16[c]	0.116	[a]Based on Stevenson (2003); [b]Annala et al. (2000); [c]Own estimate
Snapper	3[a]	0.37[b]	4.65[c]	0.033	[a]Based on Harley and Gilbert (2000) and Gillbert and Phillips (2002); [b]Banse and Mosher (1980); [c]Christensen et al. (2000).
Jack mackerel		0.22[a]	3.46[b]	0.093	[a]Annala et al. (2000); [b]Own estimate
Other pelagic		0.3[a]	4.32[b]	0.113	[a]Own estimate; [b]Christensen et al. (2000).
Flat fish		1.65[a]	4[b]	0.081	[a]Banse and Mosher (1980), [b]Own estimate.
Other fish		0.39[a]	4[b]	0.48	[a]Banse and Mosher (1980); [b]Own estimate
Juvenile fish		1.5[a]	4.5[a]		[a]Own estimate
Squid	0.046[a]	3.81[b]	22[b]	0.042	[a]Stevenson (2003); [b]Own estimate
Green mussels		2.15[a]	6.629[a]	0.003	[a]Own estimate
Scallops	5.3[a]	1.86[b]	9.8[b]	0.119	[a]Horn (2003); [b]Own estimate
Cockles		2.18[a]	10[a]	0.096	[a]Own estimate based on literature for similar species
Other shellfish	350[a]	5.1[b]	20[b]		[a]Based on data collected by Cawthron Institute; [b]Own estimate
Crabs and shrimps		4.9[a]	13[a]	0.015	[a]Own estimate based on data collected by Cawthron Institute
Other benthos	650[a]	2[b]	8[b]		[a]Based on data collected by Cawthron Institute; [b]Own estimate
Large zooplankton		5[a]	25[a]		[a]Own estimate
Small zooplankton		20[a]	60[a]		[a]Own estimate
Phytoplankton	17.5[a]	250[b]			[a]Own estimate; [b]Valiela (1995)

Catch are based on national statistics.

Table 2
The dietary composition

Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 Seals and sea lions																				
2 Birds																				
3 Sharks																				
4 Barracouta	0.001																			
5 Red cod	0.009	0.003	0.008	0.002						0.002										
6 Snapper	0.009		0.027	0.018	0.006					0.001										
7 Jack mackerel	0.07	0.096	0.024	0.049	0.017	0.034				0.058										
8 Other pelagic	0.2	0.646	0.107	0.227	0.055	0.034	0.032			0.227		0.031								
9 Flat fish	0.005		0.009	0.011	0.015	0.013				0.002		0.004								
10 Other fish	0.09	0.031	0.648	0.372	0.299	0.04				0.021		0.098					0.003	0		
11 Juvenile fish	0.016	0.052	0.056	0.114	0.01	0.024		0.013	0.001	0.091	0.004	0.093					0.004	0.001		
12 Squid	0.6	0.122	0.018	0.035	0.047	0.052	0.022	0.005	0.004	0.006		0.011					0.003	0		
13 Green mussels									0.013	0.006	0.005						0.002			
14 Scallops					0.021	0.001			0.008	0.015	0.013									
15 Cockles					0.026	0			0.013	0.017	0.03						0.007	0.001		
16 Other shellfish					0.033	0.051			0.13	0.112	0.074	0.01					0.183	0.065		
17 Crabs and shrimps		0.013	0.048	0.065	0.003	0.134	0.012	0.055	0.02	0.08	0.038	0.237					0.003	0.053		
18 Other benthos			0.054	0.106	0.355	0.579	0.066	0.151	0.44	0.168	0.26	0.34					0.296	0.088		
19 Large zooplankton		0.036	0.001	0.003	0.085		0.78	0.504		0.074	0.244	0.176					0.086	0.043	0.029	
20 Small zooplankton					0.027	0.038	0.087	0.251		0.05	0.192		0.222	0.13	0.027	0.039	0.017	0.1	0.12	0.023
21 Phytoplankton								0.02					0.5	0.667	0.275	0.189		0.159	0.55	0.577
22 Detritus									0.37	0.07	0.14		0.278	0.203	0.698	0.772	0.396	0.489	0.301	0.4

2000). Q/B ratios were calculated using the empirical equation given by Christensen et al. (2000):

$$\log(Q/B) = 7.964 - 0.204\log W_\infty - 1.965T'$$

$$+ 0.083A + 0.532h + 0.398d$$

where W_∞=asymptotic fish weight (g), T' =1000/ (°C+273), A=aspect ratio of the caudal fin (H^2/S, H is the tail height and S is the surface area of tail), h is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores) and d is also a dummy variable expressing food type (1 for detritivores, and 0 for herbivores and carnivores). When appropriate estimates were not obtainable, assumptions were made based on studies in other regions of similar latitudes. As quantitative diet information was often unavailable for the species involved, input for diet composition was generally obtained on the basis of qualitative descriptions for similar species from existing literature or unpublished reports. Table 1 shows the initial input parameters used and Table 2 summarizes the diet composition. Note that the initial mussel biomass is that naturally occurring in the region and does not include any mussel culture. The units of biomass and production are t km^{-2}, respectively.

3. Present state of the system determined from the mass balance model

3.1. Balancing the model

The model was balanced by adjusting the basic input parameters until the estimated ecotrophic efficiency (EE) was less than one. This was done as EE values greater than one are not plausible i.e. it is not possible that more biomass is used than produced by a group under conditions of steady state. Other estimates were also checked for their consistency by comparing them with data derived from laboratory experiments and similar studies.

Some of the input parameters had to be modified to balance the model (Table 3). In particular, the biomass of several groups had to be reduced by 70–90%, for example other benthos, and other shellfish and snapper. The biomass of red cod had to be increased 40 times from the original input (0.005–0.207). The original

Table 3
Changes to the input parameters required to balance the model

Group name	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE
Mammals	0.100	0.000	0.000	−0.100
Birds	−0.850	0.000	0.000	2.650
Sharks	–	0.000	0.000	0.000
Barracouta	−0.234	0.000	0.000	–
Red cod	40.400	0.000	0.000	0.000
Snapper	−0.850	0.000	0.000	
Jack mackerel	–	0.000	0.000	−0.034
Other pelagic	–	0.000	0.000	−0.066
Flat fish	–	−0.152	0.375	−0.018
Other fish	–	0.000	0.075	−0.023
Juvenile fish	–	−0.133	0.000	−0.020
Squid	14.150	−0.525	0.000	–
Green mussels	–	−0.163	0.000	–
Scallops	0.901	0.000	0.000	–
Cockles	–	−0.174	0.000	–
Other shellfish	−0.883	−0.314	0.000	–
Crabs and shrimps	–	−0.143	0.000	0.000
Other benthos	−0.701	−0.050	0.000	–
Large zooplankton	–	0.500	1.000	−0.014
Small zooplankton	–	0.000	0.333	0.000
Phytoplankton	0.000	−0.200	–	–

Values are given as (final estimate−initial input)/initial input. – indicates no initial input but calculated by the model.

input of red cod biomass of 21 t was based on trawl survey data in 2003 (Stevenson, 2003). However, this estimate must be too low since the annual catches of red cod from the two bays have varied between 100 and 1300 t during the last 13 fishing years. The final input of 0.207 t km^{-2} is more comparable to the biomass estimate of 1090 t (equivalent to 0.242 t km^{-2}) from the trawl survey conducted in 1997 (Stevenson and Hanchet, 2000). The biomass of squid also had to be increased significantly from 0.046 to 0.697 t km^{-2}. The final input of snapper biomass (0.45 t km^{-2}) is probably realistic as it lies in between 0.3 and 5 t km^{-2} as suggested by Harley and Gilbert (2000), and Gillbert and Phillips (2002). Compared to the biomass, the P/B ratios were subject to less modification during the balancing process, with the exception of squid and large zooplankton where the P/B ratios were changed more than 50%. The EE for birds were initially assumed to be 0.02 and this had to be increased 265% to 0.073.

3.2. Evaluation of the group parameters

A summary of the final input parameters and those estimated by the Ecopath model for the model with no

mussel culture is given in Table 4. The gross efficiency (P/Q or GE) is defined as the ratio between production and consumption, which in most cases should be within the range of 0.1–0.3 (Christensen et al., 2000). The P/Q ratios estimated from the present models are mostly within this range, except for a few groups such as red cod, crabs/shrimps. The P/Q ratio for wild stock green mussels calculated by the model is within the range reported for the mussel *Mytilus edulis* (0.15–0.36) in the literature (Riisgard and Randløv, 1981).

The balanced R/A ratios (ratio of respiration to assimilation) for bivalves (0.71–0.83) are higher than those suggested by Huebner and Edwards (1981) for marine bivalves (0.57–0.79) but lower than values reported by Wolff (1994) for bivalves and suspended scallops (0.81–0.85). For other shell fish (mainly gastropods), the estimated R/A ratio of 0.84 is higher than the upper range of values reported by Huebner and Edwards (1981) for marine carnivorous gastropods (0.28–0.67). The R/A ratios for pelagic groups (0.91–0.92) are slightly higher than the values (0.83–0.88) reported by

Wolff (1994). The R/B ratios estimated by the model for various benthic groups (4.5–13.4 year⁻¹) have a wider range than those (0.71–12.6 year⁻¹) reported by Bradford-Grieve et al. (2003). The R/B ratios (ratio of respiration to biomass) for pelagic groups (2.5–3.2 year⁻¹) estimated from the present model are within the range 1–10 year⁻¹ whilst the R/B ratios for zooplankton (25–44 year⁻¹) are lower than values (50–100) presented by Christensen et al. (2000).

3.3. Trophic structure and summary statistics

In terms of biomass, other benthos accounted for 45% of the total biomass, being the most important component in the system followed by wild bivalves (20%), other shellfish (9.6%) and pelagic fish (7.3%). Other benthos are also the most important component in terms of intake (29%), followed by small and large zooplankton (24% and 10%, respectively). The estimated primary production (3500 t km⁻² year⁻¹) constitutes 74% of the total system production, suggesting a phytoplankton driven system, although

Table 4
The final input parameters (in bold) and those estimated by the model

Group name	TL	B (t km⁻²)	P/B (yr⁻¹)	Q/B (yr⁻¹)	EE	P/Q	Net efficiency	R (t km⁻²)	A (t km⁻²)	R/A	P/R	R/B (yr⁻¹)	Flow to detritus
(1) Mammals	4.26	**0.044**	**0.22**	**14.886**	0.036	0.015	0.018	0.514	0.524	0.982	0.019	11.689	0.14
(2) Birds	4.1	**0.003**	**0.3**	**74.599**	0.073	0.004	0.005	0.162	0.163	0.995	0.005	59.379	0.042
(3) Sharks	4.19	0.278	**0.8**	**3.9**	**0.95**	0.205	0.256	0.644	0.866	0.744	0.345	2.32	0.228
(4) Barracouta	3.98	**0.267**	**1.26**	**4.2**	0.878	0.3	0.375	0.562	0.898	0.625	0.6	2.1	0.266
(5) Red cod	3.75	**0.207**	**1.26**	**4.16**	0.95	0.303	0.379	0.428	0.688	0.621	0.609	2.068	0.185
(6) Snapper	3.57	**0.45**	**0.37**	**4.65**	0.854	0.08	0.099	1.508	1.674	0.901	0.11	3.35	0.443
(7) Jack mackerel	3.13	11.063	**0.22**	**3.46**	**0.918**	0.064	0.079	28.188	30.622	0.921	0.086	2.548	7.856
(8) Other pelagic	3.12	19.924	**0.3**	**4.32**	**0.887**	0.069	0.087	62.882	68.859	0.913	0.095	3.156	17.888
(9) Flat fish	2.42	0.248	**1.4**	**5.5**	**0.933**	0.255	0.318	0.743	1.089	0.682	0.467	3	0.295
(10) Other fish	3.33	13.571	**0.39**	**4.3**	**0.928**	0.091	0.113	41.39	46.683	0.887	0.128	3.05	12.054
(11) Juvenile fish	3.04	2.48	**1.3**	**4.5**	**0.931**	0.289	0.361	5.705	8.93	0.639	0.565	2.3	2.455
(12) Squid	3.31	**0.697**	**3.8**	**22**	0.95	0.173	0.216	9.614	12.262	0.784	0.275	13.8	3.198
(13) Green mussels	2.23	20.676	**1.8**	**6.629**	**0.95**	0.272	0.339	78.281	109.644	0.714	0.475	3.786	23.418
(14) Scallops	2.13	**10.073**	**1.86**	**9.8**	0.779	0.19	0.237	65.012	78.972	0.823	0.288	6.454	19.104
(15) Cockles	2.03	53.457	**1.8**	**10**	**0.95**	0.18	0.225	353.78	427.658	0.827	0.272	6.618	89.381
(16) Other shellfish	2.28	**41.121**	**3.5**	**20**	0.913	0.175	0.219	549.433	657.944	0.835	0.262	13.361	141.658
(17) Crabs, shrimps	2.42	13.216	**4.2**	**13**	**0.95**	0.323	0.404	81.942	137.451	0.596	0.677	6.2	37.138
(18) Other benthos	2.47	**194.67**	**1.9**	**8**	0.915	0.238	0.297	876.02	1245.895	0.703	0.422	4.5	342.804
(19) Large zoopl.	2.03	10.431	**15**	**50**	**0.937**	0.3	0.375	260.786	417.258	0.625	0.6	25	114.139
(20) Small zoopl.	2.03	16.023	**20**	**80**	**0.95**	0.25	0.313	705.022	1025.486	0.688	0.455	44	272.395
(21) Phytoplankton	1	**17.5**	**200**	–	0.576	–	–	–	–	–	–	–	1483.71
(23) Detritus	1	–	–	–	0.854	–	–	–	–	–	–	–	–

TL: trophic level.

Table 5
Summary statistics

Parameter	Value 1	Value 2	Units
Sum of all consumption	5341.958	5449.61	t km^{-2} year^{-1}
Sum of all exports	377.393	207.202	t km^{-2} year^{-1}
Sum of all respiratory flows	3122.616	3292.882	t km^{-2} year^{-1}
Sum of all flows into detritus	2568.879	3303.056	t km^{-2} year^{-1}
Total system throughput	11411	12253	t km^{-2} year^{-1}
Sum of all production	4717	4778	t km^{-2} year^{-1}
Mean trophic level of the catch	3.33	2.01	
Gross efficiency (catch/net p.p.)	0.000504	0.057587	
Calculated total net primary production	3500	3500	t km^{-2} year^{-1}
Total primary production/total respiration	1.121	1.063	
Net system production	377.384	207.118	t km^{-2} year^{-1}
Total primary production/total biomass	8.208	5.255	
Total biomass/total throughput	0.037	0.054	
Total biomass (excluding detritus)	426.401	666.087	t km^{-2}
Total catches	1.764	201.555	t km^{-2} year^{-1}
Connectance index	0.365	0.371	
System omnivory index	0.183	0.211	

the standing phytoplankton biomass is not particularly high relative to other groups. The primary production of 3500 t km^{-2} year^{-1} is lower than the estimate of 7125 t km^{-2} year^{-1} found for Tongoy Bay (Wolff, 1994) but higher than 265 g C m^{-2} year^{-1} (equivalent to 3313 t km^{-2} year^{-1} using conversions: carbon to dry organic matter, 1:2.5; dry to wet weight organic matter, 1:5. See Parsons et al., 1977) for subantarctic
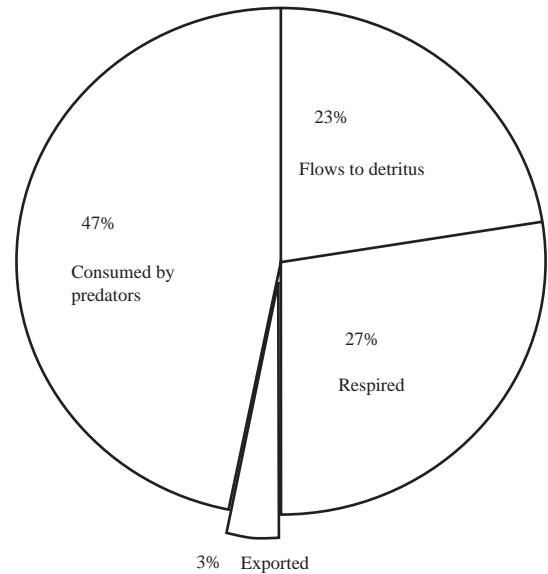

Fig. 2. Contribution of consumption by predators, flow to detritus and respiration to the total throughput.

water over the Southern Plateau, New Zealand (Bradford-Grieve et al., 2003). Small and large zooplankton, as the main phytoplankton consumer, consumed 43% of the total phytoplankton production available to the system, whereas bivalves only consumed less than 7%. Around 42% of the total phytoplankton production flowed to detritus and was recycled through detritus feeders.

Total system throughput, the sum of all flows in a system (consumption, exports, respiration and flows into detritus), was estimated to be 11 411 t·km^{-2}·year^{-1} (Table 5), which is lower than 20 835 t km^{-2} year^{-1} presented by a similar study by Wolff (1994) but higher than 10 559 t km^{-2} year^{-1}

Table 6
Throughput by trophic level

TL/Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput	%
VII	0.024	0.002	0.043	0.133	0.202	0.001803
VI	0.203	0.015	0.357	1.108	1.683	0.01502
V	1.685	0.116	2.964	8.965	13.73	0.122535
IV	13.724	0.518	23.173	72.709	110.124	0.982811
III	110.297	0.779	176.455	514.509	802.04	7.157876
II	801.052	0.334	882.102	2525.235	4208.723	37.56112
I	4209.528	375.629	1483.696	0	6068.798	54.16152

TL: trophic level.

reported by Wolff et al.(2000). About 92% of the total throughput is achieved from the trophic levels I to III: 54% from level I to II plus 37% from level II to III (Table 6). Of the total throughput, 47% goes to consumption, 27% is respired, 22% flows into detritus and 3% is exported (Fig. 2).

A total biomass of 1.76 t km^{-2} is typically harvested from the system each year and the mean trophic level of the Tasman and Golden bay fishery (i.e. the weighted average of trophic levels of all harvested species) was estimated at 3.33, about the trophic level of the other fish group. The efficiency of the fishery, the ratio of the total catch to primary production, for Tasman and Golden Bays was estimated at 0.0005, which is lower than the value (0.0089) reported by Wolff (1994) but higher than the global average 0.0002 (Christensen et al., 2000).

The transfer efficiency of the system was evaluated after the system components were grouped into discrete trophic levels (Lindeman, 1942). This was defined as the fraction of total flows at each trophic level that are either exported or transferred to upper trophic levels through predation. Table 7 shows the transfer efficiency in the Tasman and Golden Bay system. The overall transfer efficiency of 15.1% is close to the upper end of average values (8–15%) reported by Christensen and Pauly (1993), Wolff (1994), and Wolff et al. (1996), but lower than the value (23%) reported by Bradford-Grieve et al. (2003).

3.4. Mixed trophic impacts

A routine based on the method of Leontief (1951) was implemented in Ecopath to assess the effect that changes to the biomass of a particular

group will have on the biomass of the other groups in a system (Ulanowicz and Puccia, 1990). This is defined as the mixed trophic impact (MTI, Table 8). The two top predator groups (mammals and birds) are not included in Table 8 as their impact on other groups was insignificant due to their small biomasses. A small increase of phytoplankton was found to have a positive impact on bivalves and large zooplankton but a negative impact on small zooplankton. The reason for a negative impact on small zooplankton is that large zooplankton also feed on small zooplankton and the direct impact from phytoplankton is overruled by the indirect impact. The greatest impact of a small biomass change of one group on another is seen from other benthos, where a small increase of the biomass of other benthos had a negative impact on other shellfish but a positive impact on snapper. It is also worth noticing that bivalves, especially green mussels generally have a little impact on other groups, suggesting that these bivalves are presently too scarce to have any quantitative impacts (Christensen et al., 2000).

3.5. Sensitivity analysis

The sensitivity routines in Ecopath were used to evaluate the model sensitivity to the input parameters. The routine varies each input parameters in steps of 10% from −50% to 50% and the impact of the change on other parameters was assessed by a proportion, which is given as the ratio (estimated parameter−original parameter)/original. The largest impact of one parameter on another usually happens within the same group. For most of the groups, perturbing P/B ratios of 20% generally resulted in more than a 20% impact on the biomass and/or EE of the same group. The largest impact of one parameter on another was found to be with the other fish group, where a 20% change of the P/B ratio resulted in a 48.5% impact on the biomass of other fish. In addition to the large impact within groups, changing P/B ratio for other fish had a significant impact on other groups. For example, a 20% change of P/B ratio for other fish had a 45% impact on the biomass of jack mackerel, 26.6% impact on the biomass of red cod and 22.8% impact on the biomass of flat fish.

Table 7
Transfer efficiencies (the proportion of energy transferred from one trophic level to the next) for each trophic level in the system

Source/TL	II	III	IV	V	VI	VII	VIII	IX
Producer	21.7	14.2	12.7	13.1	13	12.9	12.6	
Detritus	16.6	13.4	13.2	13.1	13	12.9	12.4	
All flows	19	13.8	12.9	13.1	13	12.9	12.5	10.6

TL: trophic level.
Proportion of total flow originating from detritus: 0.46.
Transfer efficiencies (calculated as geometric mean): from primary producers, 15.8%; from detritus, 14.3; All flows, 15.1%.

Table 8
Mixed trophic impact

Impacting/impacted	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)
(3) Sharks	−0.134	−0.094	−0.047	−0.189	0.059	0.017	0.01	−0.086	−0.012	−0.016	0	0.006	0	0.009	0.003	0.001	−0.013	0	0.002
(4) Barracouta	−0.135	−0.144	−0.06	−0.055	0.021	0.004	−0.036	−0.044	−0.027	−0.016	0	0.003	0	0.004	0.002	0	−0.003	0	0
(5) Red cod	−0.052	−0.056	−0.019	−0.002	0.015	0.005	−0.034	−0.028	0.006	−0.018	0.001	0.001	0	0.003	0.002	0	−0.004	0	0.001
(6) Snapper	−0.028	0.017	0.007	−0.129	−0.021	−0.001	−0.064	−0.003	−0.001	−0.027	0.001	0.001	0.001	0.001	−0.002	−0.002	0.005	−0.001	−0.001
(7) Jack mackerel	−0.001	−0.007	−0.041	0.006	−0.134	−0.263	0.017	0.06	0.18	−0.216	0.004	0	0	−0.006	0.011	0.003	−0.094	0.018	0.009
(8) Other pelagic	0.039	−0.018	−0.033	−0.036	−0.174	−0.11	0.002	0.055	−0.307	−0.168	0.039	0.047	0.042	0.029	−0.06	−0.026	−0.178	−0.015	0.036
(9) Flat fish	−0.028	−0.032	−0.006	0.021	−0.003	0	−0.012	0.003	0.001	0.001	0	0	0	0	0	−0.001	0.001	0	0
(10) Other fish	0.246	0.039	−0.203	−0.26	−0.491	−0.242	−0.288	−0.312	0.036	0.183	−0.013	−0.059	−0.01	−0.075	−0.019	0.004	0.137	0.004	−0.02
(11) Juvenile fish	0.024	0.086	0.003	0.008	0.007	0.01	−0.013	−0.027	−0.052	0.063	0.006	0	0.005	0.003	−0.005	−0.006	−0.017	−0.001	0.004
(12) Squid	−0.082	−0.038	0.07	0.08	0.138	0.024	−0.101	−0.181	−0.377	−0.208	0.01	0.023	0.009	0.026	−0.013	−0.008	−0.033	0.002	0.002
(13) Green mussels	0	0.001	0.001	−0.001	0.002	−0.013	−0.008	−0.001	−0.004	0.001	−0.027	−0.008	−0.018	−0.014	−0.02	0.009	0.011	−0.076	0.019
(14) Scallops	0.002	0.001	0.018	−0.003	−0.011	−0.013	−0.005	0.007	0.006	0.005	−0.016	−0.022	−0.009	−0.008	−0.006	0.003	−0.002	−0.042	−0.007
(15) Cockles	−0.039	−0.042	0.002	0.002	−0.02	−0.019	−0.079	−0.01	0.007	−0.019	−0.075	−0.047	−0.097	−0.076	−0.083	0.001	−0.029	−0.049	−0.024
(16) Other shellfish	0.043	−0.065	−0.112	−0.144	−0.095	−0.089	−0.161	0.14	0.032	−0.034	0.208	0.196	0.185	0.067	0.138	−0.322	0.066	−0.09	−0.057
(17) Crabs and shrimps	0.022	0.036	−0.015	0.087	−0.038	0.02	−0.049	−0.001	−0.09	0.077	0.007	0.008	0	−0.076	−0.083	−0.011	−0.059	−0.006	0.02
(18) Other benthos	0.012	0.184	0.231	0.3	−0.076	0.027	0.06	−0.007	0.015	0.152	−0.767	−0.64	−0.776	−0.466	−0.499	−0.19	−0.15	0.001	0.126
(19) Large zooplankton	0.019	0.005	0.032	−0.008	0.534	0.194	−0.035	0.059	0.118	−0.081	−0.057	−0.073	−0.034	−0.035	0.009	−0.002	−0.236	−0.111	−0.08
(20) Small zooplankton	0.011	0.018	0.003	0.025	−0.118	0.078	−0.008	0.002	0.042	−0.006	0.016	−0.145	−0.099	−0.054	−0.003	0.023	−0.229	−0.316	−0.317
(21) Phyto-plankton	0.025	0.007	0.03	0.003	0.265	0.199	−0.09	0.076	0.131	−0.068	0.269	0.458	0.118	0.073	−0.018	0.007	0.377	0.423	−0.343

4. Predicted carrying capacity from the mass balance model

The overall goal of this programme was to attempt to determine the ecological and production carrying capacity of mussel culture in the marine ecosystem. In order to investigate this with the mass balance model, the biomass of green mussels was increased (and catch increased accordingly) to represent the introduction of the culture, and the system response investigated. It was found that the mussel biomass could be increased to 65 t km^{-2} $year^{-1}$, after which the model would not balance as the EE for detritus becomes unrealistic (>1). Of interest is that the model parameter estimates for other groups were generally not changed up to this level of mussel biomass except for the biomass of small zooplankton and the EE for phytoplankton, whereas the biomass of small zooplankton increased from 16 to 20 and the EE for phytoplankton increased from 0.58 to 0.68. Therefore, the mass balance model suggests that Tasman and Golden Bay system could support an average green mussel biomass of 65 t km^{-2} $year^{-1}$ without significantly changing flows and biomass of other components within the system and this may be thought of as an estimate of the ecological carrying capacity (as defined in section 1). This is equivalent to a total mussel culture biomass of 292 500 t. For comparison, this predicted green mussel density can be supported by Tasman and Golden Bay system is significantly lower than the estimate for scallops (500 t km^{-2} $year^{-1}$) by Wolff (1994) for Northern Chile.

The introduction of large-scale mussel aquaculture could potentially lead to large changes in the energy fluxes occurring within the bays. Since the culture will be suspended it will compete directly with zooplankton for the resources. Furthermore, since zooplankton are the present dominant grazers, an estimate of the production carrying capacity can be performed by considering the case where suspended mussels completely replace zooplankton. Therefore, Ecopath was reconfigured for the case where the mussels replace small and large zooplankton. Note that is performing this exercise, the model accounts for differences in the physiology and efficiency of zooplankton as opposed to mussels. Ecopath predicted that the resulting modification to the dietary matrix focused on changes to pelagic groups and this is

logical since these groups are the primary consumers of zooplankton. The model was then re-balanced and pelagic fishes were forced to increase consumption of other prey (other groups) and consequently, predation pressure on these prey (other groups) was increased and the ecotrophic efficiency of these groups became larger than one. The biomass of the predator groups therefore had to be reduced to balance the model. During the iterative balancing process, the biomass of mussels was increased gradually. Table 9 summarizes the parameter estimates after large-scale mussel farms were introduced into the system. It was found that the model could be balanced until the biomass of mussels reach 310 t km^{-2} $year^{-1}$.

During the iterative re-balancing the biomasses of some groups increased, whilst the biomasses of the others decreased (Tables 4 and 9). The most striking reduction in biomass took place for other pelagics and mackerel, where the biomasses reduced to about one tenth of their original biomasses. Corresponding to the increase of mussel biomass, the contribution of other benthos to the total biomasses decreased to 29% compared to 45% before mussel culture was intro-

Table 9
Parameter estimates after zooplankton were replaced with green mussels

Group name	TL	B (t km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q
(1) Mammals	4.15	0.002	0.22	14.886	0.909	0.015
(2) Birds	3.88	0	0.3	74.599	0.894	0.004
(3) Sharks	4.07	0.278	0.8	3.9	0.95	0.205
(4) Barracouta	3.69	0.246	1.26	4.2	0.95	0.3
(5) Red cod	3.63	0.174	1.26	4.16	0.95	0.303
(6) Snapper	3.45	0.381	0.37	4.65	0.95	0.08
(7) Jack mackerel	3.92	1	0.22	3.46	0.95	0.064
(8) Other pelagic	2.72	2.181	0.3	4.32	0.95	0.069
(9) Flat fish	2.39	0.292	1.4	5.5	0.835	0.255
(10) Other fish	3.19	7.216	0.39	4.3	0.95	0.091
(11) Juvenile fish	2.97	3.248	1.3	4.5	0.95	0.289
(12) Squid	3.16	0.874	3.8	22	0.95	0.173
(13) Green mussels	2	310	1.8	6.629	0.43	0.272
(14) Scallops	2	10.073	1.86	9.8	0.871	0.19
(15) Cockles	2	60.683	1.8	10	0.95	0.18
(16) Other shellfish	2.23	43.331	3.5	20	0.95	0.175
(17) Crabs and shrimps	2.3	13.937	4.2	13	0.95	0.323
(18) Other benthos	2.36	194.67	1.9	8	0.95	0.238
(21) Phytoplankton	1	17.5	200	–	0.409	–
(23) Detritus	1	–	–	–	0.998	–

TL: trophic level.

duced. Due to the increased biomass of green mussels, phytoplankton consumption by bivalves increased from 7% to 33%. It is also noticed that the proportion of total phytoplankton production flow to detritus increased to 59% from 42%.

A comparison of the summary statistics for the system before and after mussel farms introduced into the system is presented in Table 5. Interestingly, the overall yield of fisheries resources in the bays would increase owing to the dominant role of mussels in the total harvest. The mean trophic level of the catch reduced from 3.33 to 2.01 and as a result the fishery efficiency increased significantly (Table 5). The total system throughput increased from 11 411 to 12 253 t km^{-2} year^{-1}, of which 96% was achieved from trophic levels I to III: 56.4% from level I to II plus 39.1% from level II to III. Of the total system throughput, 45% went to consumption and fishery catch, 27% flowed into detritus and 27% to respiration.

Ecopath is a steady state model and therefore cannot be used to simulate changes to flows with time. By contrast, the model has been used to investigate the present functioning of the system and how this may change if intensive aquaculture were to be introduced. For example, one of the likely responses of the system would be that suspended mussel culture would act to out-compete zooplankton (the present dominant grazers) and the extreme case would be if the culture completely replaced the ecological role of zooplankton. Under this scenario almost all of the primary resources in the bay would be used to grow mussels and this represents the maximum production carrying capacity in the bay (unless new nutrients are introduced). Of interest is the large difference between this theoretical production carrying capacity of 310 t km^{-2} year^{-1}, and the estimate of the ecological carrying capacity where little change occurs if the culture is introduced (65 t km^{-2} year^{-1}).

5. Summary

Inspection of the marine literature indicates that apart from a small number of hydrodynamic modelling systems, the present generation of marine models are unable to accurately and consistently forecast the behaviour of marine ecosystems. Therefore, the most robust way to apply deterministic models in the marine environment is to use them as prognostic tools to undertake numerical experiments in order to elucidate particular aspects and processes in the system in question. Following this approach, here we use a mass balance model to investigate the potential carrying capacity of bivalve shellfish culture in a region in New Zealand. Rather than attempt to predict how the carbon flows may respond to different levels of introduced culture through time, here we attempt to determine what levels of culture could be introduced until predefined changes occurred. The two levels of change map onto the theoretical maximum level of culture possible (the production carrying capacity), and the level of culture that could be introduced without leading to any significant changes to the food web structure and flows.

The configuration of the present state of the system indicated that the total production of Tasman and Golden Bay system was dominated by primary production (74%), among which 43% was directly consumed by zooplankton, whilst 42% flowed to detritus and recycled in the system. The most important component in the system in terms of biomass was other benthos, which was also the most important component in terms of intake. The total system throughput was estimated to be 11 411 t km^{-2} year^{-1} and 92% of the throughput was achieved from the trophic levels I to III. Nearly half of the total throughput went to consumption and fishery catch, whereas 22% flowed into detritus and 27% to respiration.

The mean trophic level of the Tasman and Golden bay fishery was estimated at 3.33. A total biomass of 1.76 t km^{-2} is typically harvested from the system each year. The group other fish made up 28% of the total catch, being the most important component, followed by barracouta (16%) and sharks (12%). Combined, scallops and cockles constituted 12.5% of the total harvest, whilst wild green mussels contributed less than 1%. Nevertheless, the model suggested that up to 65 t km^{-2} of green mussels could be supported by the system without significantly changing the food web structure in the region. The corresponding total biomass would increase from 426 to 474 t km^{-2}. As a result, the catch would increase significantly. For the present analysis, the model estimated that a total catch of 26.7 t km^{-2}

could be harvested, compared to a total catch of 1.76 t before mussel culture was introduced into the system.

The carrying capacity analysis involved perturbating the model until the suspended culture replaces the ecological role of zooplankton, as this was predefined as the ultimate production carrying capacity. In this case, the food web essentially collapses down to a nutrient–phytoplankton–bivalve culture–detritus system in which zooplankton and higher pelagic trophic levels that are underpinned by zooplankton are extinct. The model analysis suggests that for Tasman and Golden Bays, this corresponds to an absolute theoretical maximum stocking density of 310 t km^{-2}, by contrast to 65 t km^{-2}— the biomass that could be introduced without significantly changing the fluxes or structure of the ecosystem. In addition to the increase of mussel biomass, the model also reveals other changes after large-scale mussel aquaculture was introduced into the system. The total system throughput, for example, increased from 11 411 to 12 253 t km^{-2} year^{-1}, of which 45% went to consumption and fishery catch, 27% flowed into detritus and 27% to respiration.

It must be highlighted that the carrying capacity estimates from the present analysis serve only as a guide and the objective was to investigate resource management and coastal allocation issues rather than production planning issues here as the model does not investigate for example marketable cohorts. Furthermore, the true production carrying capacity is likely to be determined by other factors not explicitly addressed here. For example, as the production carrying capacity is approached, the growth rates of the culture are likely to decrease and hence this may lead to less profitability, and hence less incentive to further develop the culturing activities. In addition, it is also reasonable to expect that as the system collapses down to a system dominated by the bivalve monoculture, the resilience may decrease and the system may become more susceptible to disease or biological invasions that may reduce the yield performance of the culture. Climatological variability may also lead to variability in the input of new nutrients that may also ultimately influence the carrying capacity. However once again it is difficult to predict how such variability will manifest itself in the food web.

Apart from above mentioned factors, bias resulting from estimating the model parameters would also have an impact on the carry capacity estimates. The accuracy of parameter estimates, however, depends on information available for the components. Some components (e.g. other fish and other benthos) may include hundreds even thousands of species and it is almost impossible to have an accurate parameter estimate for such groups. Even for commercially harvested species, data needed to estimate the model parameters (including dietary composition) are often incomplete and estimates have to be based on studies conducted elsewhere for similar species, or rely on qualitative descriptions. These would certainly affect the model output. However, the present model has utilised the best information available and hence represents our present best guess of the food web structure of Tasman and Golden Bay ecosystem.

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