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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.

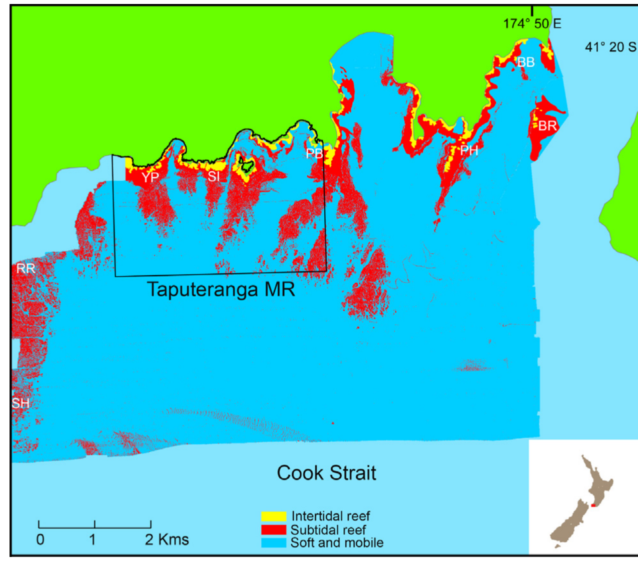

Fig. 1. Map of Taputeranga Marine Reserve, Wellington south coast model area, study sites and substrate types. Location of Taputeranga MR within New Zealand as red square in bottom right panel. Main figure – map of the area for which the model was developed showing location of Taputeranga MR (black box, 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.)

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.

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