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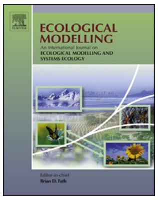

Lobsters as keystone: Only in unfished ecosystems?

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ABSTRACT

No-take marine reserves (MRs) are a useful tool to study the ecosystem effects of fishing as many MRs have allowed ecosystems to recover to pre-fished states. Established in 2008, the Taputeranga MR, located on the south coast of Wellington, New Zealand, provides full no-take protection to the nearshore marine environment. Commercial, recreational, and customary fisheries are important in this region and commercial catch records for the last 70 years indicate that exploitation has greatly reduced the biomass of some species. We employed an ecosystem modelling approach to analyse the food web linkages on this coast immediately prior to MR establishment (the pre-MR state) for comparison to reconstructed historical and predicted future ecosystem states. Our results suggest that the organisation and function of the pre-MR ecosystem have changed since the 1940s, notably in terms of the role played by lobster (*Jasus edwardsii*). Historically, lobster were at least four times more abundant, and played a keystone role by directly negatively impacting the abundance of prey species, and indirectly positively influencing the abundance of the prey of their prey. While the fishery for lobster that operates today is well managed and sustainable from a single-species perspective, our results indicate that the fishery has reduced lobster biomass sufficiently to have significant impacts on the organisation and function of the nearshore temperate reef ecosystem along Wellingtons's south coast. Our results predict that over the next 40 years, the Taputeranga MR is capable of restoring the protected ecosystem to a state more similar to that observed in the past, prior to large-scale commercial exploitation. This finding has implications for the management of fisheries in other areas, as we have demonstrated the inability of the single species fisheries model to manage the ecosystem effects of fishing.

1. Introduction

Given the extent of worldwide fishing pressure on marine species, habitats, and entire ecosystems, studies that have compared current exploited states to historical or pristine states have invariably found that large-scale changes to species abundances and ecosystem structure and function have occurred as a result of fishing (Jackson et al., 2001; Pandolfi et al., 2003; Lotze et al., 2006). Traditional fisheries management practices have mostly focussed on single-species approaches to conduct stock assessments to determine the maximum sustainable yield (MSY) that can be harvested (Browman et al., 2004; Pikitch et al., 2004). However, more recently, the ecosystem-based fisheries management (EBFM) approach is increasingly being used by fisheries management agencies following a widespread call from the scientific and academic communities for its implementation (Browman et al., 2004; Pikitch et al., 2004; Pitcher et al., 2009). EBFM is broadly defined as the recognition of the need to move towards a management system that recognises the importance of food web linkages and an understanding of how human activity affects the integrity and sustainability of all components of marine ecosystems (Pitcher et al., 2009).

Implicit in this broader view of fisheries management is the need to quantify food web linkages, the flow of energy through the ecosystem, and the ecosystem effects of fisheries. Recent fisheries studies have applied ecosystem models to assess the impact of fisheries on marine ecosystems worldwide (Worm et al., 2009; Smith et al., 2011; Garcia et al., 2012). Results from such studies indicate that entire ecosystems are directly and indirectly impacted as a result of fishing activities (Worm et al., 2009; Smith et al., 2011;

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Garcia et al., 2012). Historical ecosystem reconstructions have been undertaken for northern British Columbia, Canada (Ainsworth et al., 2008), and for the North Adriatic (Coll et al., 2009a), South Catalan, (Coll et al., 2009b), and North Sea regions in Europe (Mackinson and Daskalov, 2007). These model reconstructions have documented large-scale ecosystem-wide changes that have occurred as a result of fishery harvest along with other human-mediated disturbances (Coll et al., 2009a, 2009b). Many ecosystem models have also been used to predict the ecosystem impacts of EBFM strategies for ecosystems (Worm et al., 2009; Smith et al., 2011; Garcia et al., 2012).

In New Zealand, Māori peoples settled approximately 760 years ago, about 600 years before European arrival (Wilmshurst et al., 2010). These first settlers had a high reliance on coastal marine resources (Leach, 2006; Smith, 2011a,b), as evidenced by remains of lobster (*Jasus edwardsii*) and other invertebrates and vertebrates in middens located on Wellington's south coast and throughout New Zealand, which were harvested by diving, pots, and hoop nets (Leach, 2006; Booth, 2008). At the beginning of the 20th century, the commercial lobster fishery on Wellington's south coast was one of the first lobster fisheries in the country (Booth, 2008). In the late 1940s, most lobster were harvested from rocky inshore areas between depths of 5 and 25 m, but the late 1970s lobster were fished to depths of 50 m (Booth, 2008). In addition to this depth change, there is evidence that the average size of a lobster is smaller today than in the 1940s (Booth, 2008). Commercial fishing of lobster through the use of pots represents the main source of fishery revenue within the Wellington region and the fishery has been managed through the quota management system (QMS) since 1986. There is also a substantial recreational lobster fishery, taken by both potting and diving within the region. The lobster fishery in New Zealand is the country's most valuable export fishery, worth $229 million for 2.7 million kg of lobster landed in 2010 (Ministry of Fisheries, 2011). In addition to lobster fishing on Wellington's south coast, there are commercial and recreational fisheries for many finfish and shellfish species.

The exploitation of coastal marine resources affects not only the targeted species, but also other species and habitats in the ecosystem (Jackson et al., 2001; Pandolfi et al., 2003; Lotze et al., 2006). By studying trophic dynamics in areas protected by no-take MRs in comparison to exploited areas, it is possible to understand the ecosystem effects of fishing and how exploited ecosystems recover. Keystoneness, an indicator for identifying keystone speices, is one of many useful indicators for understanding how ecosystems respond to changes in abundance of certain species (Paine 1966; Paine 1969; Power et al., 1996; Libralato et al., 2006, 2010; Link et al., 2010a,b). A keystone species is defined as a species whose effect on an ecosystem is disproportionately large relative to its abundance and is important for understanding how individual species affect ecosystems (Power et al., 1996). In New Zealand, a top-down trophic cascade has been observed at a MR, where urchin (*Evechinus chloroticus*) grazed areas have been reduced in spatial extent through top-down predation on the urchin population by recovering populations of protected predators such as lobster (*J. edwardsii*) and fish (snapper – *Chrysophrys auratus*) (Cole and Keuskamp, 1998; Shears and Babcock, 2002, 2003).

In 2008, the Taputeranga MR was established on Wellington's south coast (Pande and Gardner, 2009). This full no-take MR protects 854.79 hectares of coastal waters, including habitats suitable for lobster and other harvested reef species. In order to understand the ecosystem effects of fishing and ecosystem response to MR protection on the south coast of Wellington, we have constructed ecosystem models for three time frames: historical past, pre-MR establishment, and distant future. Using fisheries catch records and stock assessments, we constructed a historical ecosystem model for 1940 prior to large-scale commercial exploitation. Using extensive field observations, a model was constructed to represent the ecosystem prior to implementation of the Taputeranga MR in 2008 (exploited state). This model was used to simulate the future ecosystem in 2050 following 42 years of protection by the Taputeranga MR. These three models were analysed to determine the ecosystem effects of fisheries, and how the ecosystem responds to MR protection. We then compared our results to other ecosystems protected by MRs in New Zealand (Shears and Babcock, 2003; Pinkerton et al., 2008), and ecosystem responses to lobster fisheries worldwide.

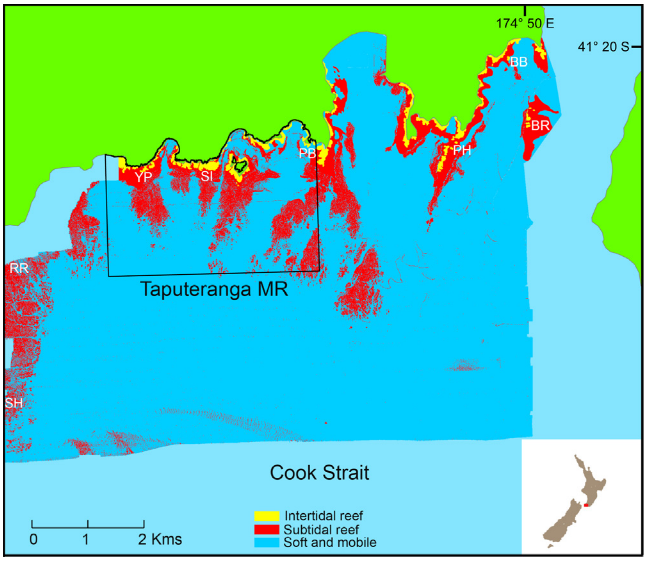

Fig. 1. Map of Taputeranga Marine Reserve, Wellington south coast model area, study sites and substrate types. Location of Taputeranga MR within New Zealand as red square in bottom right panel. Main figure – map of the area for which the model was developed showing location of Taputeranga MR (black box, labelled Taputeranga MR). Model area is characterised by substrates: intertidal reef (yellow); subtidal reef (red); and soft and mobile substrates (darker blue). Study sites for biomass data collection are shown in white letters; BR: Barrett Reef; BB: Breaker Bay; PH: Palmer Head; PB: Princess Bay; SI: Sirens; YP: Yungh Pen; RR: Red Rocks; SH: Sinclair Head. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. Study area

The study area on Wellington's south coast includes the Taputeranga MR (41°20 S, 174°45 E). This full no-take reserve extends from Princess Bay on the eastern boundary to Quarry Bay on the western boundary (Fig. 1) and was officially designated in August 2008. We conducted research in the Taputeranga MR in collaboration with, and permission from, the Department of Conservation that manages the MR. The marine environment that the Taputeranga MR protects is representative of the temperate Cook Strait region (Pande and Gardner, 2009); a highly dynamic area receiving frequent wave energy from the south, as well as the zone of convergence for the East Cape, D'Urville, and Southland currents (Eddy et al., 2008). Habitats represented in the study area include wave-exposed rocky reef, wave-sheltered rocky reef, cobble beach, and sandy shore (Eddy et al., 2008).

Wellington's south coast is home to a diverse assemblage of macroalgal species including kelp forests (dominated by *Lessonia variegata* and *Macrocystis pyrifera*), which provide habitat for a large number of invertebrate and vertebrate species. These brown (Phaeophyceae), red (Rhodophyceae), and green (Chlorophyceae) macroalgae are all speciose on Wellington's south coast, with close to 50% of all of New Zealand's species recorded in the region (Nelson, 2008). Much of the substratum type is characterised by greywacke reef, which is structurally complex with crevices and gullies that provide habitat for a number of commercially and recreationally targeted invertebrates including lobster (*J. edwardsii*), paua (abalone – *Haliotis iris* and *Haliotis australis*), and kina (urchin – *Evechinus chloroticus*). The combination of macroalgae and rocky reef provides habitat for many fish species typical of Cook Strait temperate assemblages (Francis, 2008). Encrusting communities are composed of sponges, hydroids, ascidians, and bryozoans. The Wellington south coast is characterised by an absence of mussels, which is thought to be due to bottom-up food limitation (Gardner, 2000; Helson and Gardner, 2004; Helson et al., 2007; Gardner, 2013). Elsewhere in the reserve, the substratum is sand with its associated, but poorly known, epifaunal and infaunal assemblages (Gardner and Bell, 2008).

We used a backscatter map produced by the National Institute of Water and Atmospheric Sciences Research (NIWA) using side-scan sonar (Wright et al., 2006) for the Taputeranga MR to delimit the area of the model. The GIS version of this map made it possible to determine the extent of physical bottom type by depth range. In order to ensure that the interpretation of the bottom-type parameter 'slope' was valid, we ground-truthed and reclassified the map with the 'Wellington South Coast Substrates Map' (New Zealand Oceanographic Institute, 1993). This map was also used to determine areas of 'intertidal reef' and 'intertidal soft and mobile substrates' as the intertidal zone was not included the side-scan sonar map. We sub-divided the model area into six regions to input region-specific information about the biomass of different species, where available, and the extent of each substrate type. This allowed estimation of biomass for each species for each region in the model area based on substrate type (hard or soft and mobile) and depth range inhabited when spatially resolved information was available (see Appendix A for more detail on spatial sampling methods).

The model area is 5428 ha in size, of which the Taputeranga MR comprises 15.7% (854.79 ha; Fig. 1). 'Subtidal reef' accounts for 580 ha (10%) of model area, while 'subtidal soft and mobile substrates' cover 4289 ha (79%). 'Intertidal reef' accounts for 308.5 ha (6%) of the model area, 'intertidal soft and mobile substrates' account for 265 ha (5%). Maximum depth within the model area is approximately 100 m, while average depth is approximately 25 m. 'Subtidal reef' mostly occurs between 0 and 25 m with a few smaller areas found at greater depths.

2.2. Ecosystem modelling

Ecopath with Ecosim (EwE) version 6 modelling software was used for the construction of historical (1940s) and pre-MR establishment (2008) ecosystem models, and for future (2050) ecosystem simulation prediction (Walters et al., 1997; Christensen and Walters, 2004). EwE uses a mass-balance approach to account for production and consumption of a set of defined functional trophic groups (species or groups) within the ecosystem (Eq. (1)).

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum_j B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \quad (1)$$

Parameters are described by; B_i = biomass of functional group i; P/B = production per unit of biomass of the functional group i; $(Q/B)_j$ = consumption per unit of biomass of the predator j of biomass B_j; DC_{ij} = proportion of prey i in the diet of predator j; Y_i = exports from the system as fishery catches; E_i = net migration; EE_i = ecotrophic efficiency of the functional group i. Losses of energy intake for each functional group are represented by Eq. (2).

$$B_j \cdot \left(\frac{Q}{B}\right)_i = B_j \cdot \left(\frac{P}{B}\right)_j + B_j \cdot \left(\frac{R}{B}\right)_j + \left(\frac{U}{Q}\right)_j \quad (2)$$

Parameters are described by; $(R/B)_j$ = respiration rate per unit of biomass; $(U/Q)_j$ = fraction of food consumption that is not assimilated. Functional groups are balanced energetically such that consumption for each trophic group is the sum of production, respiration, and unassimilated food (Walters et al., 1997; Christensen and Walters, 2004).

EwE uses Eqs. (1) and (2) in combination with a predator/prey diet matrix to describe the ecosystem that can be integrated over time to run dynamic simulations, represented by Eq. (3).

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum_{j=1} Q_{ji} - \sum_{j=1} Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \quad (3)$$

Eq. (3) is described by parameters: dB_i/dt = biomass growth rate of group i during the time interval dt; $(P/Q)_I$ = net growth efficiency; M_i = non-predation natural mortality rate, F_i = fishing mortality rate; e_i = emigration rate; I_i = immigration rate; $I_i - e_iB_i$ = net migration rate. Detailed information about EwE and its strengths and weaknesses have been documented (Walters et al., 1997; Christensen and Walters, 2004).

2.3. Ecosystem structure and function

EwE analyses provide information about ecosystem structure and function. EwE employs mixed trophic impact (MTI) analysis, similar to a sensitivity analysis, which determines ecosystem-wide impacts of increasing individual groups by small amounts. The MTI for living groups is calculated by constructing an $n \times n$ matrix, where the i,jth element representing the interaction between the impacting group i and the impacted group j is:

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \quad (4)$$

where $DC_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i, and $FC_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i as a predator (Leontief, 1951; Christensen et al., 2008). When calculating the host compositions the fishing fleets are included as 'predators' (Christensen et al., 2008). This analysis can also be used to understand and predict how individual species or trophic groups can cause trophic cascades. The Lindeman spine flow diagram shows transfer efficiency, the proportion of production for a given integer trophic level compared to the trophic level that preceeds it, which has been identified as a key ecosystem indicator (Lindeman, 1942; Coll et al., 2009a, 2009b). Ascendency is an information theory metric that is a measure of the average mutual information in a system scaled to the total system throughput (Ulanowicz, 1986), which in an ecoystem modelling context, indicates the amount of energy in reserve in the ecosystem to respond to unexpected perturbations.

EwE software is able to identify keystone groups or species, which are defined as having a structuring role for much larger biomasses within the food web and are often mediated through habitat changes (although habitat changes are not explicitly represented in EwE). EwE calculates keystoneness from MTI analysis as above following the approach by Power et al. (1996; referred to by EwE as keystone index #2):

$$KS_i = \varepsilon_i \cdot \frac{1}{p_i} \quad (5)$$

where Eq. (5) is described by parameters: KS_i = keystoneness of functional group i; ε_i = relative total impact of functional group i; p_i = contribution of the functional group i to the total biomass of the food web. Libralato et al. (2006) developed an approach to calculate relative total impact from EwE MTI analysis:

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2} \tag{6}$$

where m_{ij} is calculated from the MTI analysis as the product of all net impacts for all the possible pathways in the foodweb linking prey, i, and predators, j. The keystoneness of functional group i, (referred to by EwE as keystone index #1) is calculated as:

$$KS_i = \log[\varepsilon_i \cdot (1 - p_i)] \tag{7}$$

Using the Libralato et al. (2006) approach, a keystone functional group is one that has a KS_i value close to or greater than zero.

2.4. Model parameterisation

We used the 22 trophic functional groups from an ecosystem model constructed for coastal northeastern New Zealand (Lundquist and Pinkerton, 2008; Pinkerton et al., 2008), with the addition of two further groups (Table 1). The 22 trophic groups were chosen based on similarities of morphology, and in the case of consumers based on diet composition (Lundquist and Pinkerton, 2008; Pinkerton et al., 2008). We added the trophic groups ‘paua’ and ‘kina’ (abalone and urchins, respectively) as these animals are observed in relatively high biomass on the Wellington south coast, in contrast to the Te Tapuwae o Rongokako MR, which is depauperate in terms of invertebrate grazers (Lundquist and Pinkerton, 2008; Pinkerton et al., 2008). We parameterised biomasses of trophic groups using observational data collected within the model area for the following 17 trophic groups: lobster, mobile invertebrates – herbivores, paua, kina, mobile invertebrates – carnivores, sea cucumbers, sponges, sessile invertebrates, fish – cryptic, fish – invertebrate feeders, fish – piscivores, fish – planktivores, fish – herbivores, macroalgae – canopy, macroalgae – foliose, macroalgae–crustose, and phytoplankton (Appendix A for detailed methods). In the absence of data from the model area for depths deeper than those surveyed on SCUBA, we have also used information from locations in the Wellington region for the three trophic groups: fish – invertebrate feeders, fish – piscivores, and fish – planktivores groups (Appendix A for detailed methods). For the trophic group: phytal/infaunal invertebrates, data were collected outside the model area, but from the Wellington region (Appendix A for detailed methods). For the six trophic groups lacking local information – birds, microphytes, meso/macrozooplankton, microzooplankton, bacteria and detritus – biomasses were estimated from the literature (Lundquist and Pinkerton, 2008; Appendices A and B for detailed methods). In the absence of information about the import/export of biomass of organisms within the model area, we assume that imports are equal to exports.

Diet, production, and consumption values (Tables 1–3) were obtained for New Zealand taxa when available (Appendix B). Lundquist and Pinkerton (2008; and references therein) produced an extensive report compiling and reviewing both New Zealand and international biomass, diet, production, and consumption data for a food web model of the Te Tapuwae o Rongokako Marine Reserve. We used their diet, production, and consumption parameters in our model as the majority of species are found in both locations (Appendix B). In the absence of information from New Zealand, they provide estimates of values from the literature that are most appropriate to be used for New Zealand species (Appendix B). In addition, we have used local lobster diet information from within the model area (Kelly et al., unpublished manuscript). We document the data types (pedigree), coefficients of variation, and key references for each parameter estimate (Walters et al., 1997; Christensen et al., 2008; Appendices B and C).

2.5. Model balancing

Following guidelines laid out by Link (2010), we have employed the pre-balancing routine (PREBAL) to ensure that model parameters obeyed energetic laws for ecosystem structure. Production, consumption, and diet parameters were adjusted to values within confidence intervals for the trophic groups: birds, lobster, mobile invertebrates – herbivores, kina, mobile invertebrates – carnivores, phytal/infaunal invertebrates, sponges, and bacteria (initial estimates are described in Appendices D and E). We incrementally changed the value of the most uncertain parameters first in order to achieve model balance in order to minimise the change in initial parameter esimates. This process gave insight into which trophic groups were consuming a large proportion of prey available to them. We compared trophic levels for trophic groups resulting from initial model parameterisation to literature values. It was necessary to adjust the diet of fish planktivores to values within its confidence interval to produce a trophic level closer to the value published by Fishbase (Froese and Pauly, 2005).

2.6. Parameterisation of fisheries

The most important commercial fishery operating within the model area is the lobster fishery. We used landings data from the 915 statistical area of the CRA4 management region where the model area is located, scaled for the size of the model area to determine harvested annual lobster biomass (Ministry of Fisheries, 2009a). The most recent estimate of recreational take of lobster is approximately 10% of commercial landings (Ministry of Fisheries, 2009a). This value was used to parameterise the recreational lobster fishery. Important finfish species harvested in the model area are blue cod (*Parapercis colias*) and butterfish (*Odax pullus*). Blue cod is harvested commercially throughout New Zealand, but not within the model area boundary (Francis, 2008). In terms of biomass, blue cod is the most important species landed by recreational fisheries in New Zealand (Ministry of Fisheries, 2009a). For recreational catch of this species, we have used recent estimates of recreational harvest from the BCO_2 management area scaled to the model area (Ministry of Fisheries, 2009a). Recreational harvest of butterfish is estimated at approximately 10% of commercial harvest for the management area BUT2 (Ministry of Fisheries, 2009a). Thus, to estimate recreational catch of butterfish from the study area, we have applied the percentage to landings from this management area scaled to model area. Within the model area paua are extensively harvested recreationally, but not commercially, so to estimate paua harvest we have used recreational landings estimates for the PAU2 management area scaled to the model area (Ministry of Fisheries, 2009a). Recreational and commercial landings of other finfish and shellfish species were estimated using Ministry of Fisheries catch data (Ministry of Fisheries, 2009b).

2.7. Reconstruction of the historical ecosystem

While it is difficult to determine the exact unfished biomass (B_0; biomass prior to exploitation) of lobster for the model region, there is evidence that lobster biomass in the 1940s was considerably higher than at present. Breen and Kim (2006) report that vulnerable lobster biomass was approximately four times greater in the 1940s compared to present for the CRA4 management area in which the model area is located. We have used this estimate for the historical ecosystem model. In order to reflect the higher

Table 1
Inputs for the historical and pre-MR ecosystem models. *B*: initial biomass ($\mathrm{g\,C\,m^{-2}}$); L_{rec}: recreational fishery landings; L_{com}: commercial fishery landings; *P*/*B*: production/biomass ratio ($\mathrm{yr^{-1}}$); *Q*/*B*: consumption/biomass ratio ($\mathrm{yr^{-1}}$).

	Functional group	Historical	Pre-MR				
		B	*B*	L_{rec}	L_{com}	*P*/*B*	*Q*/*B*
1	Birds	0.00022	0.00022			0.10	89.70
2	Lobster	1.64	0.41	0.02	0.18	0.50	7.40
3	Mob inverts herb	1.91	0.97			1.30	7.94
4	Abalone (paua)	0.46	0.23	0.15		1.50	15.00
5	Urchins (kina)	0.12	0.06			1.10	7.50
6	Mob invert carn	0.61	0.61			1.76	5.97
7	Sea cucumber	0.35	0.35			0.60	3.40
8	Phytal/infaunal inverts	0.54	0.54			3.67	12.00
9	Sponges	1.59	1.59			0.20	0.80
10	Sessile inverts	1.56	1.56			1.50	6.00
11	Fish cryptic	0.04	0.04			2.40	15.60
12	Fish inverts	0.13	0.09			0.41	3.59
13	Fish piscivores	0.03	0.01	0.0025		0.43	2.62
14	Fish planktivores	0.22	0.15			0.50	6.33
15	Fish herbivores	0.37	0.25	0.010	0.080	0.40	9.52
16	Microphytes	7.64	7.64			21.00	0.00
17	Macroalgae canopy	37.66	37.66			2.87	0.00
18	Macroalgae foliose	18.19	18.19			13.00	0.00
19	Macroalgae crustose	1.36	1.36			25.40	0.00
20	Meso/macrozooplankton	0.17	0.17			17.70	51.50
21	Microzooplankton	0.06	0.06			220.00	624.00
22	Phytoplankton	0.48	0.48			324.00	0.00
23	Bacteria	0.60	0.60			100.00	400.00
24	Detritus	1.00	1.00				

biomasses of other species that have also been exploited over the last 60 years, we also increased the biomasses of trophic groups that contain targeted species; kina, mobile invertebrate – herbivores, paua, and piscivorous fishes, fish – invertebrate feeders, fish – herbivores, and fish – planktivores. These estimates were scaled from Ministry of Fisheries (2009b) unfished biomass estimates and exploitation histories for these fisheries. The 'historical' model refers to the period in the 1940s before large-scale commercial removal of marine species occurred. While there is anecdotal evidence that hapuku (*Polyprion oxygeneios*) inhabited nearshore waters of the Cook Strait prior to intensive exploitation which now restricts it to greater depths, we could not find any records to give an indication in which areas it was found and at what abundance, and therefore have not included it in the past ecosystem model.

In the past model, higher lobster biomass brings a corresponding increase in predation by lobster on prey species. In order to supply prey biomass for the increased lobster biomass, its diet composition was changed to reflect an increase in herbivory (Tables 2 and 3). This change was based on observations (Lundquist and Pinkerton, 2008) from the Te Tapuwae o Rongokako MR (northeast New Zealand) following increases in lobster density, which resulted in a diet that consisted of a greater proportion of macroalgae than did the diet of lobster in neighbouring, unprotected areas. We also adjusted the diets of piscivorous fish, planktivorous fish, and invertebrate feeding fish in order to provide sufficient prey biomass for these trophic groups (Tables 2 and 3, Appendix C).

In the absence of information about biomasses, diets, production, and consumption rates for all species in the ecosystem for the time period that we examined, our historical model is based on information about the diets and biomasses of species for which we have evidence. In the absence of information for other parameters, we use parameter estimates from the pre-MR establishment model. While it is entirely possible that parameters for other species may have also changed as a result of the increased biomass of presently exploited species, in this study we have based our historical model on the available information about biomasses and diets of exploited species.

2.8. *Prediction of the future ecosystem*

To evaluate the likelihood of the Taputeranga MR ecosystem returning to its historical state, we ran a simulation from the exploited, pre-MR establishment state into the future for 42 years using EwE (Walters et al., 1997; Christensen et al., 2008). The 'future' ecosystem state refers to the results of model predictions for the year 2050 for only the MR portion of the model area to observe the response following exclusion of fishing. This simulation makes two key assumptions: first, that there is no illegal fishing or poaching from within the MR, and second that there is no density-dependent related movement out of the MR. The purpose of this simulation is to determine if the absence of exploitation of marine resources could return the ecosystem to its past ecosystem state, which includes higher biomasses of targeted species. Diet proportions were allowed to vary in the EwE model to allow for changing biomasses of different trophic groups. Simulations of the MR (fishery mortality of 0) were performed using parameter estimates for the entire model area, which is representative of the MR.

Vulnerability (*V*) is one of the most sensitve parameters for EwE dynamic simulations, and determines basic model stability and diversity properties (Christensen and Walters, 2004; Christensen et al., 2008). It is suggested that species that have been exploited throughout time and are at low biomass in comparison to historical times may not recover if they have a low vulnerability value (Christensen et al., 2008). As the trophic group 'lobster' falls into this category, we checked that a positive lobster response as predicted by the model was similar to observations from other MRs throughout New Zealand (Ministry of Fisheries, 2009b). We tuned the vulnerability parameters of trophic groups using the historical model, which was run for 63 years (1945 until 2008) and then fitted it independently to a time series of lobster biomass and a time series of fishery mortality (Ministry of Fisheries, 2009a) to minimise the sum of squares (SS) between observed and predicted data (Appendices F and G). During the model run from 1945 to 2008, the biomasses of other trophic groups also changed as a result of connected food web linkages (Appendix H).

Table 2
Diet matrix for the pre-MR ecosystem model. Diets are expressed as a proportion of total diet. Diets highlighted in yellow indicate cannibalizing trophic groups.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	20	21	23
1	birds	-	-	-	-	-	$1*10^{-6}$	-	-	-	-	-	-	-	-	-	-	-	-
2	lobster	-	-	-	-	-	$4*10^{-4}$	-	-	-	-	-	-	-	-	-	-	-	-
3	mob inverts herb	0.20	0.21	-	-	-	0.15	-	-	-	-	-	0.12	-	-	-	-	-	-
4	paua	0.03	0.01	-	-	-	0.04	-	-	-	-	-	0.02	-	-	-	-	-	-
5	kina	0.01	0.01	-	-	-	0.01	-	-	-	-	-	0.01	-	-	-	-	-	-
6	mob invert carn	0.29	0.15	-	-	-	0.14	-	-	-	-	-	0.31	-	-	-	-	-	-
7	sea cucumber	-	-	-	-	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-
8	phytal/infaunal inverts	0.31	0.32	-	-	-	0.10	-	-	-	-	0.58	0.17	-	0.03	-	-	-	-
9	sponges	-	-	-	-	-	0.07	-	-	-	-	-	0.04	-	-	-	-	-	-
10	sessile inverts	-	-	-	0.05	0.05	0.43	-	-	-	-	0.24	0.33	-	-	-	-	-	-
11	fish cryptic	0.16	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
12	fish inverts	-	-	-	-	-	-	-	-	-	-	-	-	0.21	-	-	-	-	-
13	fish piscivores	-	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
14	fish planktivores	-	-	-	-	-	-	-	-	-	-	-	-	0.53	-	-	-	-	-
15	fish herbivores	-	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
16	microphytes	-	-	0.25	0.05	0.05	-	-	0.25	-	-	-	-	-	-	-	-	-	-
17	macroalgae canopy	-	0.10	0.35	0.20	0.60	-	-	0.25	-	-	-	-	-	-	0.24	-	-	-
18	macroalgae foliose	-	-	0.20	0.35	0.15	-	-	-	-	-	-	-	-	-	0.67	-	-	-
19	macroalgae crustose	-	0.20	0.20	0.35	0.15	-	-	-	-	-	-	-	-	-	0.09	-	-	-
20	meso/macrozooplankton	-	-	-	-	-	-	-	-	-	-	0.17	-	-	0.71	-	0.06	-	-
21	microzooplankton	-	-	-	-	-	-	-	-	0.30	0.30	-	-	-	-	-	0.72	0.10	-
22	phytoplankton	-	-	-	-	-	-	-	0.25	0.40	0.40	-	-	-	-	-	0.21	0.67	-
23	bacteria	-	-	-	-	-	-	1.00	0.25	0.30	0.30	-	-	-	0.26	-	-	0.23	0.18
24	detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.82

2.9. Sensitivity analysis

We performed sensitivity analyses on the most uncertain parameters (estimated by EwE, other models, guesstimates, based on empirical relationships or general knowledge for same group/species) that had pedigree scores of 1–3 for biomass, catch, and diet and 1–4 for *P*/*B*, *Q*/*B*, and conversion factor pedigrees, as well as vulnerability parameters (*V*) for exploited trophic groups (38 parameter values for 23 different parameters; Appendices C and I). For each parameter estimate that qualified for sensitivity analysis, we ran an ecosystem simulation as above, but replaced the 'best estimate' parameter with either the high or low value of the estimated parameter range. For the conversion factor parameter estimates, we did not have a range of the estimate, so we used the coefficient of variation (CV) for that data source as indicated by EwE (80%) (Walters et al., 1997; Christensen et al., 2008) to estimate high and low parameter estimate bounds (±1 CV respectively). Using the high and/or low estimate bound for some parameters resulted in an unbalanced model, in which case we increased or decreased the parameter value to achieve model balance. For some parameters, there was not a higher or lower value other than the 'best estimate' that would result in a balanced model. We discuss these parameters specifically in Section 3. For each parameter bound sensitivity analysis run, the biomasses of all trophic groups were compared to

Table 3
Diet matrix for the historical ecosystem model. Diets are expressed as a proportion of total diet. Diets highlighted in yellow indicate cannibalizing trophic groups.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	20	21	23
1	birds	-	-	-	-	-	$1*10^{-6}$	-	-	-	-	-	-	-	-	-	-	-	-
2	lobster	-	-	-	-	-	$4*10^{-4}$	-	-	-	-	-	-	-	-	-	-	-	-
3	mob inverts herb	0.20	0.13	-	-	-	0.15	-	-	-	-	-	0.18	-	-	-	-	-	-
4	paua	0.03	0.01	-	-	-	0.04	-	-	-	-	-	0.03	-	-	-	-	-	-
5	kina	0.01	-	-	-	-	0.01	-	-	-	-	-	0.01	-	-	-	-	-	-
6	mob invert carn	0.29	0.04	-	-	-	0.14	-	-	-	-	-	0.20	-	-	-	-	-	-
7	sea cucumber	-	-	-	-	-	0.06	-	-	-	-	-	-	-	-	-	-	-	-
8	phytal/infaunal inverts	0.31	0.09	-	-	-	0.10	-	-	-	-	0.58	0.12	-	0.04	-	-	-	-
9	sponges	-	-	-	-	-	0.07	-	-	-	-	-	0.06	-	-	-	-	-	-
10	sessile inverts	-	-	-	0.05	0.05	0.43	-	-	-	-	0.24	0.41	-	-	-	-	-	-
11	fish cryptic	0.16	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
12	fish inverts	-	-	-	-	-	-	-	-	-	-	-	-	0.21	-	-	-	-	-
13	fish piscivores	-	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
14	fish planktivores	-	-	-	-	-	-	-	-	-	-	-	-	0.53	-	-	-	-	-
15	fish herbivores	-	-	-	-	-	-	-	-	-	-	-	-	0.09	-	-	-	-	-
16	microphytes	-	-	0.25	0.05	0.05	-	-	0.25	-	-	-	-	-	-	-	-	-	-
17	macroalgae canopy	-	0.24	0.35	0.20	0.60	-	-	0.25	-	-	-	-	-	-	0.24	-	-	-
18	macroalgae foliose	-	-	0.20	0.35	0.15	-	-	-	-	-	-	-	-	-	0.67	-	-	-
19	macroalgae crustose	-	0.49	0.20	0.35	0.15	-	-	-	-	-	-	-	-	-	0.09	-	-	-
20	meso/macrozooplankton	-	-	-	-	-	-	-	-	-	-	0.17	-	-	0.82	-	0.20	-	-
21	microzooplankton	-	-	-	-	-	-	-	-	0.30	0.30	-	-	-	-	-	0.70	0.10	-
22	phytoplankton	-	-	-	-	-	-	-	0.25	0.40	0.40	-	-	-	-	-	0.10	0.65	-
23	bacteria	-	-	-	-	-	-	1.00	0.25	0.30	0.30	-	-	-	0.14	-	-	0.25	0.18
24	detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.82

the biomasses of all trophic groups from the 'best estimates' run. We calculated the proportion of trophic groups within the entire ecosystem that differed by at least 20% (±20% biomass) and investigated which individual trophic groups contributed to these results (Appendix I).

3. Results

3.1. Ecosystem structure and function

The pre-MR, exploited ecosystem model is described by 24 trophic groups linked by 77 predator–prey interactions, and approximately five trophic levels (Fig. 2 and Table 1), with the majority of biomass within the ecosystem being made up of primary producers (Fig. 2). Macroalgal trophic groups accounted for 78% of the biomass in the ecosystem, being made up of 51% canopy, 25% foliose and 2% crustose species. Microphytes accounted for 10% of ecosystem biomass. The benthic invertebrate trophic groups accounted for 8% of ecosystem biomass, made up of 2.1% sessile taxa, 2.1% sponges, 1.3% mobile herbivores, 0.8% mobile carnivores, 0.7% phytal/infaunal, 0.6% lobster, 0.3% paua, and 0.1% kina. Detritus made up 1.3% of ecosystem biomass. Plankton made up 1% of ecosystem biomass, being composed of 0.7% phytoplankton, 0.2% meso/macrozooplankton, and 0.1% microzooplankton.

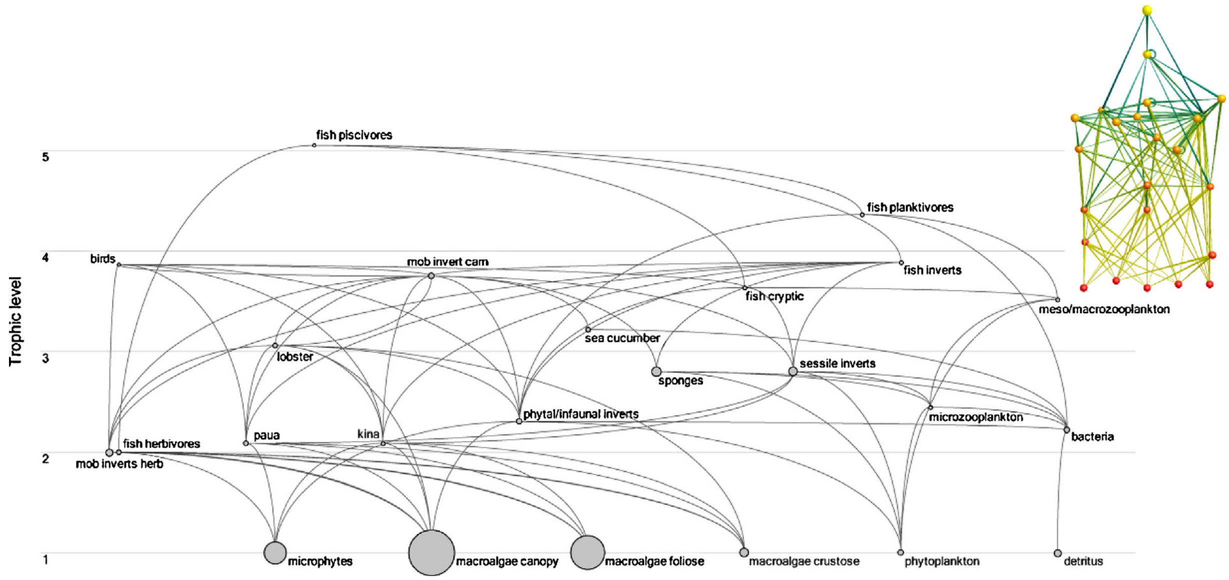

Fig. 2. Flow diagrams for the Wellington south coast ecosystem model. Circle size of each trophic group is proportional to amount of biomass. Direction of energy flow is represented by position of line with relation to circle: flows positioned on the top of a trophic group indicate biomass outgoing, while flows positioned on the side indicate entering biomass. Coloured insert shows a 3D representation of the food web with energy flowing from the small to the large end of each food web link. Canabalising trophic groups are indicated by a closed loop food web link. 3D Image produced with FoodWeb3D; Yoon I, Williams RJ, Levine E, Yoon S, Dunne JA, Martinez ND (2004). Webs on the Web (WoW): 3D visualisation of ecological networks on the WWW for collaborative research and education. Proceedings of the IS&T/SPIE Symposium on Electronic Imaging, Visualisation and Data Analysis 5295: 124–132.

Bacteria accounted for 0.8% of ecosystem biomass. Fish trophic groups accounted for 0.5%, made up of 0.2% herbivores fishes, 0.1% planktivores, 0.1% invertebrate feeders, 0.1% cryptic reef fishes and less than 0.1% piscivores. Birds accounted for less than 0.001% of ecosystem biomass. In the historical ecosystem model, biomass is distributed slightly differently, with 75% accounted for by macroalgae, 11% by invertebrates, 10% by microphytes, 1.3% by detritus, 1% by fishes, 0.9% by plankton, 0.8% by bacteria, and less than 0.001% by birds.

The historical ecosystem model resulted in a 4% greater average biomass per unit area in comparison to the pre-MR, exploited ecosystem (77.3 g C m^{-2} vs. 74.5 g C m^{-2} respectively). The historical ecosystem model differed from the pre-MR ecosystem model by having higher biomasses for the trophic groups: lobster, mobile invertebrate – herbivores, paua, kina, fish – invertebrate feeders, fish – piscivores, fish – planktivores, and fish – herbivores (Table 1). The diet matrix for the historical and pre-MR ecosystem models differed as a result of having greater biomass of some trophic groups in the historical model, which require a greater quantity of prey biomass not supplied by the present diet matrix (Tables 2 and 3).

For the historical and pre-MR ecosystem models, the top predators were fish – piscivores, with trophic levels of 4.75 and 4.77, respectively (Table 4). The future ecosystem simulation predicts that fish – planktivores will be the top predator with a trophic level of 3.91. For the historical and pre-MR ecosystem models, fish – planktivores, fish – invertebrate feeders, and birds made up the next highest trophic level groups. For the future ecosystem simulation, fish – invertebrate feeders, birds, and fish – piscivores had the next highest trophic levels. The trophic level of lobster increased from 2.36 in the past ecosystem model to 3.06 in the pre-MR ecosystem model as a result of decreased herbivory following the four-fold decrease in lobster biomass (Table 4). The trophic level of fish – piscivores decreased from 4.77 in the pre-MR model to 3.79 in the future model due to increased predation on the lower trophic level prey such as fish – herbivores, which increased in biomass due to the absence of exploitation (Table 4).

The keystoneness plot indicates that the two most keystone trophic groups (having a keystone index 1 value greater than

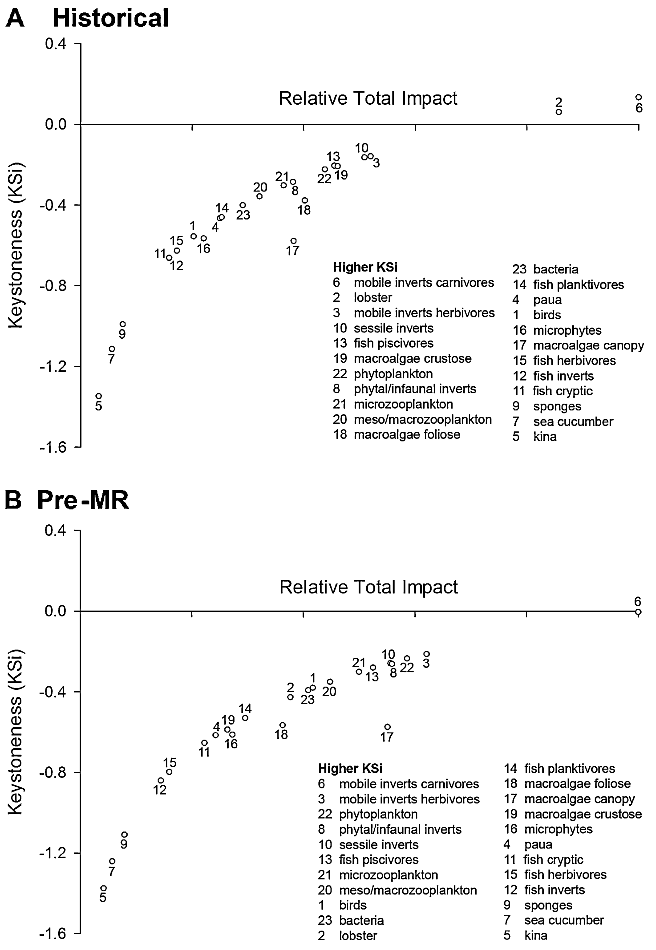

Fig. 3. Keystoneness (KS_i) of each functional group for the historical and pre-MR ecosystem models. Keystone groups are those with higher relative total impact (ε_i) and higher KS_i (value close to or greater than zero). Higher KS_i shows rank of trophic group by KS_i value.

Table 4
Model outputs for the historical, pre-MR, and future periods. TL = trophic level; EE = ecotrophic efficiency; M = predation mortality (yr^{-1}); F = fishery mortality (yr^{-1}); B = biomass.

	Trophic group	Historical			Pre-MR			Future			
		TL	EE	M	TL	EE	M	F	B	TL	M
1	Birds	3.85	0.17	0.02	3.85	0.17	0.02	0	0.00024	3.82	0.10
2	Lobster	2.36	0	0	3.06	0.98	0	0.48	5.14	3.05	0.03
3	Mob inverts herb	2.00	0.89	1.16	2.00	0.78	1.02	0	0.93	2.00	1.30
4	Paua	2.09	0.35	0.52	2.09	0.92	0.73	0.65	0.37	2.08	1.36
5	Kina	2.09	0.51	0.56	2.09	0.69	0.76	0	0.06	2.08	1.10
6	Mob invert carn	3.75	1.00	1.76	3.75	0.82	1.45	0	0.64	3.71	1.76
7	Sea cucumber	3.22	0.97	0.58	3.22	0.97	0.58	0	0.34	3.22	0.60
8	Phytal/infaunal inverts	2.30	1.00	3.65	2.30	0.72	2.65	0	0.54	2.31	3.66
9	Sponges	2.79	0.89	0.18	2.79	0.84	0.17	0	1.56	2.79	0.20
10	Sessile inverts	2.79	1.00	1.50	2.79	0.88	1.32	0	1.46	2.79	1.51
11	Fish cryptic	3.57	0.09	0.22	3.57	0.065	0.16	0	0.04	3.57	2.41
12	Fish inverts	3.67	0.30	0.12	3.88	0.25	0.10	0	0.07	3.87	0.42
13	Fish piscivores	4.75	0.54	0.23	4.77	0.99	0.26	0.17	0.05	3.79	0.42
14	Fish planktivores	3.89	0.37	0.19	3.89	0.31	0.15	0	0.13	3.91	0.52
15	Fish herbivores	2.00	0.05	0.02	2.00	0.94	0.02	0.36	1.98	2.00	0.09
16	Microphytes	1.00	0.04	0.76	1.00	0.02	0.49	0	7.64	1.00	21.01
17	Macroalgae canopy	1.00	0.12	0.34	1.00	0.06	0.16	0	37.11	1.00	2.89
18	Macroalgae foliose	1.00	0.03	0.44	1.00	0.02	0.24	0	17.89	1.00	13.11
19	Macroalgae crustose	1.00	0.34	8.68	1.00	0.10	2.50	0	1.30	1.00	25.97
20	Meso/macrozooplankton	3.17	0.54	9.58	3.17	0.89	15.75	0	0.18	3.17	17.61
21	Microzooplankton	2.42	0.99	217	2.42	0.97	213.09	0	0.06	2.42	220.49
22	Phytoplankton	1.00	0.21	69.37	1.00	0.20	65.74	0	0.49	1.00	323.60
23	Bacteria	2.22	0.97	97.39	2.22	0.98	98.19	0	0.60	2.22	99.47
24	Detritus	1.00	0.28	0	1.00	0.28	0	0	1.00	1.00	0.00

or close to 0) for the historical ecosystem model were mobile invertebrate carnivores (keystone index 1 = 0.133, Libralato et al., 2006), followed by lobster (keystone index 1 = 0.0601; Fig. 3A). The pre-MR ecosystem model indicates that mobile invertebrate carnivores were the only keystone trophic group (keystone index 1 = −0.00478; Fig. 3B). In the pre-MR model, lobster are no longer keystone (keystone index 1 = −0.427; Fig. 3B).

The mixed-trophic impact analysis displays direct and indirect impacts of very small increases in biomasses of groups (impacting groups) on the biomasses of other groups (impacted groups) (Fig. 4). These impacts are relative, but comparable among groups within any one time period, and form the basis for keystone index calculations. For the historical ecosystem model, mobile invertebrate carnivores were the most keystone trophic group, negatively impacting all prey species except mobile invertebrate herbivores and phytal/infaunal invertebrates. Lobster were the second most keystone trophic group, resulting in negative impacts for their prey (except macroalgae canopy) and positive impacts on the prey of their prey, indicating a trophic cascade (Figs. 2 and 4). Mobile invertebrate herbivores were the third most keystone species and negatively impacted their prey species and also competitors that consume the same prey items. Mobile invertebrate herbivores positively impacted three of their predators, namely birds, mobile invertebrate carnivores, and fish – invertebrate feeders.

For the pre-MR ecosystem model, the keystone trophic group – mobile invertebrate – carnivores – had a negative effect on all of its prey species, with the exception of lobster (Figs. 2–4). Positive impacts exerted by mobile invertebrate – carnivores were observed for the prey of their prey and were smaller in magnitude compared to the negative impacts (Figs. 2 and 4). Mobile invertebrate – herbivores displayed negative effects on both their prey and also on other grazing trophic groups that compete for the same resources (Figs. 2 and 4). Phytoplankton displayed mostly positive effects for impacted groups throughout all trophic levels presumably as a result of increased carbon production flowing through the entire ecosystem (Figs. 2 and 4). Although lobster was the second most keystone group for the historic ecosystem model, this group played a much smaller role in the pre-MR ecosystem (it no longer had a keystone value greater than or close to 0), because of its greatly reduced biomass (Figs. 2 and 3). In the historical ecosystem, macroalgae – crustose, phytoplankton, and macroalgae – foliose were the most important producers, while in the pre-MR ecosystem model phytoplankton was the most important producer group (Fig. 3).

The Lindeman spine indicates equal or higher biomass for all of the trophic levels in the historical ecosystem model in comparison to the pre-MR model, with a large difference in the second trophic level (secondary producers; Fig. 5). Transfer efficiencies were lower on average for the historical ecosystem model (24.9% for historical and 25.4% for pre-MR; Fig. 5). Ascendancy was lower for the historical ecosystem model at 36.1% in comparison to 36.7% in the pre-MR model, indicating that less energy was available to respond to unexpected perturbations in the historical ecosystem.

3.2. *Impacts of fisheries and MR protection*

Results from the pre-MR ecosystem model indicate that commercial fisheries for lobster and butterfish operating in the model area had the greatest impacts on the ecosystem (Fig. 4B). Of the recreational fisheries, those for paua and blue cod had the greatest impacts on the ecosystem (Fig. 4B). Of the harvested species, lobster required the greatest proportion of primary production to support them at 1.79%, followed by piscivorous fish (0.48%), herbivorous fish (0.17%), and paua (0.15%). The majority of biomass removed by fisheries is from secondary producers of trophic level II, followed by trophic levels III, IV, and V (Fig. 5).

Results from the future ‘no fishing’ simulation predict that the biomasses of previously targeted trophic groups will increase in the absence of fishing (Table 4). Overall, total ecosystem biomass predicted by the future model is 78.6 $g\,C\,m^{-2}$, which is 5.5% greater than prior to MR establishment and 1.7% greater than occurred historically. Along with exploited trophic groups, other groups that the future model suggests will increase in biomass are birds, meso/macrozoplankton, sea cucumber, sponges, sessile invertebrates, microphytes, macroalgae canopy, and phytoplankton (Table 4). Trophic groups that are predicted to decline in biomass in the future simulation are microzooplankton, mobile

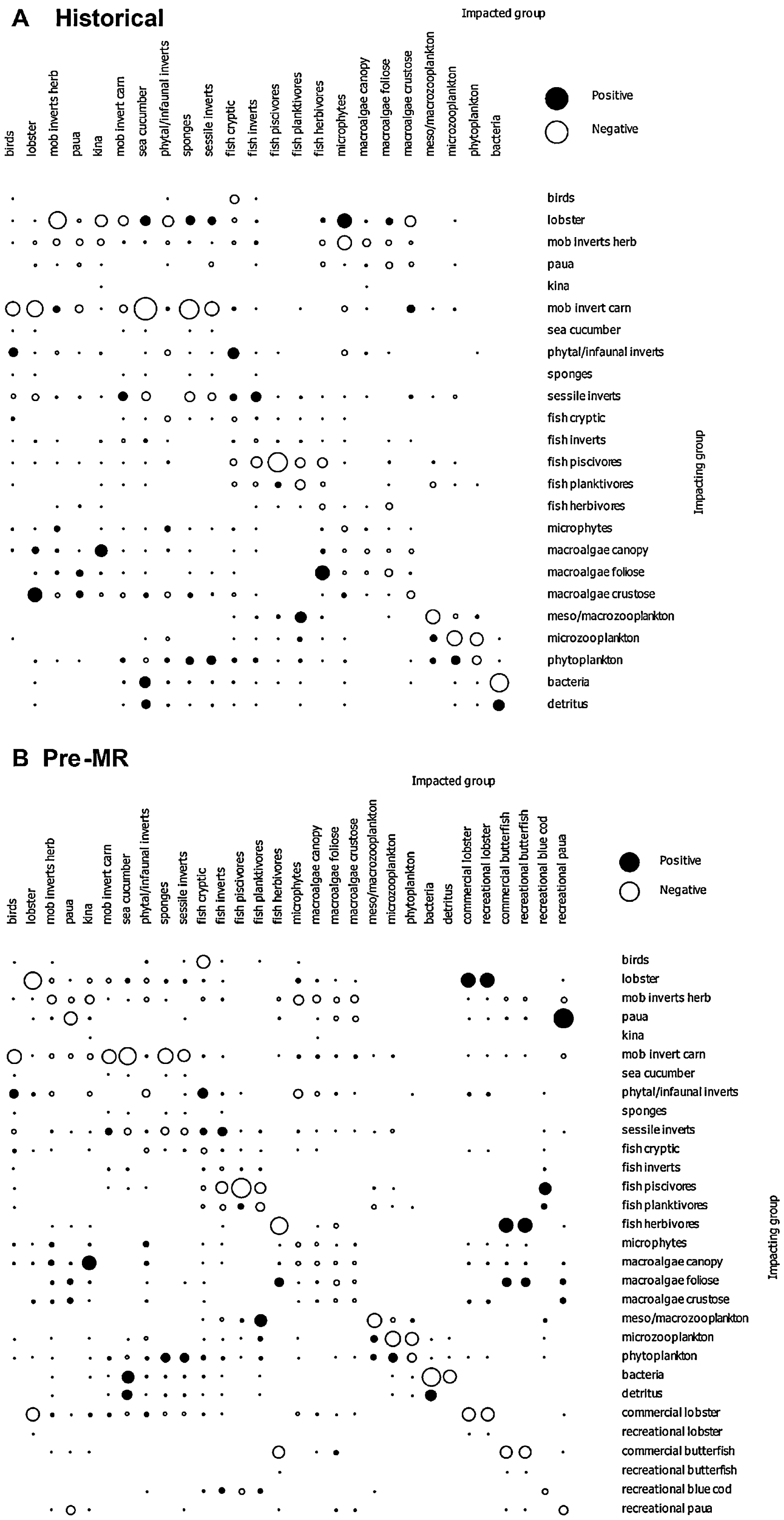

Fig. 4. Mixed trophic impacts (MTI) for historical and pre-MR models. Plots indicate the combined direct and indirect trophic impacts that an infinitesimal increase of any of the trophic groups in rows (impacting group) is predicted to have on the groups in columns (impacted group) in the historical (A) and pre-MR (B) models. Size of the circle is proportional to the degree of change.

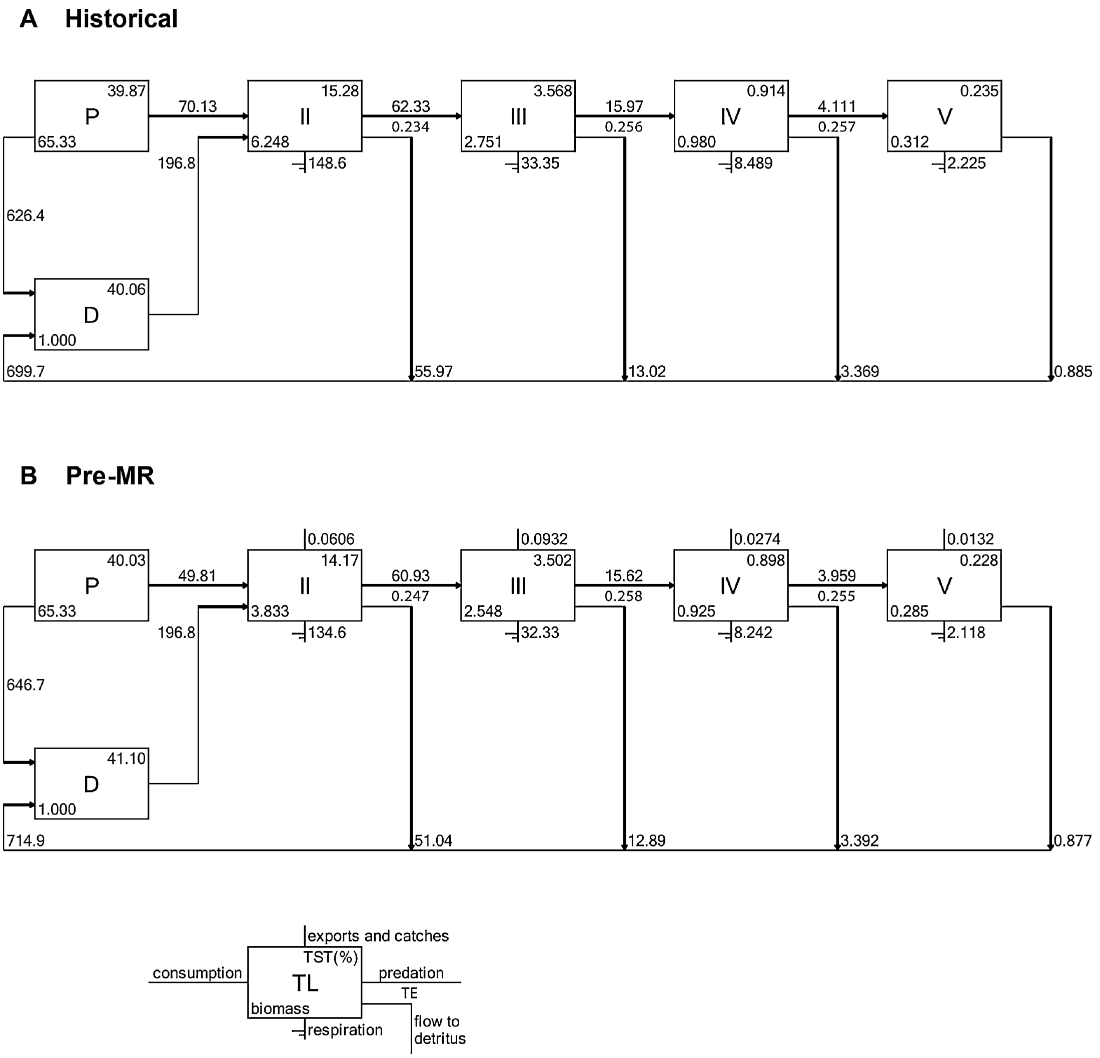

Fig. 5. Lindeman spine for historical and pre-MR ecosystem models. Lindeman spline indicates flows between trophic levels and export of biomass due to catch at each trophic level.

invertebrates – carnivores, kina, phytal/infaunal invertebrates, mobile invertebrates – herbivores, macroalgae – foliose, macroalgae – crustose, fish – planktivores, fish – invertebrate feeders, and fish – cryptic (Table 4).

Trophic control within the predicted ecosystem under the future MR scenario is closer to the historical ecosystem reconstruction following biomass recoveries of trophic groups exploited in the pre-MR model. Overall, the future ecosystem model predicts that the keystone role of lobster will increase from the pre-MR keystone index 1 value of −0.427 to −0.24, thereby restoring ecosystem function to levels associated with the historical model.

3.3. Sensitivity analyses

Results from the sensitivity analysis indicate that the parameter 'lobster high *V* (vulnerability)' is the most sensitive parameter, which results in 7 trophic groups being impacted by a change in biomass of least 20% biomass in comparison to the results from the 'best estimate' parameters (birds; lobster; mobile invertebrates herbivores; kina; sea cucumber; phytal/infaunal invertebrates; fish cryptic: Appendix I). Other parameters that impacted trophic groups by at least 20% changes in biomass other than the trophic group associated with the parameter are all fish – herbivores parameters, which also impact fish – piscivores for the parameters low *P*/*B*, high *P*/*B*, high *B*, and low *V* (Appendix I). Parameters that impacted only the trophic group with which they were associated by at least 20% biomass were paua low *V*, fish – cryptic low *B*, fish – cryptic high *B*, fish – invertebrates low *B*, fish – invertebrates high *B*, fish – piscivores high *B*, fish – planktivores low *B*, and fish – planktivores high *B* (Appendix I).

4. Discussion

4.1. Historical, pre-MR establishment, and future ecosystem states

The degree of ecosystem exploitation and change that has taken place during the last 70 years of fishing activity along the Wellington south coast is not as severe as has been documented at European locations, which have in some cases been subjected to 2500 years of exploitation (Coll et al., 2009a, 2009b). The degree of exploitation that we have observed is more similar to marine ecosystems with shorter and less intense exploitation histories, such as in northern British Columbia, Canada (Ainsworth et al., 2008). Historically, not all forms of human exploitation lead to ecosystem degradation. For example, in Hawai'i, following a period of decline, coral reef ecosystems recovered from the 1400s to the 1800s as a result of changes in underlying human social systems (Kittinger et al., 2011). Although our analyses of fishery impacts have been constrained to the commercial and recreational fisheries operating in the last 70 years in the Wellington region, estimates of the annual exploitation of 100 species of marine shellfish, fish, shore and sea birds, and marine mammals by pre-European Māori (Smith, 2011a,b), including all the harvested species we have modelled, provide an indication of fishing impacts prior to European arrival. Therefore, given the known impact of Maori communities on coastal resources, it seems likely that the historical model that we have parameterised for the Wellington south coast in 1945 was not based on a pristine ecosystem. There are present modelling efforts underway to parametise New Zealand coastal ecosystems for five time periods over the last millennium in order to understand how humans have impacted marine ecosystems since first settlement (Matt Pinkerton, NIWA, Wellington, unpublished data).

In the historical and future ecosystem states, due to decreased exploitation, lobster biomass was or will be greater than that prior to MR establishment. Increased biomass results in lobster having a stronger influence on ecosystem trophic interactions, thereby increasing this group's keystone role. The extent to which lobster are able to change their diet and become more or less herbivorous has been demonstrated at the Te Tapuwae o Rongokako MR, New Zealand, using stable isotope analysis (Lundquist and Pinkerton, 2008), where there is a greater abundance of lobster inside the MR in comparison to neighbouring areas (Freeman et al., 2009). Furthermore, lobster inside the Te Tapuwae o Rongokako MR display different feeding behaviour compared to lobster at neighbouring unprotected locations by foraging on the intertidal platform at night for a range of macroalgal species (Freeman, 2007). At the Cape Rodney – Okakari Point MR (Leigh or Goat Island MR) in northeast New Zealand, predation by large rock lobster has been found to potentially account for the distributional patterns of certain bivalve populations (Langlois et al., 2006a), and it has been shown that larger lobster are able to prey on a larger size range of prey species (Langlois et al., 2006b). The increased lobster biomass expected to occur in the future at the Taputeranga MR will likely require a change in their diet to include a greater proportion of macroalgae due to the absence of mussels on Wellington's south coast (Gardner, 2000, 2013; Helson and Gardner, 2004; Helson et al., 2007), typically a staple diet component.

The recovery of lobster populations within the Te Tapuwae o Rongokako MR that has resulted in their recolonisation of the intertidal zone (Freeman, 2007) reflects historical accounts of lobster observed in the intertidal and shallow subtidal zones at Great Mercury Island, New Zealand in 1872. "There are quite a lot [of lobster] in the seaweed that fringes the beaches and reefs around the Island" (Anon., 1977). Traditional fishing practices were described by the observation: "The Māori felt for the crayfish [lobster] with their feet, then reached down and caught them by their feelers and threw them onto the beach. In about 20 min, they caught about 12–15 crayfish [lobster]" (Anon., 1977). Similar observations of previously high lobster abundance in the intertidal zone during historical times have also been made of a closely-related lobster species (*Jasus frontalis*) in the Juan Fernández Archipelago, Chile (Eddy et al., 2010). We suggest that as lobster biomass in the Taputeranga MR increases, lobster will also be observed foraging in the intertidal zone.

While the biomasses of exploited species and trophic groups along Wellington's south coast (including the newly established Taputeranga MR) have been substantially depleted, our modelling predicts that overall ecosystem biomass and the biomasses of lobster, paua and some fishes will respond positively to MR protection over several decades and return to a state closer to the historical levels of 1940. Overall, ecosystem structure and function such as transfer efficiency are predicted to return to historical levels. This is in line with findings from other comparisons of protected and exploited ecosystems, such as in the Adriatic Sea (Libralato et al., 2010). Ascendency, a measure of the amount of energy in reserve in the ecosystem to respond to unexpected perturbations, was predicted to be higherest in the pre-MR ecosystem. However, not all trophic groups and species are predicted to increase in biomass due to the complex nature of food-web linkages in marine ecosystems. This is represented in the MTI analysis, which indicates that as the biomasses of exploited trophic groups change, so do the biomasses of other trophic groups. Thus, the structure and function of the entire ecosystem may change through direct (predator–prey) and indirect (trophic cascade) mechanisms. Other mechanisms potentially explaining changing biomasses of trophic groups may be prey avoidance and shifts in vulnerability as predator biomass increases. Predictions from the future simulation indicate that the ecosystem can support increased biomasses of previously targeted species following exclusion of fishing pressure in the Taputeranga MR. We have not included the recent addition of harvest for the kelp, *Macrocystis pyrifera*, to the New Zealand QMS in our ecosystem model, but note that this trophic group forms the majority of primary production in the coastal ecosystem and should therefore be managed accordingly.

Building EwE models for an area has value in that it requires the collection of a wide range of data across all species in the ecosystem. This collection procedure highlights areas that are information poor, and this study was no exception. The temperate rocky reef community on the south coast of Wellington is well studied, but there is much less information available for the soft sediment community. Further research in this area will provide useful information not only for understanding the biology and ecology of the local soft sediment community, but also to inform future ecosystem modelling. Production (P/B) and consumption (Q/B) rates for most fishes and some invertebrates in New Zealand have not been quantified, with the result that future research will undoubtedly provide a valuable contribution to the scientific literature. We have represented one hypothesis of the historical model based on the available information for biomasses of exploited species. We have also adjusted the diet of the trophic group 'lobster' to balance the model, which has been observed to change with increased biomass (Lundquist and Pinkerton, 2008). It is possible that other parameters have also changed, but in the absence of this information we have used values that were estimated for the pre-MR establishment model. The sensitivity analysis has provided insight about how alternative parameter estimates affect model output. The future model is one representation of many potential hypotheses, given that there is uncertainty in the model input data. Researchers have studied the potential effects of parameter uncertainty on ecosystem models to show that multiple outcomes may be predicted (Mackinson et al., 2003; Hill et al., 2007; Link et al., 2010a,b; McElhany et al., 2010).

4.2. The future perspective

The purpose of the future ecosystem model was to determine if exclusion of fishery exploitation will return the existing ecosystem to a state more similar to that observed in the past. The EwE trophic web ecosystem model often suggests that ecosystems 'rewind' on simple recovery trajectories when fishing pressures are eliminated (Pitcher, 2005; Ainsworth and Pitcher, 2010; criticised by Campbell et al., 2009). In the real world, more complex non-linear ecological interactions, especially those associated with habitat changes, may prevent such a simple recovery. Also, the future ecosystem model does not take into account spillover from the Taputeranga MR to neighbouring fished locations, an outcome that is probable given observations of lobster movement out of other MRs in New Zealand

(Kelly and MacDiarmid, 2003) and the configuration of the Taputeranga MR boundaries that cross reef habitat patches (e.g. Freeman et al., 2009). For these reasons, the predicted magnitude of change within the Taputeranga MR may be exaggerated, particularly for the reef system at the eastern end of the MR that is bisected by the MR boundary (Fig. 1). However, the value of the future model is that it suggests how relative ecosystem structure will change in the absence of exploitation. Evidence from the Te Tapuowae o Rongokako MR suggests that annual growth rates for adult lobster are greater inside the MR in comparison to neighbouring fished areas, likely due to the indirect effects of fishing (Lundquist and Pinkerton, 2008). If a similar response occurs at the Taputeranga MR, then our model predictions may be underestimating the rate of lobster biomass increase.

There are many factors that need to be considered when making predictions about future ecosystem states, including, interannual seasonal variability, the El Nino Southern Oscillation (ENSO), climate change, food availability, habitat quality and quantity, larval supply, larval recruitment, predation pressure, and environmental controls (currents, temperature, nutrient levels). However, evidence from other MRs in New Zealand has shown that the size and abundance of previously exploited species typically increase after MR implementation (Kelly et al., 2000; Pande et al., 2008; Diaz et al., 2012), and our results indicate that this will also be the case for the Taputeranga MR. In the context of MRs as biodiversity conservation tools, such a finding is encouraging both at the level of the response of individually targeted species and also at the ecosystem level.

4.3. New Zealand coastal ecosystems

Trophic control of reef ecosystems has been studied at three North Island New Zealand MRs; Cape Rodney – Okakari Point MR, Te Tapuwae o Rongokako MR and Taputeranga MR, and three South Island MRs; Te Awaatu Channel MR, Kutu Parera MR, and Taipari Roa MR. A fourth-order trophic cascade (Langlois and Ballantine, 2005) observed at the warm-temperate and moderately wave-sheltered Cape Rodney – Okakari Point MR (established in 1975) followed the recovery of lobster (*J. edwardsii*) and snapper (*C. auratus*) populations within the MR (Shears and Babcock, 2003). At the Te Awaatu Channel and Kutu Parera MRs, located in Fiordland, on the South Island of New Zealand, more lobster were found within MRs, compared to surrounding open fishing areas (Jack et al., 2009). At the Taipari Roa MR, located in the same region, lobster abundance was lower inside the MR compared to the Te Awaatu Channel and Kutu Parera MRs, likely due to a lower abundance of bivalve prey species (demonstrated using stable isotope analysis), resulting in resource limitation and a greater proporation of primary producers in lobster diet (Jack et al., 2009).

The waters of the Cook Strait, where our study was focused are subject to high wave, wind, and current energy, and host a different community of marine species to other regions studied to date (Shears and Babcock, 2007; Pande and Gardner, 2009). Consequently, trophic linkages are also likely to differ compared to trophic linkages from other regions, and importantly, kina (urchins; *Evechinus chloroticus*) do not form large aggregations on Wellington's south coast, and extensive urchin grazed areas reported farther north are not present here (Pande, 2001; Shears and Babcock, 2003; Pande and Gardner, 2009). For this reason, we do not expect to see a similar trophic cascade as observed at the Cape Rodney – Okakari Point MR, but we do predict at least a second-order change following increases in exploited species and decreases in their prey items (Langlois and Ballantine, 2005). In the pre-MR establishment ecosystem model, mobile invertebrate carnivores such as crabs, asteroids, gastropods, and octopus exerted the greatest trophic control on the ecosystem. In the historical model, trophic control of the ecosystem was more evenly shared by lobster and mobile invertebrate carnivores, indicating that both groups played keystone roles.

Like the Te Tapuwae o Rongokako MR that is located 300 km to the northeast, the Taputeranga MR has a high biomass of macroalgae, but Taputeranga MR also has three-fold more lobster and ten-fold more mobile invertebrate carnivores (Lundquist and Pinkerton, 2008; Pinkerton et al., 2008). In contrast, Te Tapuwae o Rongokako has higher biomasses of three fish groups: invertebrate feeders, piscivores, and planktivores. Notably, despite geographic differences in the composition of reef communities at all three North Island locations where trophic control has been studied, lobster play or played a keystone role in trophic control of the ecosystem. It also appears that lobsters are showing similar effects in the South Island MRs, where lobster diet has been studied (Jack et al., 2009). Given the wide distribution and high abundance of lobster (*J. edwardsii*) around the New Zealand coastline, we suggest that when at sufficient abundance, this species plays an important ecological structuring role throughout its range.

4.4. Ecosystem impacts of lobster fisheries

Before implementation of the Taputeranga MR in 2008, lobster biomass was estimated to be, at most, approximately one quarter of that compared to the 1940s, and may have been less given that the biomass was probably in decline at the start of the historical time series (Breen and Kim, 2006). If this is the case, then our historical estimate of lobster biomass is likely to be conservative. The reduction of lobster biomass has resulted in a changed role for lobster in the ecosystem. Historically, lobster played a keystone role in the ecosystem, influencing overall ecosystem structure, dynamics, and function. This organising role had negative impacts on the trophic groups: crustose macroalgae, mobile invertebrate carnivores, urchins (kina), and mobile invertebrate herbivores through direct predation relationships, while microphytes, sessile invertebrates, sponges, and sea cucumbers benefitted by this keystone role through indirect relationships such as reduced predation. Removing three quarters or more of the biomass of a keystone species such as lobster has large impacts on the structure and function of the ecosytem. This finding indicates the inadequacy of single species fisheries management to address the ecosystem effects of exploitation, even for an information rich, high-value fishery that is co-managed by fishers and considered to be well managed (Yandle, 2006; Breen et al., 2009). While establishment of the Taputeranga MR has displaced fishing effort from the 855 ha of the reserve which may have increased pressure on the accessible stock outside the reserve but within the same quota management area (Rojas-Nazar, 2013), it has been shown that as lobster populations recover in MRs (Kelly et al., 2000; Pande et al., 2008; Diaz et al., 2012), surrounding lobster fisheries may experience a ‘spillover’ effect which can maintain catches (Kelly et al., 2002), and is influenced by the relationship of MR boundaries to subtidal and intertidal rocky reefs (Freeman et al., 2009). Given the rapid global expansion of invertebrate fisheries, which are often characterised by poor information bases (Anderson et al., 2011), our findings about the importance of the role played by lobster within a temperate reef ecosystem highlight the need for the EBFM of all species, including invertebrates.

At MRs in Tasmania, Australia, there have been similar observations about the recovery of *J. edwardsii* from heavy fishing pressure, and corresponding changes in feeding behaviour (Barrett et al., 2009a, 2009b; Guest et al., 2009). Combined chemical tracer analysis indicated that the trophic level of lobster was higher in fished areas compared to MRs, explained by greater intraspecific competition for food resources in MRs, resulting in greater consumption of lower trophic level prey species (Guest et al., 2009). It has also been found that lobster inside MRs can control abundances of prey species such as urchins and abalone (Barrett et al., 2009a), and that the removal of large predatory lobster in nearby fished areas has reduced the resilience of kelp beds against the climate-driven threats of sea urchin propagation, thereby increasing risk of a shift to widespread urchin grazed areas (Ling et al., 2009; Ling and Johnson, 2012).

Similar trophic interactions have been observed on the south-west coast of South Africa, where an area characterised by urchin grazed areas was invaded by the commercially exploited lobster, *Jasus lalandii*, resulting in a trophic cascade where urchins were virtually eliminated by lobster predation, and macroalgae increased by more than 450% (Blamey et al., 2010). This regime shift to a macroalgae dominated state had economic implications, as the juveniles of the commercially important abalone, *Haliotis midae*, are closely associated with urchins (Blamey et al., 2010). Interestingly, at two islands located on the west coast of South Africa, there appears to be alternative stable states dominated by either the lobster, *Jasus lalandii* or by whelks (mostly *Burnupena* spp.) (Barkai and McQuaid, 1988). In the lobster-dominated state, whelks are preyed upon by lobster, and in the whelk-dominated state, lobster are preyed upon by whelks (Barkai and McQuaid, 1988). Reduction of lobster abundance by fisheries in these regions is therefore expected to have strong ecosystem impacts.

These examples of complex ecosystem dynamics provide further support for the EBFM paradigm. Ecosystem models such as EwE are an invaluable tool to assess EBFM. Surveying the global evidence, it is apparent that when occurring in sufficient abundance, lobsters (*Jasus* spp.) are keystone, exterting top-down control on ecosystem structure and function, and that the reduction of lobster through fishing, diminishes this keystone role. MRs are a tool that have been proven successful in restoring the keystone role of lobster in New Zealand and Australia.

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Appendix A. Methods for parameterisation of trophic groups

A.1. Subtidal invertebrates and algae

Subtidal invertebrate and macroalgal area cover and abundance data were collected between 5 and 15 m depth using a 1 m^2 quadrat placed at 5 m intervals along a 50 m transect at 8 sites within the model area during the summer seasons of two years (2007/08 and 2008/09; Byfield, In progress; Table A1). Collections of macroalgae – canopy (*Cystophora scalaris*, *Carpophyllum flexuosum*, *Carpophyllum maschalocarpum*, *Ecklonia radiata*, *Landsburgia quercifolia*, *Lessonia variegata*, *Macrocystis pyrifera*, *Marginariella borynana*, *Marginariella urvilliana*, *Sargassum sinclairii*, *Caulerpa brownii*, *Caulerpa flexilis*, and *Zonaria turneriana*), paua (*Haliotis iris* and *Haliotis australis*), and kina (*Evechinus chloroticus*) were conducted during four sampling events (Winter 2007; Summer 2007/08; Winter 2008; Summer 2008/2009) at three sites in the model area. During each sampling event, 20 individuals of each species were collected at each site when possible ($n \sim 60$ individuals for each species during each sampling event), measured for size, and mass of wet weight in order to determine biomass to length/per cent cover ratios to covert abundance survey data to biomass per unit area (Byfield, In progress).

A.2. Intertidal invertebrates and macroalgae

Intertidal invertebrate and macroalgal area cover and abundance data to species level were collected by randomly locating a 0.5 m by 0.5 m quadrat five times at each of low, middle, and high intertidal zones, which were then fixed positions for future surveys (Tam, 2012; Jones, In progress; Table A2). Six sites were surveyed within the model area during the summer season of 2008. Conversion of area cover and abundance data to biomass of macroalgal and invertebrates species that were not collected, were determined using ratios from Lundquist and Pinkerton (2008) and Shears and Babcock (2007). Biomass was converted into g C m^{-2} using ratios for individual species (Lundquist and Pinkerton, 2008) and then pooled across trophic groups.

A.3. Subtidal fishes

Underwater observations of reef fish size and abundance were conducted seasonally from 2007 to 2008 between 5 and 15 m depth (Eddy, 2011). The 10 most abundant species included: banded wrasse (*Notolabrus fucicola*), blue cod (*Parapercis colias*), blue moki (*Latridopsis ciliaris*), butterfish (*Odax pullus*), leatherjacket (*Parika scaber*), marblefish (*Aplodactylus arctidens*), red moki (*Cheilodactylus spectabilis*), scarlet wrasse (*Pseudolabrus miles*), spotty (*Notolabrus celidotus*), and tarakihi (*Pseudolabrus macropterus*). Data for all species were averaged across all seasons. Fish species were assigned to one of four trophic groups; herbivores, planktivores, invertebrate feeders or piscivores (Table A3; Francis, 2001; Froese and Pauly, 2005). Size-frequency data were converted into biomass using non-linear length to weight relationships for north-eastern New Zealand reef fishes (Taylor and Willis, 1998; Froese and Pauly, 2005).

Commercial fishery landings data for lobster were obtained from the Ministry of Fisheries (Ministry of Fisheries, 2009b) to provide information about abundance at depths deeper than those surveyed on SCUBA (>20 m). Data for the bottom trawl demersal finfish fishery that occurred within 100 km of, and at depths found within the model area (to a maximum depth of 100 m), from 1999 to 2009 were obtained from the Ministry of Fisheries commercial fishers logbook database to provide information about abundance for demersal species (Ministry of Fisheries, 2009b; Table A.4). Biomass per unit area by depth stratum for each species was determined from the catch, area swept and catchability data (Ministry of Fisheries, 2009b). Data for pelagic finfish species occurring within 100 km of the model area from 1999 to 2009 were obtained from the Ministry of Fisheries aerial sight database (Ministry of Fisheries, 2009c; Table A.5). Biomass was converted into g C m^{-2} using a ratio of 8.3% carbon to wet weight (Lundquist and Pinkerton, 2008).

A.4. Cryptic reef fishes

The biomass of the trophic group 'cryptic reef fishes' was estimated from an intertidal study that was conducted within the model area (Willis and Roberts, 1996) and from New Zealand

Table A1
Trophic group composition by species/group observed during subtidal surveys of algae and invertebrates.

Trophic group	Family	Species/group
Mob invert carn	Actiniidae	*Phlyctenactis tuberculosa*
	Archidorididae	*Archidoris wellingtoniensis*
	Asteriidae	*Astrostole scabra*
		Coscinasterias calamaria
	Asterinidae	*Patiriella regularis*
	Buccinidae	*Buccilinum* sp.
		Buccinulum linea
		Cominella virgata
	Chromodorididae	*Chromodoris aureomarginata*
	Discodorididae	*Aphelodoris luctuosa*
	Echinasteridae	*Stegnaster inflatus*
	Grapsidae	*Plagusia chabris*
	Muricidae	*Haustrum haustorium*
	Octopodidae	*Octopus vulgaris*
	Odontasteridae	*Diplodontias dilatatus*
	Ophiodermatidae	*Pectinura maculata*
	Pentagonasterinae	*Pentagonaster pulchellus*
	Ranellidae	*Argobuccinum pustulosum tumidum*
		Cabestana spengleri
	Stichasteridae	*Stichaster australis*
Kina	Echinometridae	*Evechinus chloroticus*
Lobster	Palinuridae	*Jasus edwardsii*
Macroalgae canopy	Alariaceae	*Ecklonia radiata*
		Macrocystis pyrifera
		Undaria pinnatifida
	Cystoseiraceae	*Cystophora scalaris*
		Landsburgia quercifolia
	Lessoniaceae	*Lessonia variegata*
	Sargassaceae	*Carpophyllum flexuosum*
		Carpophyllum maschalocarpum
		Sargassum sinclairii
	Seirococcaceae	*Marginariella* sp.
Macroalgae crustose	Corallinaceae	*Corallina officinalis*
		Geniculate coralline algae (GCA)
		Jania micrarthrodia
	Corallinaceae, Hapalidiaceae, Sporolithaceae	Crustose coralline algae (CCA)
Macroalgae foliose	Caulerpaceae	*Caulerpa geminata*
		Caulerpa brownii
		Caulerpa flexilis
	Champiaceae	*Champia laingii*
	Desmarestiaceae	*Desmarestia ligulata*
	Dictyotaceae	*Glossophora kunthii*
		Zonaria turneriana
	Fucaceae	*Xiphophora gladiata*
	Gelidiaceae	*Pterocladia lucida*
	Gigartinaceae	*Gigartina circumcincta*
		Gigartina decipiens
	Plocamiaceae	*Plocamium microcladioides*
	Rhodomelaceae	*Cladhymenia oblongifolia*
		Rhodymenia dichotoma
	Scytosiphonaceae	*Colpomenia sinuosa*
	Sporochnaceae	*Carpomitra costata*
	Stypocaulaceae	*Halopteris congesta*
		Halopteris funicularis
		Halopteris virgata
	Ulvaceae	*Ulva sp.*
Mob invert herb	Callochitonidae	*Eudoxochiton nobilis*
	Chitonidae	*Chiton glaucus*
		Sypharochiton pelliserpentis
	Fissurellidae	*Scutus breviculus*
	Ischnochitonidae	*Ischnochiton maorianus*
	Mopaliidae	*Plaxiphora obtecta*
	Trochidae	*Cantharidus opalus*
		Cantharidus purpureus
		Trochus viridis
	Turbinidae	*Cookia sulcata*
		Modelia granulosa
		Turbo smaragdus
Paua	Haliotidae	*Haliotis australis*
		Haliotis iris
Sea cucumber	Stichopodidae	*Stichopus mollis*
Sessile inverts		Class Hydrozoa
		Genus Ascidia
		Phylum Bryozoa
Sponges		Phylum Porifera

Table A2
Trophic group composition by species/group observed during intertidal surveys of algae and invertebrates.

Trophic group	Family	Species
Macroalgae canopy	Alariaceae	*Undaria pinnatifida*
	Durvillaeaceae	*Durvillaea antarctica*
	Lessoniaceae	*Lessonia variegata*
	Sargassaceae	*Carpophyllum maschalocarpum*
		Cystophora scalaris
		Cystophora sp.
Macroalgae crustose	Corallinaceae	*Corallina officinalis*
		Encrusting coralline pink
	Gelidiaceae	*Gelidium pusillum*
	Hildenbrandiaceae	*Hildenbrandia* sp.
	Liagoraceae	*Helminthocladia* spp.
	Ralfsiaceae	*Ralfsia verrucosa*
Macroalgae foliose	Adenocystaceae	*Adenocystis utricularis*
	Bangiaceae	*Porphyra* sp.
	Caulacanthaceae	*Caulacanthus ustulatus*
	Champiaceae	*Champia novozealandia*
	Chordariacea	*Leathesia difformis*
	Codiaceae	*Codium convolutum*
		Codium sp.
	Dictyotaceae	*Glossophora kunthii*
		Zonaria aureomarginata
	Gigartinaceae	*Gigartina decipiens*
	Homosiraceae	*Hormosira banksii*
	Rhodomelaceae	*Bryocladia ericoides*
	Scytosiphonaceae	*Colpomenia sinuosa*
	Splachnidiaceae	*Splachnidium rugosum*
	Stypocaulaceae	*Halopteris* sp.
	Xiphophoraceae	*Xiphophora gladiata*
Mob invert carn	Asterinidae	*Patiriella regularis*
	Muricidae	*Haustrum haustorium*
		Haustrum scobina
	Stichasteridae	*Stichaster australis*
Mob invert herb	Callochitonidae	*Eudoxochiton nobilis*
	Chitonidae	*Sypharochiton pelliserpentis*
	Littorinidae	*Austrolittorina antipodum*
		Austrolittorina cincta
		Risellopsis varia
	Lottiidae	*Patelloida corticata*
	Nacellidae	*Cellana denticulata*
		Cellana ornata
		Cellana radians
	Siphonariidae	*Siphonaria* sp.
Sessile invert	Chthamalidae	*Chamaesipho brunnea*
		Chamaesipho columna

Table A3
Trophic group composition by species/group observed during subtidal surveys of reef fishes.

Trophic group	Family	Scientific name	Common name
Fish herbivores	Aplodactylidae	*Aplodactylus arctidens*	Marblefish
	Odacidae	*Odax pullus*	Butterfish
Fish inverts	Clinidae	*Cristiceps aurantiacus*	Weedfish
	Girellidae	*Girella fimbriata*	Parore
	Labridae	*Notolabrus fucicola*	Banded wrasse
		Pseudolabrus milnes	Scarlet wrasse
		Notolabrus celidotus	Spotty
	Latridae	*Latridopsis ciliaris*	Blue moki
		Latridopsis forsteri	Copper moki
		Cheilodactylus spectabilis	Red moki
	Cheilodactylidae	*Nemadactylus macropterus*	Tarakihi
	Monacanthidae	*Parika scaber*	Leatherjacket
Fish piscivores	Arripidae	*Arripis trutta*	Kahawai
	Carangidae	*Trachurus novaezelandiae*	Jack mackeral
	Pinguipedidae	*Parapercis colias*	Blue cod
Fish planktivores	Carangidae	*Decapterus koheru*	Koheru

subtidal observations (Lundquist and Pinkerton, 2008). Size-frequency data were converted into biomass data using non-linear length to weight relationships (Lundquist and Pinkerton, 2008; Froese and Pauly, 2005; Taylor and Willis, 1998). Biomass was converted into $\mathrm{g\,C\,m^{-2}}$ using a ratio of 8.3% carbon to wet weight (Lundquist and Pinkerton, 2008).

A.5. Phytoplankton

Phytoplankton biomass was estimated using Chl *a* concentration data from the SeaWifs ocean colour satellite for the period 1997–2006 for an offshore location within the model area (centroid 41° 20 S, 174° 30 E) to minimise impact of coastal

Table A.4
Trophic group composition by species/group recorded in trawl fishers' logbooks. Data extract from the New Zealand Ministry of Fisheries logbook database.

Trophic group	Family	Scientific name	Common name
Fish inverts	Bramidae	*Brama brama*	Ray's bream
	Callorhinchidae	*Callorhinchus milii*	Elephant fish
	Centrolophidae	*Seriolella brama*	Common warehou
		Seriolella punctata	Silver Common warehou
		Hyperoglyphe antarctica	Bluenose
	Chimaeridae	*Hydrolagus novaezealandiae*	Ghost shark
	Gempylidae	*Thyrsites atun*	Barracouta
	Latridae	*Latridopsis ciliaris*	Blue moki
	Latridae	*Nemadactylus macropterus*	Tarakihi
	Macrouridae		Rattails
	Merlucciidae	*Macruronus novaezelandiae*	Hoki
	Monacanthidae	*Parika scaber*	Leatherjacket
	Ophidiidae	*Genypterus blacodes*	Ling
	Rajidae & Arhynchobatidae		Skates
	Triakidae	*Galeorhinus galeus*	School shark
		Mustelus lenticulatus	Rig
	Triglidae	*Chelidonichthys kumu*	Gurnard
Fish piscivores	Carangidae	*Seriola lalandi*	Kingfish
		Trachurus spp.	Jack mackerel
	Congridae	*Conger* spp.	Conger eel
	Diodontidae	*Tragulichthys jaculiferus*	Porcupine fish
	Moridae	*Pseudophycis bachus*	Red cod
	Pinguipedidae	*Parapercis colias*	Blue cod
	Polyprionidae	*Polyprion americanus*	Bass
		Polyprion oxygeneios	Hapuku
	Scorpaenidae	*Helicolenus* spp.	Sea perch
	Squalidae	*Squalus acanthias*	Spiny dogfish
	Uranoscopidae	*Kathetostoma* spp.	Giant stargazer
	Zeidae	*Zeus faber*	John dory
Fish planktivores	Carangidae	*Pseudocaranx dentex*	Trevally

Table A.5
Trophic group composition by species/group observed during aerial surveys of pelagic fishes. Data extract from the New Zealand Ministry of Fisheries aerial survey database.

Trophic group	Family	Scientific name	Common name
Fish piscivores	Scombridae	*Katsuwonus pelamis*	Skipjack tuna
Fish planktivores	Arripidae	*Arripis* spp.	Kahawai
	Carangidae	*Trachurus novaezelandiae*	Jack mackeral
	Scombridae	*Scomber australasicus*	Blue mackeral

runoff (Lundquist and Pinkerton, 2008). Phytoplankton production was determined using a vertically generalised production model (Behrenfeld and Falkowski, 1997). Production data were converted from averaged production per unit area from the centroid location to total monthly primary production over the model area.

A.6. Other invertebrates, bacteria, and detritus

Phytal invertebrate (organisms living on macroalgae) biomass was estimated as a proportion of macroalgal biomass (Lundquist and Pinkerton, 2008). Infaunal invertebrate biomass was estimated from studies of soft-sediment research that had taken place at Fitzroy Bay which is located ~5 km from the model area and is also exposed to high wave energy (Anderlini and Wear, 1990). In the absence of data for the model area, microphyte, meso/macrozooplankton, microzooplankton and bacterial biomasses were estimated from the literature (Lundquist and Pinkerton, 2008). Detritus biomass was estimated by EwE from mass-balance requirements.

A.7. Marine mammals

Marine mammals that are observed in the model area are New Zealand fur seals (*Arctocephalus forsteri*) seasonally, and orcas (*Orcinus orca*) rarely. There is a fur seal winter haul-out site on the western edge of the model area (Kaplan, 2003; Fig. 1), but fur seals feed off the continental shelf in waters deeper than those included in our model (Harcourt et al., 2002). Because marine mammal feeding in the model area is likely to be minimal if it occurs at all, we have not included marine mammals in our models.

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Appendix B. References for parameter estimates for Wellington south coast EwE models. Numbered references listed below

	Functional group	Historical	Pre-MR							
		B	*B*	*Lrec*	*Lcom*	*P/B*	*Q/B*	*U*	*Conversion factors*	*Diet matrix*
1	Birds	1	1			2	2	3, 4	2	2
2	Lobster	5, 6	5, 6	5	5, 6	7, 8, 9	7, 8	3, 4	10	59
3	Mob inverts herb	11, 12, 13	11, 12, 13			7	7	3, 4	2	2
4	Paua	11, 12, 13	11, 12, 13	5		2, 14, 15	16	3, 4	13	2
5	Kina	11, 12, 13	11, 12, 13			8, 17	8	3, 4	13	2
6	Mob invert carn	11, 12, 13	11, 12, 13			7	7	3, 4	7	2
7	Sea cucumber	13	13			8	8	3, 4	10, 18	2
8	Phytal/infaunal inverts	2, 7, 13, 19–23, 54	2, 7, 13, 19–23, 54			24, 25	26–29	3, 4	2, 13, 10, 19	7, 20
9	Sponges	13	13			30–33	33	3, 4	2, 19	31, 34
10	Sessile inverts	11, 12, 13	11, 12, 13			8, 24, 35	8, 35	3, 4	19	2, 36
11	Fish cryptic	2, 37	2, 37			38	39, 40	3, 4	41–44	45
12	Fish inverts	6, 40, 46, 47	6, 40, 46, 47			38	39, 40	3, 4	41–44	2, 48–50
13	Fish piscivores	6, 40, 46, 47	6, 40, 46, 47	5		38	39, 40	3, 4	41–44	2, 48–50
14	Fish planktivores	6, 40, 46, 47	6, 40, 46, 47			38	39, 40	3, 4	41–44	2, 48–50
15	Fish herbivores	6, 40, 46, 47	6, 40, 46, 47	5	5	38	39, 40	3, 4	41–44	2, 48–50
16	Microphytes	51–53	51–53			51	N/A	N/A	51–53	N/A
17	Macroalgae canopy	11, 12, 13	11, 12, 13			2, 19	N/A	N/A	19	N/A
18	Macroalgae foliose	11, 12, 13	11, 12, 13			2, 19	N/A	N/A	19	N/A
19	Macroalgae crustose	11, 12, 13	11, 12, 13			2, 19	N/A	N/A	19	N/A
20	Meso/macrozooplankton	55–57	55–57			58	58	3, 4	10	2, 56, 58
21	Microzooplankton	58	58			58	58	3, 4		2, 56, 58
22	Phytoplankton	2	2			2	N/A		2	N/A
23	Bacteria					2	2	3, 4		
24	Detritus									

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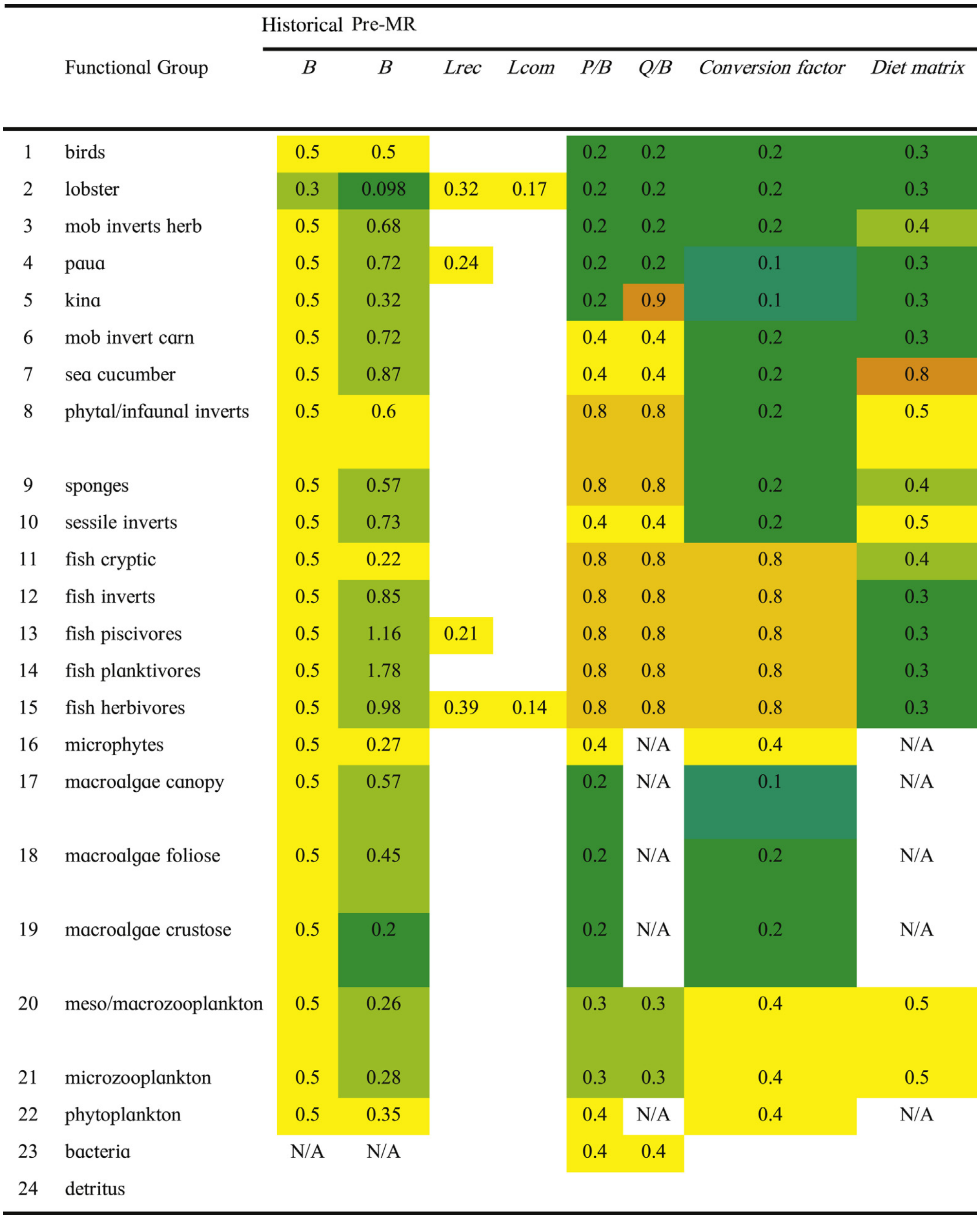
Appendix C. Pedigree describing quality of parameter estimate sources (represented by colour, refer to accompanying legends) with coefficients of variation (CVs) for Wellington south coast EwE models. Pedigree categories, scores, and CVs as indicated by Ecopath with Ecosim software where CVs were not able to be determined from raw data.



	Functional Group	Historical	Pre-MR						
		B	*B*	*Lrec*	*Lcom*	*P/B*	*Q/B*	*Conversion factor*	*Diet matrix*
1	birds	0.5	0.5			0.2	0.2	0.2	0.3
2	lobster	0.3	0.098	0.32	0.17	0.2	0.2	0.2	0.3
3	mob inverts herb	0.5	0.68			0.2	0.2	0.2	0.4
4	paua	0.5	0.72	0.24		0.2	0.2	0.1	0.3
5	kina	0.5	0.32			0.2	0.9	0.1	0.3
6	mob invert carn	0.5	0.72			0.4	0.4	0.2	0.3
7	sea cucumber	0.5	0.87			0.4	0.4	0.2	0.8
8	phytal/infaunal inverts	0.5	0.6			0.8	0.8	0.2	0.5
9	sponges	0.5	0.57			0.8	0.8	0.2	0.4
10	sessile inverts	0.5	0.73			0.4	0.4	0.2	0.5
11	fish cryptic	0.5	0.22			0.8	0.8	0.8	0.4
12	fish inverts	0.5	0.85			0.8	0.8	0.8	0.3
13	fish piscivores	0.5	1.16	0.21		0.8	0.8	0.8	0.3
14	fish planktivores	0.5	1.78			0.8	0.8	0.8	0.3
15	fish herbivores	0.5	0.98	0.39	0.14	0.8	0.8	0.8	0.3
16	microphytes	0.5	0.27			0.4	N/A	0.4	N/A
17	macroalgae canopy	0.5	0.57			0.2	N/A	0.1	N/A
18	macroalgae foliose	0.5	0.45			0.2	N/A	0.2	N/A
19	macroalgae crustose	0.5	0.2			0.2	N/A	0.2	N/A
20	meso/macrozooplankton	0.5	0.26			0.3	0.3	0.4	0.5
21	microzooplankton	0.5	0.28			0.3	0.3	0.4	0.5
22	phytoplankton	0.5	0.35			0.4	N/A	0.4	N/A
23	bacteria	N/A	N/A			0.4	0.4		
24	detritus								

Biomass pedigree	
1	Estimated by ecopath
2	Estimated from other model
3	Guesstimate
4	Approximate or indirect method
5	Sampling based, low precision
6	Sampling based, high precision

Catch pedigree	
1	Guesstimates
2	From other model
3	FAO statistics
4	National statistics
5	Local study, low precision/incomplete
6	Local study, high precision/complete

P/B, Q/B and Conversion factor pedigree	
1	'Missing' parameter (estimated by Ecopath)
2	Guesstimates
3	From other model
4	Empirical relationships
5	Similar group/species, similar system
6	Similar group/species, same system
7	Same group/species, similar system
8	Same group/species, same system

Diet pedigree	
1	General knowledge of related group/species
2	From other model
3	General knowledge for same group/species
4	Qualitative diet composition study
5	Quantitative but limited diet composition study
6	Quantitative, detailed, diet composition study

Appendix D. Initial parameter estimates before model balancing for Wellington south coast EwE models

	Functional group	Historical	Pre-MR				
		B	*B*	*Lrec*	*Lcom*	*P/B*	*Q/B*
1	Birds	0.00022	0.00022			0.1	89.7
2	Lobster	1.64	0.41	0.02	0.18	0.44 (0.50)	7.4
3	Mob inverts herb	1.91	0.97			1.3	7.94 (7.40)
4	Paua	0.46	0.23	0.15		1.5	15
5	Kina	0.12	0.06			1.1	7.5
6	Mob invert carn	0.61	0.61			1.76	5.97
7	Sea cucumber	0.35	0.35			0.6	3.4
8	Phytal/infaunal inverts	0.54	0.54			3.05 (3.67)	12
9	Sponges	1.59	1.59			0.2	0.8
10	Sessile inverts	1.56	1.56			1.5	6
11	Fish cryptic	0.04	0.04			2.4	15.6
12	Fish inverts	0.13	0.09			0.41	3.59
13	Fish piscivores	0.03	0.01	0.0025		0.43	2.62
14	Fish planktivores	0.22	0.15			0.5	6.33
15	Fish herbivores	0.37	0.25	0.01	0.08	0.4	9.52
16	Microphytes	7.64	7.64			21	0
17	Macroalgae canopy	37.66	37.66			2.87	0
18	Macroalgae foliose	18.19	18.19			13	0
19	Macroalgae crustose	1.36	1.36			25.4	0
20	Meso/macrozooplankton	0.17	0.17			17.7	51.5
21	Microzooplankton	0.06	0.06			220	624
22	Phytoplankton	0.48	0.48			324	0
23	Bacteria	0.6	0.6			100	400
24	Detritus	1	1				

Appendix E. Initial diet parameter estimates before model balancing for Wellington south coast EwE models

	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	20	21	23
1	Birds	–	–	–	–	–	0.01 (1×10^{-6})	–	–	–	–	–	–	–	–	–	–	–	–
2	Lobster	–	–	–	–	–	0.10 (4×10^{-4})	–	–	–	–	–	–	–	–	–	–	–	–
3	Mob inverts herb	0.25 (0.20)	0.26 (0.21)	–	–	–	0.30 (0.15)	–	–	–	–	–	0.16 (0.12)	–	–	–	–	–	–
4	Paua	0.03	0.01	–	–	–	0.04	–	–	–	–	–	0.02	–	–	–	–	–	–
5	Kina	0.01	0.01	–	–	–	0.01	–	–	–	–	–	0.01	–	–	–	–	–	–
6	Mob invert carn	0.30 (0.29)	0.14 (0.15)	–	–	–	0.25 (0.14)	–	–	–	–	–	0.30 (0.31)	–	–	–	–	–	–
7	Sea cucumber	–	–	–	–	–	0.01 (0.06)	–	–	–	–	–	–	–	–	–	–	–	–
8	Phytal/infaunal inverts	0.35 (0.31)	0.28 (0.32)	–	–	–	0.08 (0.10)	–	–	–	–	0.64 (0.58)	0.17	–	0.22 (0.03)	–	–	–	–
9	Sponges	–	–	–	–	–	0.10 (0.07)	–	–	–	–	–	0.04	–	–	–	–	–	–
10	Sessile inverts	–	–	–	0.05	0.05	0.15 (0.43)	–	–	–	–	0.21 (0.24)	0.32 (0.33)	–	–	–	–	–	–
11	Fish cryptic	0.10 (0.16)	–	–	–	–	–	–	–	–	–	–	–	0.09	–	–	–	–	–
12	Fish inverts	–	–	–	–	–	–	–	–	–	–	–	–	0.21	–	–	–	–	–
13	Fish piscivores	–	–	–	–	–	–	–	–	–	–	–	–	0.09	–	–	–	–	–
14	Fish planktivores	–	–	–	–	–	–	–	–	–	–	–	–	0.53	–	–	–	–	–
15	Fish herbivores	–	–	–	–	–	–	–	–	–	–	–	–	0.09	–	–	–	–	–
16	Microphytes	–	–	0.25	0.05	0.05	–	–	0.25	–	–	–	–	–	–	–	–	–	–
17	Macroalgae canopy	–	0.19 (0.10)	0.35	0.20	0.60	–	–	0.25	–	–	–	–	–	–	0.24	–	–	–
18	Macroalgae foliose	–	–	0.20	0.35	0.15	–	–	–	–	–	–	–	–	–	0.67	–	–	–
19	Macroalgae crustose	–	0.13 (0.20)	0.20	0.35	0.15	–	–	–	–	–	–	–	–	–	0.09	–	–	–
20	Meso/macrozooplankton	–	–	–	–	–	–	–	–	–	–	0.15 (0.17)	–	–	0.72 (0.71)	–	0.20 (0.06)	–	–
21	Microzooplankton	–	–	–	–	–	–	–	–	0.30	0.30	–	–	–	–	–	0.70 (0.72)	0.10	–
22	Phytoplankton	–	–	–	–	–	–	–	0.25	0.40	0.40	–	–	–	–	–	0.10 (0.21)	0.65 (0.67)	–
23	Bacteria	–	–	–	–	–	–	1.00	0.25	0.30	0.30	–	–	–	0.06 (0.26)	–	–	0.25 (0.23)	0.50 (0.18)
24	Detritus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.50 (0.82)

Appendix F. Vulnerabilities (V) of lobster prey used to tune the Wellington south coast model run from 1945 to 2008. Vulnerabilities were determined by minimising the sum of squares (SS) between observed and predicted data for the 63 year historical lobster biomass and fisher mortality time series, from 1945 until 2008. Default vulnerabilities of 2.00 for the prey of all other consuming trophic groups were used.

Prey	V
Mob inverts herb	1.00
Paua	1.00
Kina	1.00
Mob invert carn	1.00
Phytal/infaunal inverts	1.00
Macroalgae canopy	1.15
Macroalgae crustose	1.15

Appendix G. Model fit for historical run (1945–2008) of lobster biomass. Observed lobster biomass data is from the New Zealand Ministry of Fisheries database and predicted data is from the historical Wellington south coast EwE model, forced with a time series of lobster fishing mortality (F)

Fig. A6

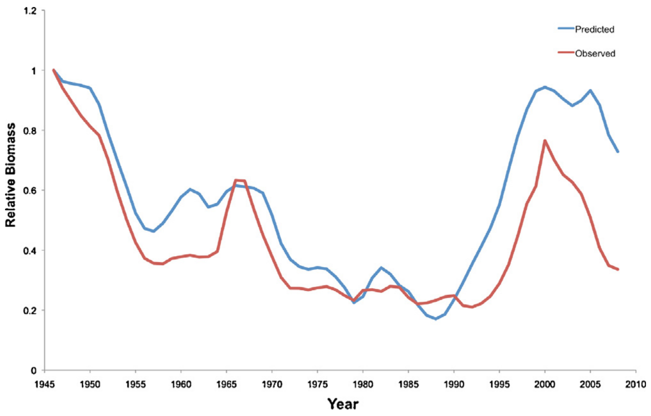


Fig. A6.

Appendix H. Biomass parameters for the pre-MR model compared to biomass parameters predicted for the pre-MR model using the historical model run from 1945 to 2008. The differences between the predicted and actual are proportional to the actual biomass.

	Functional group	Pre-MR biomass	Predicted biomass	Difference proportional to pre-MR
1	Birds	0.00022	0.00034	0.37
2	Lobster	0.41	1.20	0.66
3	Mob inverts herb	0.97	2.52	0.62
4	Paua	0.23	0.46	0.50
5	Kina	0.060	0.13	0.53
6	Mob invert carn	0.61	0.80	0.24
7	Sea cucumber	0.35	0.29	−0.20
8	Phytal/infaunal inverts	0.54	0.66	0.18
9	Sponges	1.59	1.34	−0.19
10	Sessile inverts	1.56	1.32	−0.18
11	Fish cryptic	0.040	0.065	0.38
12	Fish inverts	0.090	0.15	0.41
13	Fish piscivores	0.010	0.032	0.68
14	Fish planktivores	0.15	0.23	0.33
15	Fish herbivores	0.25	0.37	0.32
16	Microphytes	7.64	7.51	−0.017
17	Macroalgae canopy	37.66	36.81	−0.023
18	Macroalgae foliose	18.19	18.06	−0.0071
19	Macroalgae crustose	1.36	1.37	0.0072
20	Meso/macrozooplankton	0.17	0.18	0.039
21	Microzooplankton	0.060	0.064	0.065
22	Phytoplankton	0.48	0.48	0.0056
23	Bacteria	0.60	0.60	−0.0076
24	Detritus	1.00	0.99	−0.0080

Appendix I. Sensitivity analysis results for the most uncertain and sensitive parameter estimates. Parameter estimate uncertainty was determined by the data pedigree (Table S6). Table indicates the number of trophic groups whose biomass was impacted by at least ± 20%

Parameter	Parameter value	Number of trophic groups impacted	%
Lobster high V	2 for prey of lobster	7	29.17
Paua low V	1 for prey of paua	1	4.17
Kina low Q/B	5	0	0
Kina high Q/B	10	0	0
Phytal/infaunal low P/B	3	0	0
Phytal/infaunal low Q/B	9.66	0	0
Phytal/infaunal high Q/B	18.1	0	0
Sponges low P/B	0.17	0	0
Sponges high P/B	0.24	0	0
Sponges low Q/B	0.64	0	0
Sponges high Q/B	1.2	0	0
Fish cryptic low P/B	1.92	0	0
Fish cryptic high P/B	2.88	0	0
Fish cryptic low Q/B	12.5	0	0
Fish cryptic high Q/B	23.5	0	0
Fish cryptic low B	0.068	1	4.17
Fish cryptic high B	0.612	1	4.17
Fish inverts low P/B	0.33	0	0
Fish inverts high P/B	0.5	0	0
Fish inverts low Q/B	2.87	0	0
Fish inverts high Q/B	5.39	0	0
Fish inverts low B	0.03	1	4.17
Fish inverts high B	0.1746	1	4.17
Fish pisc high P/B	0.51	0	0
Fish pisc high B	0.02953	1	4.17
Fish pisc low V	1 for prey of fish pisc	0	0
Fish plank low P/B	0.4	0	0
Fish plank high P/B	0.6	0	0
Fish plank low Q/B	5.06	0	0
Fish plank high Q/B	8.8	0	0
Fish plank low B	0.05	1	4.17
Fish plank high B	0.2	1	4.17
Fish herb low P/B	0.38	2	8.33
Fish herb high P/B	0.48	2	8.33
Fish herb low Q/B	7.61	0	0
Fish herb high Q/B	14.3	0	0
Fish herb high B	0.5004	2	8.33
Fish herb low V	1 for prey of fish herb	2	8.33

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