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# Lobster fishery and marine reserve interactions in central New Zealand

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ABSTRACT

Full no-take marine reserves (MRs) act as tools for biodiversity protection that reduce or remove human-induced disturbances and support the recovery of harvested species. Even if not designed specifically for fisheries management, MRs have the potential to enhance locally and distantly fished populations. This study quantified contemporary catch per unit effort (CPUE) of rock lobsters (RLs) with respect to weight and abundance inside and outside two central New Zealand MRs (Kapiti MR established in 1992, Taputeranga MR established in 2008) using commercial fishing methods (pots), and compared it to historical CPUE data. On average, mean CPUE and mean RL size were significantly greater inside than outside at both MRs. Contemporary CPUE at both MRs was approximately twice that of historical CPUE prior to the reserves being established. At Taputeranga, but not at Kapiti MR, we observed a gradient in CPUE with distance from the centre of the reserve. MRs had higher CPUE at reefs that were fully protected (entire reef in the MR) than at partially protected reefs (reef spans the MR boundary), which in turn had higher CPUE than unprotected reefs (entire reef outside the MR). Our results indicate that RL populations are responding positively to protection, but that factors such as the amount of reef area protected and proximity to reserve boundary contribute differently to RL responses. Our findings contribute to the design of MRs with respect to the habitat they protect and to a better understanding of the interactions between MRs and local fisheries.

## 1. Introduction

Anthropogenic activities such as fishing, pollution and habitat modification can have major negative impacts on marine environments, particularly in coastal regions [1,2]. To mitigate such impacts, many nations are working to establish networks of marine protected areas (MPAs), including full no-take areas, such as marine reserves (MRs) [3–5]. MRs around the world are created for a number of reasons including conservation, biodiversity and habitat protection, fisheries management, and to protect historical or cultural features. In New Zealand (NZ), MRs are established under the Marine Reserves Act [6] for the purposes of conducting research in the absence of most human pressures, but with the ultimate aim of ecosystem protection [7–10]. This legislation is currently being reviewed and is likely to be replaced by a Marine Protected Areas Act, which is expected to support international conservation targets to which NZ is a signatory, including the Convention of Biological Diversity, which has a goal of 10% marine protection by 2020.

Outcomes from MR designations in NZ have been described for communities and species, including those targeted by both commercial and recreational fishing (e.g. Refs. [7,9–15]). Internationally, many such studies have reported increases in the mean abundance and size, total weight, individual weight and size of species inside MRs compared to outside, as well as direct and indirect effects on communities [5,16–18]. While 'more' and 'bigger' responses, in particular of targeted species, are now routinely reported from international work when fishing pressure is removed [14,18,19], the relative contribution of individual factors such as reserve age, size, placement, shape, policing (enforcement), proximity to major urban centers, and extent of protection are only now starting to be understood [5].

Interactions between full no take MRs and local fisheries can be difficult to quantify. Baseline biological data (before MR establishment) are often not available [9,10,15,20] for sites inside and outside MRs, and fisheries data may not be collected at a sufficiently fine spatial scale to permit testing of hypotheses of change in abundance or biomass at an appropriate scale. In addition, countries such as NZ where commercial

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fishing data may be available, catch data for recreational and for customary (Māori) catch are generally not available [21,22]. From a management (regulatory) perspective, trying to balance the often competing needs of biodiversity protection or habitat conservation against those of the different fishing sectors can be hard, and understanding how MRs interact with local fisheries is often particularly difficult [but see Refs. [23,24]]. Future planning of individual reserve location, size and shape, in particular in the context of a national network of reserves, needs to move beyond the establishment of a simple *ad hoc* closed area approach to include consideration of effects such as extent of reef protection, levels of historical and contemporary local fishing pressure, spatial coverage of representative habitat types, and connectivity [25–27].

A commonly employed harvesting strategy once MRs are established is called ‘fishing the line’, where fishing effort is concentrated at the boundaries of MRs [28–30]. Fishers use this strategy because there is an inherent assumption that catch rates at the boundaries will be enhanced by the net export of individuals from the reserve, the so called ‘spillover effect’ [26,29]. While this harvesting tactic may benefit some fishers when the total number of fishers is small, if the effort is large, there may be declines in both the fished stock and the protected population [29,31,32]. Species with high site fidelity that spend long periods on inshore reefs, but move seasonally offshore (e.g. for reproduction or moulting), are known to be vulnerable to capture at MR boundaries [29,33,34]. The Southern or red rock lobster (RL) *Jasus edwardsii* (Hutton, 1975) (Palinuridae), which is found throughout NZ and southern Australia, is one such species. In NZ it exhibits gregarious behaviour during the day [20,35], with high site fidelity as well as seasonal inshore/offshore migrations [20,26,36–38]. RLs can forage on a wide range and size of prey [39]. In addition, RL translocation experiments have shown immediate cohabitation and fidelity to the release site, with no evidence of displacement or avoidance between prior residents and larger size and new RLs [40], with the result that MR populations of RLs may be vulnerable to capture when they migrate. This knowledge has led to the suggestion that MR boundaries need to be set around subtidal rocky reef regions to encompass all, or as much as possible, of the reef to afford protection to lobsters because it has been shown that they are less likely to cross soft sediment habitats [26].

RLs are ecologically important in NZ and southern Australia and are considered to be a keystone species in temperate reef communities, playing an important role in trophic cascades [9,26,41–43], as well as in structuring soft sediment communities [44]. From an economic perspective, RLs are the most important invertebrate targeted for commercial and recreational fishing, supporting large fisheries in Australia and NZ [9,37,38,45]. In NZ, RLs have been managed under the Quota Management System (QMS) since 1991 [45,46]. Regulations include minimum legal sizes for males and females, gear regulations (undersize escape gaps required), local closures, and the return of berried (egg-bearing) females and soft-shelled RLs to the water [22]. RLs are the second highest valued inshore seafood export, worth over NZ$116 m in 2017, a decline of 21% since 2016 [47]. During 2017, most NZ RLs were exported live to China (56%) and Hong Kong (9%) [47]. It is therefore important to understand and quantify how RLs respond to MR protection to better understand the ecological role of RLs and the impacts of the fishery on local stocks, as well as to understand the potential effects of MRs on adjacent fisheries.

Research from Australia has shown increased weight of legal-sized RLs of more than 20 times inside compared to outside MRs [48]. Similar results have been reported in NZ, with larger and more abundant RLs inside than outside MRs [13,38,49]. In addition, meta-analyses of RL responses to MR protection in NZ have demonstrated that there is a strong positive site-specific effect on abundance and size [7,14]. This substantial inside versus outside MR response may result, at least in part, because MRs may be isolated from their surrounding environments due to fishing pressure at the boundaries [50–55]. This response may create gradients of population density and mean size across MR boundaries, such that highest densities and greatest mean sizes are found at the MR centre, and lowest densities and smallest mean sizes at the MR boundaries. It has been suggested that this response will be influenced by the size and location of habitats relative to MR boundaries [20,26].

Using commercial fishing methods, this study reports the biological responses of RL populations to the protection afforded by two MRs in central New Zealand. First, comparisons of RLs in terms of mean size, abundance and sex ratios inside versus outside the two MRs were conducted. Then, boundary effects on catch per unit effort (CPUE) of RLs were tested for an effect based on proportion of reef protected. Finally, levels of historical CPUE from the commercial fishery before the reserves were established were compared with contemporary estimates of CPUE after reserve establishment. This research was conducted in two MRs of different ages and sizes, but of similar habitat type. Like all MRs in NZ, the two reserves were established indirectly for ecosystem protection and not specifically for the protection of RLs or any other single species. Our results highlight the importance of an understanding of fishing effort in the context of extent of reef protection and site-specific proximity to the reserve boundary to better understand the complex interactions between reserve protection and fishing pressure.

## 2. Methods

### 2.1. Study locations

RL responses to protection were studied at two MRs in central New Zealand. Taputeranga Marine Reserve (TMR) was gazetted in 2008. It protects 854.79 ha of coastal waters, and is the first rocky reef MR in NZ located adjacent to a major city (Wellington). The marine environment is representative of the temperate Cook Strait region, a highly dynamic system, experiencing substantial wave energy from the south as well as being a zone of convergence for the East Cape, D'Urville and Southland currents [10,56] (Fig. 1). Kapiti Marine Reserve (KMR) was gazetted in 1992. It is located approximately 60 km north of Wellington. KMR is divided into two parts: the larger portion (1,750 ha) is on the eastern side of the island extending to the mainland at Paraparaumu, whilst the smaller portion (340 ha) is located on the western side of the island and does not connect with the mainland (Fig. 1). Our study was carried out in the western side of the reserve, where more complex reef structures exist compared to the eastern side [57]. Sites on the western side of Kapiti Island have similar reef (in terms of geology and complexity) and habitat types, and historical RL fishing sites are located on this side of the island (Fig. 1). In addition, Stewart and MacDiarmid [58] reported that the majority of RLs are found on the western side of the island.

### 2.2. Contemporary rock lobster pot survey

Eight commercial rock lobster pots (RLPs) were deployed along the Wellington south coast (one RLP per site) during summer (mid December–February) 2010–2011 and 2012, winter (June–August) 2010–2011, and spring (September–November) 2010–2011. At TMR, each RLP was sampled 27 times during the entire study, totalling 216 RLP lifts across all eight sites (108 pot lifts inside and 108 outside). At KMR, RLPs were deployed in winter 2010–2011, spring 2010–2011, and summer 2011–2012, with a total of 17 RLP lifts at each sampling site, totalling 136 RLP lifts across all eight sites (68 pot lifts inside and 68 outside). The pot type used was the standard, legal, commercial RL fishery pot, with a rectangular steel frame and 52-mm mesh and a bait box inside. Each RLP had a 20 m rope with buoy attached, and two minimum size escape gaps (one on each side) to permit small RLs to escape, as specified by the national requirements for the commercial RL fishery in the management unit CRA4 [21,22]. Consistent with commercial fishing practice, different bait types, either single or mixed species, were employed (Appendix A), following the untested

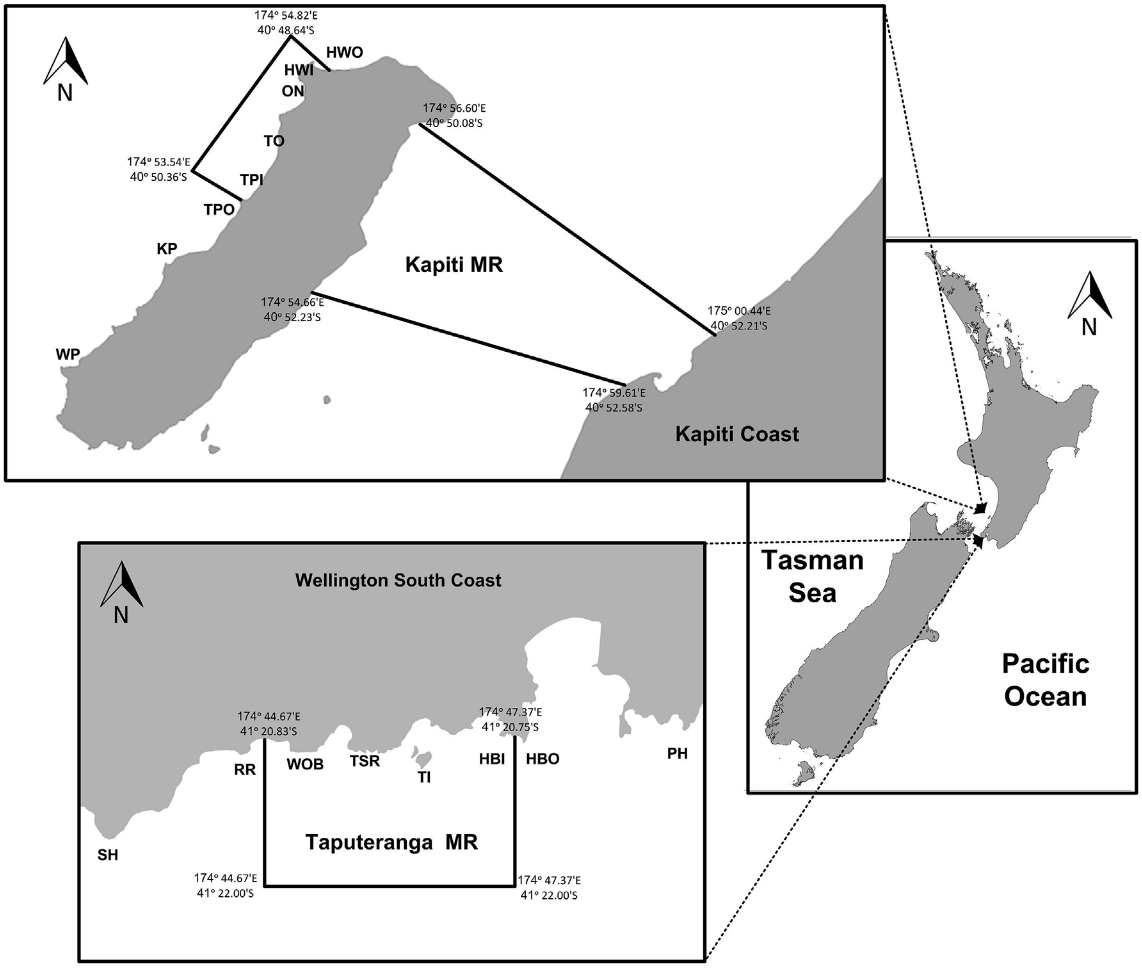

**Fig. 1.** Maps showing the two marine reserves and study sites at each marine reserve used as in Wellington region, New Zealand. For Taputeranga MR: **PH**: Palmer Head, **HBO**: Houghton Bay Outside, **HBI**: Houghton Bay Inside, **TI**: Taputeranga Island, **TSR**: The Sirens Rock, **WOB**: Western Owhiro Bay, **RR**: Red Rocks and **SH**: Sinclair Head. For Kapiti MR: **HWO**: Hole in the wall outside; **HWI**: Hole in the wall inside; **ON**: Onepoto; **TO**: Te Oneroa; **TPI**: Trig Point inside; **TPO**: Trig Point outside; **KP**: Kaiwharawhara Point; **WP**: West Point.

assumption of commercial fishers that bait type does not influence RL capture. The RLPs were deployed in 10–15 m water depth, on rocky reefs. Pots were normally set one day and retrieved the next (less than 24 h soak time). The effect of soak time was not tested on RL captures, but given that variance in soak times was small, this factor is not expected to be important. Because of the legal requirements of using RLPs with escape gaps for under-sized RL, CPUE was assessed solely for legal-sized lobsters.

Rocky reef sampling sites inside and outside the MRs were selected based on historical fishing site information provided by local fishers. Eight sites were selected per location (one RLP per site), four inside and four outside the MR. Based on historical fishing sites at TMR, RLP were deployed at two sites on the east side and another two on the west side of the MR, as well as at four sites inside the reserve (Fig. 1). Due to the geographic complexity of the marine environment around Kapiti Island, RLPs were deployed at three sites south and one north of the MR, as well as four sites inside the reserve (Fig. 1). The number of sampling days in every season at each MR varied between two and six and was dependent on weather and sea conditions.

RL abundance was measured as total number of lobsters per pot lift inside and outside each MR. RL weight was measured at sea using a scale, as total kilograms caught (total weight) at each MR (inside and outside), and as catch per unit effort (CPUE) defined as total kilograms per pot lift (kg pot lift$^{-1}$). To compare abundance inside and outside each MR, a two-tailed *t*-test ($\alpha = 0.05$) was employed. Total weight caught inside/outside each reserve was compared with a $\chi^2$ test for independence ($\alpha = 0.05$). For CPUE, comparison between seasons and inside/outside each MR, a two-way ANOVA ($\alpha = 0.05$) was employed, where season and status (inside/outside) were treated as fixed factors.

### *2.3. Rock lobster morphometric and sex ratio indices*

In the central NZ region where the TMR and KMR reserves are located, the minimum legal size (tail width) is 54 mm for males and 60 mm for females [59]. Individual RL weight was recorded to the nearest gram. Tail width was measured with Vernier calipers as a straight line between the tips of the two large (primary) spines on the second segment of the tail. RL sex was determined using industry guidelines [21,22]. After being weighed, measured and sexed, all RLs were released where they were caught.

Morphometric data for RLs inside and outside both MRs were investigated using a two-tailed *t*-test ($\alpha = 0.05$). Because weight was not normally distributed, it was normalised using a log transformation. Seasonal differences in RL morphometric measures inside and outside the reserves were compared using a two way ANOVA ($\alpha = 0.05$). Differences in the numbers of male and female RLs inside and outside each MR were tested using a permutational 2 × 2 contingency test [60].

To determine if both sexes had similar seasonal patterns, a permutational RxC test (2 × 3 contingency test) was used for sex (male vs female) against season (summer, winter, spring) at each MR separately [60]. For this analysis, male and female data were pooled from inside and outside the MR.

### 2.4. Gradient of CPUE response from the centre of each marine reserve

The geographic centre of each MR was identified using Google Earth as the point that was equidistant from the boundaries of the MR that are perpendicular to the shoreline, that is, the east-west boundaries at TMR and the north-south boundaries for the western portion of KMR. The distance of each sample site, whether inside or outside the reserve, from the centre of the reserve was calculated in Google Earth (Appendix B). For the two MRs separately, this index of distance from the centre of the MR was used as the independent variable in analyses of the dependent variable (CPUE) to test for the effect of proximity to the MR boundary. Both, linear and non-linear responses of CPUE were tested as a function of distance from the centre of each MR using regression analyses: best fit was judged on the basis of the correlation coefficient [61]. Because the CPUE data contained many zero values, the data were transformed by adding one to each value for the non-linear analysis (zeros were untransformed and remained in the linear analysis).

### 2.5. Changes in historical and contemporary CPUE

Commercial RL fishing in this part of NZ is designated as the CRA4 fisheries management area [62]. CRA4 is divided into statistical subareas; TMR and the Wellington south coast are in area 915, KMR and the Kapiti Island region are in area 934. The size of area 915 is 1,902.82 km$^2$ and includes 130 km of coast line, whereas area 934 is 3,124.89 km$^2$ and includes 190 km of coast line [63].

Historical monthly commercial RL data from 1989 to 2005 for areas 915 and 934 were provided by the NZ Ministry for Primary Industries (Fig. 2), which only included legal-sized lobsters. The historical RL catch data from the Wellington and Kapiti regions were compared with our contemporary CPUE data using a two factor permutational multivariate analysis of variance (PERMANOVA) with $\alpha = 0.05$. The factors incorporated in the PERMANOVA design were 'time' (two levels: historical (=commercial) and contemporary data), and 'season' (three levels: summer, winter and spring). Based on local knowledge, autumn was not considered in this study, because at this time RLs migrate to deeper waters. The analysis was based on similarity matrices calculated using the Bray-Curtis coefficient. To check differences of the historical CPUE amongst seasons at sites inside and outside each MR separately, a pair-wise comparison in PERMANOVA ($\alpha = 0.05$) was used to identify the location of differences. Tests were run using the statistical package PRIMER-E v6 [64].

### 2.6. Analysis of CPUE for MR reef systems with differing levels of protection

Because the configuration of MR boundaries with respect to habitats such as reefs can affect the response of exploited species [5,26], this was explored for RLs at TMR and KMR. At TMR, there have been two efforts to map habitat type, the first, a habitat substratum map [65], and the second, a backscatter map produced using side-scan sonar [66]. These two maps were combined using GIS and the TMR boundaries were overlaid to show the reserve location in relation to different substratum types [9]. The intertidal and subtidal hard substratum types were ground-truthed during subtidal surveys undertaken with SCUBA, which corresponded to 'rocky reef' habitat [9]. Two of the reefs surveyed for CPUE were fully protected, that is, totally included within the boundaries of the reserve (The Sirens and Taputeranga Island), two of the reefs were partially protected by the reserve, with boundaries that bisected the reefs (Houghton Bay and western Owhiro Bay), while three reefs that were surveyed were unprotected (Sinclair Head, Red Rocks and Palmer Head) because they are all outside TMR. CPUE survey data were used for all seasons and years to determine if CPUE differed among the three protection levels (fully protected, partially protected, unprotected). Data were analysed by analysis of variance (ANOVA) using Statistica [61]. Data were tested for normality and homogeneity of variances and were found to meet both assumptions of parametric testing. Variation in CPUE (dependent variable) was tested as a function of percentage of protected reef (independent variable, three groups of 0%, 50% and 100%).

At KMR, recent efforts have provided side-scan sonar coverage of the nearshore environment [67,68]. Despite a lack of coverage in shallow water close to shore, it was still possible to determine if reefs were fully protected and continuous within the reserve, were bisected by the reserve boundaries and therefore partially protected, or were unprotected and outside the MR boundaries. At KMR the majority of the nearshore reef structure is continuous, with the only obvious break in hard substratum occurring within the reef itself. This means that all of the reserve sites are considered to be 'partially protected', and the statistical analysis was therefore equivalent to testing between protected and unprotected (inside *versus* outside), as above.

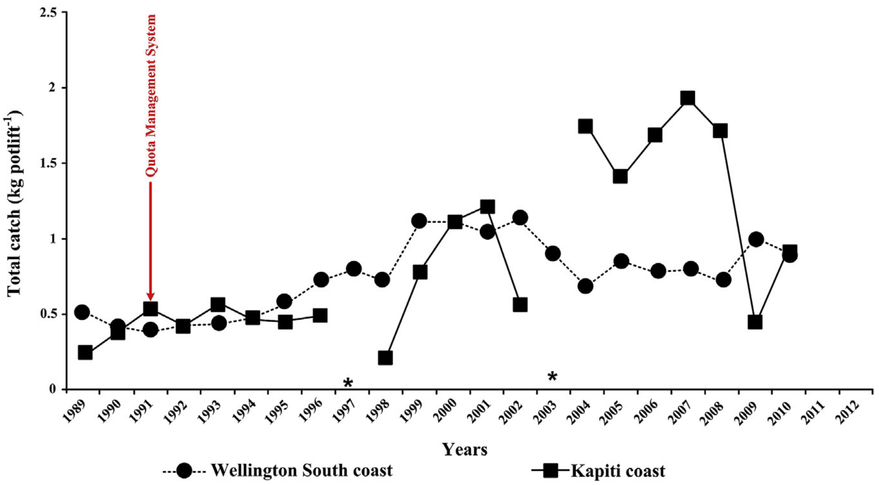

**Fig. 2.** Historical CPUE (kg rock lobster per pot lift; sex and seasons pooled) along the Wellington south coast (statistical area 915) and Kapiti coast (statistical area 934) from 1989 to 2010. The asterisk (*) indicates that no data were reported for Kapiti coast in 1997 and 2003.

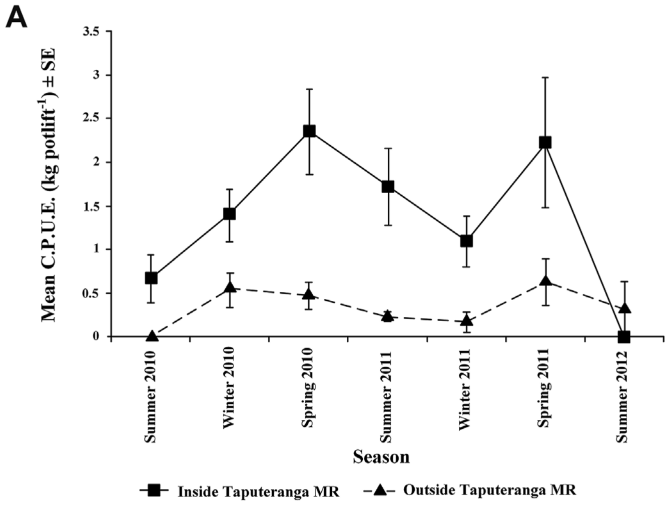

**Fig. 3A.** Mean CPUE (kg rock lobster per pot lift; males and females pooled) during three seasons from 2010 to 2012 for Taputeranga Marine Reserve.

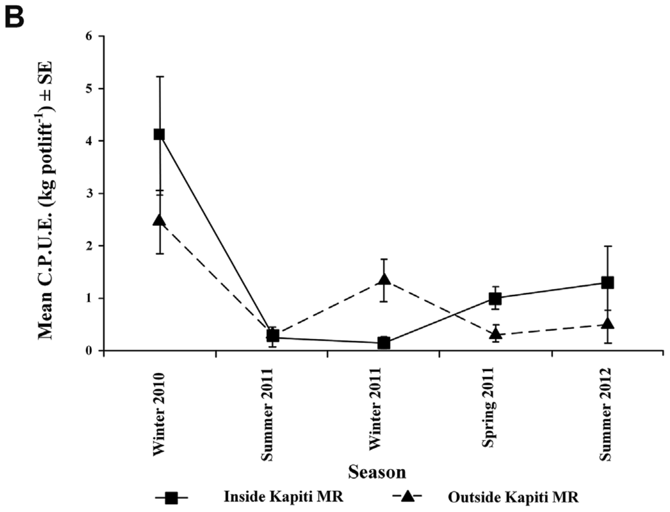

**Fig. 3B.** Mean CPUE (kg rock lobster per pot lift; males and females pooled) during three seasons from 2010 to 2012 for Kapiti Marine Reserve.

## 3. Results

### 3.1. Contemporary rock lobster survey

#### 3.1.1. Abundance and CPUE

At TMR, a total of 234 RLs were caught during the period summer 2010 to summer 2012, from a total of 216 pot lifts (108 pot lifts inside and 108 pot lifts outside TMR). Of the 234 RLs, 183 were caught inside (78%) and 51 (22%) outside TMR ($\chi^2 = 74.462$, df = 1, $p < 0.001$). Most RLs were caught in spring 2010, with a catch rate of 2.5 RL pot$^{-1}$ (± 0.4 SE) inside and 0.5 RL pot$^{-1}$ (± 0.2) outside the reserve. At KMR, a total of 118 RLs were caught during the period winter 2010 to summer 2012, from a total of 136 pot lifts (68 pot lifts inside and 68 pot lifts outside KMR). Of the 118 RLs, 76 were caught inside (64%) and 42 (36%) were caught outside KMR ($\chi^2 = 9.797$, df = 1, $p < 0.01$). Most RLs were caught in winter 2010, when the catch rate was 1.4 RL pot$^{-1}$ (± 0.3) inside and catch rate was 2.4 RL pot$^{-1}$ (± 0.5) outside the reserve.

At TMR the CPUE was 2.8 times higher inside than outside the reserve, with a mean of 1.30 kg pot lift$^{-1}$ (± 0.2) inside and 0.46 kg pot lift$^{-1}$ (± 0.2) outside ($t = 2.864$, df = 54, $p < 0.006$; Fig. 3A). At KMR, the mean CPUE was 1.4 times higher inside (1.34 kg pot lift$^{-1}$ ± 0.5) than outside the MR (0.98 kg pot lift$^{-1}$ ± 0.2) ($t = 0.705$, df = 38, $p = 0.485$; Fig. 3B).

#### 3.1.2. Total and mean weight

The total weight of the catch inside TMR was 182 kg, while outside it was 37 kg. At KMR, the total weight was 108 kg inside and 68 kg outside the reserve. At TMR, mean individual RL weight was 0.86 kg ± 0.02 inside and 0.67 kg ± 0.02 outside the reserve ($t = 4.619$, df = 264, $p < 0.001$), and at KMR it was 1.37 kg ± 0.1 inside and 1.66 kg ± 0.2 outside the reserve ($t = 1.830$, df = 118, $p = 0.070$).

### 3.2. Rock lobster morphometric and sex ratio indices

For RLs from both regions, tail width and individual weight were strongly correlated ($p < 0.0001$ for male and for female lobsters). Mean values of tail width and individual weight were greater inside than outside both reserves. These differences were significant at TMR, but no differences were found at KMR (Table 1).

RL size and weight frequency histograms revealed that the majority of males and females inside and outside both reserves were larger than the minimum legal size for capture (MLS - tail width is 60 mm for females and 54 mm for males). Inside TMR, 86.8% of female and 91.2% of male RLs were larger than MLS, while 56% of female and 83% of male RLs were larger than the MLS outside the MR. At KMR, all RLs caught within and outside the reserve were larger than MLS (Figs. 4 and 5).

At TMR, more male (136 versus 23) and female (76 versus 32) RLs were caught inside versus outside the reserve, a response that was highly significant (permutation test, $p = 0.0035$, SE = 0.0009). In contrast, at KMR, more male (57 versus 10) but fewer female (21 versus 31) RLs were caught inside versus outside the reserve, another response that was highly significant ($p < 0.0001$, SE < 0.0001). The ratio of males to females caught inside TMR was 1:1.7, while the ratio outside the reserve was 1:1.4. This ratio varied seasonally, with more males caught in winter inside and outside both MRs, when the ratio was 3:1 males to females. In spring, more males were caught inside TMR (2.3:1 males to females), while more females were caught outside TMR (1:2 males to females). At KMR, the sex ratio of RLs caught inside the MR was 1:2.8 males to females. Outside the MR, the sex ratio was 3:1 males to females. There were fluctuations in the sex ratio of the catches amongst seasons, but no consistent pattern was evident.

#### 3.2.1. Seasonal and annual variation in mean tail width

Inside TMR, mean tail width values increased steadily during the sampling period (2010–2012). In summer 2010, mean tail width was 56.2 mm (± 2.5) and by the end of spring 2011 it was 66.5 mm (± 2.4). In addition, outside the reserve mean tail width had increased by ~6 mm (mean size) from summer 2010 (58.5 mm ± 2.4 mm) to summer 2012 (64.5 ± 2.4 mm). At KMR the mean tail width values did not show pronounced changes over the sampling period (Fig. 6).

### 3.3. Gradient of CPUE response from the centre of each marine reserve

Linear and non-linear regression analyses revealed that at TMR, CPUE declined significantly with distance from the centre of the reserve (Fig. 7). The linear fit was statistically significant ($r^2 = 0.136$, $p = 0.005$), but was surpassed by the best non-linear fit ($r^2 = 0.257$, $p < 0.0001$). However, CPUE at KMR did not show this general trend (Fig. 8). Both the linear ($r^2 = 0.002$, $p = 0.769$) and the best non-linear fit ($r^2 = 0.006$, $p = 0.625$) were not significant, providing no evidence of a relationship between CPUE and distance from the centre of KMR.

### 3.4. Changes in historical and contemporary CPUE data

At TMR, contemporary CPUE (i.e. CPUE estimated during this study) both inside and outside the reserve was significantly greater than

**Table 1**
Mean size of tail width and weight for rock lobsters caught inside and outside Taputeranga and Kapiti marine reserves (mean ± s.e.).

| | Taputeranga MR | | | | Kapiti MR | | | |
|---|---|---|---|---|---|---|---|---|
| | Inside | Outside | p-value | DF | Inside | Outside | p-value | DF |
| Tail width (mm) | 63.11 ± 3.03 | 59.84 ± 2.3 | 0.022 | 265 | 78.20 ± 3.11 | 72.45 ± 4.2 | 0.33 | 87.5 |
| Weight (g) | 860.1 ± 17.1 | 669.6 ± 13.2 | 0.0001 | 265 | 1360.6 ± 27.5 | 982.7 ± 19.7 | 0.082 | 65.9 |

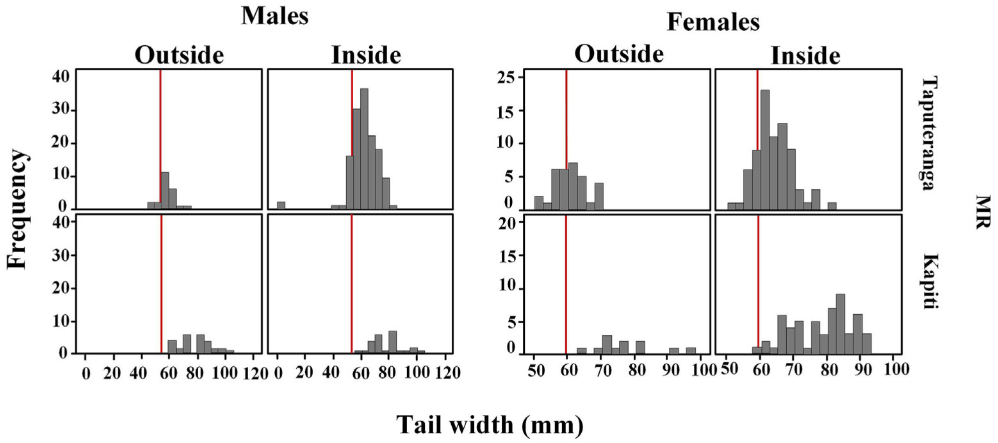

**Fig. 4.** Size frequency histograms (% frequency) for male and female rock lobsters tail width (mm) surveyed on the Wellington south coast and Kapiti Island within and outside Taputeranga and Kapiti MRs. Vertical red lines indicate minimum legal sizes for each sex (54 mm for males and 60 mm for females). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

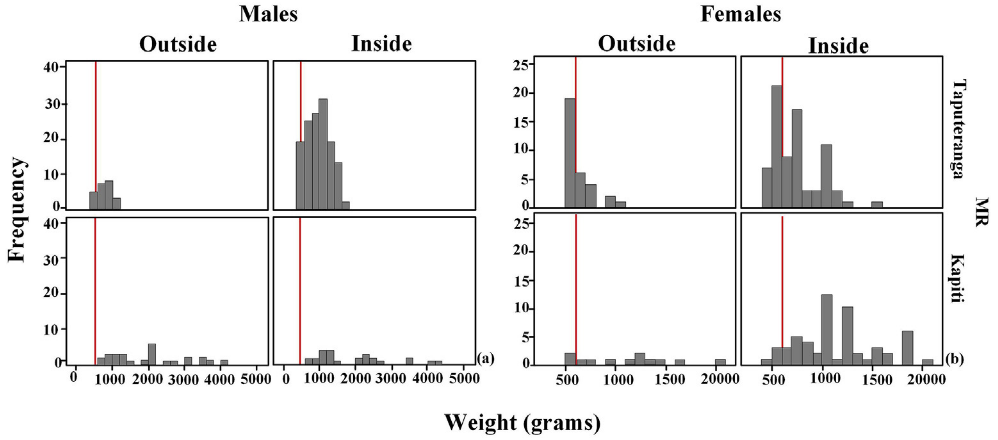

**Fig. 5.** Weight frequency histograms (% frequency) for male (a) and female (b) rock lobsters surveyed at Wellington south coast and Kapiti Island within and outside the Taputeranga and Kapiti MRs. The size measure is individual weight of rock lobster caught (grams). Vertical red lines are the minimum legal sizes for either sex (expressed here in grams equivalent to tail width). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

historical CPUE (i.e. commercial fisheries catch before TMR was established) for the region (inside: PERMANOVA, *pseudo-F* = 12.488, $p < 0.001$; outside: PERMANOVA, *pseudo-F* = 40.057, $p < 0.001$) (Table 3). The contemporary mean CPUE (inside and outside) was twice as high as the historical CPUE (1998–2005) (mean historical CPUE was 0.8 kg pot lift$^{-1}$ ± 0.05 SE). In addition, significant differences were also observed between the contemporary and historic CPUE data amongst seasons (Table 2) inside and outside the reserve (inside: PERMANOVA, *pseudo-F* = 7.012, $p < 0.001$; outside: PERMANOVA, *pseudo-F* = 3.7461, $p = 0.010$) (Table 3). Testing of TMR historical

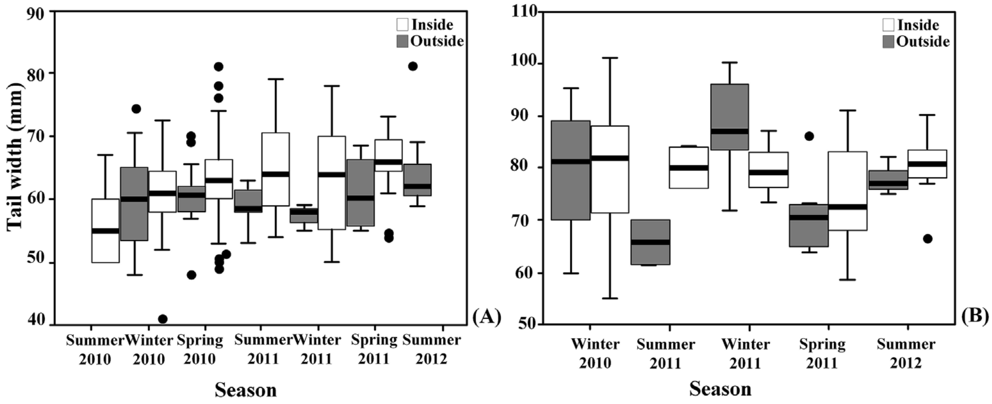

**Fig. 6.** Box plots of data for all rock lobsters caught inside and outside of Taputeranga (A) and Kapiti (B) Marine Reserves respectively. Box plots show the median interquartile range (box) for tail width (mm) for different seasons and years for rock lobsters inside and outside the Taputeranga Marine Reserve and Kapiti Marine Reserve.

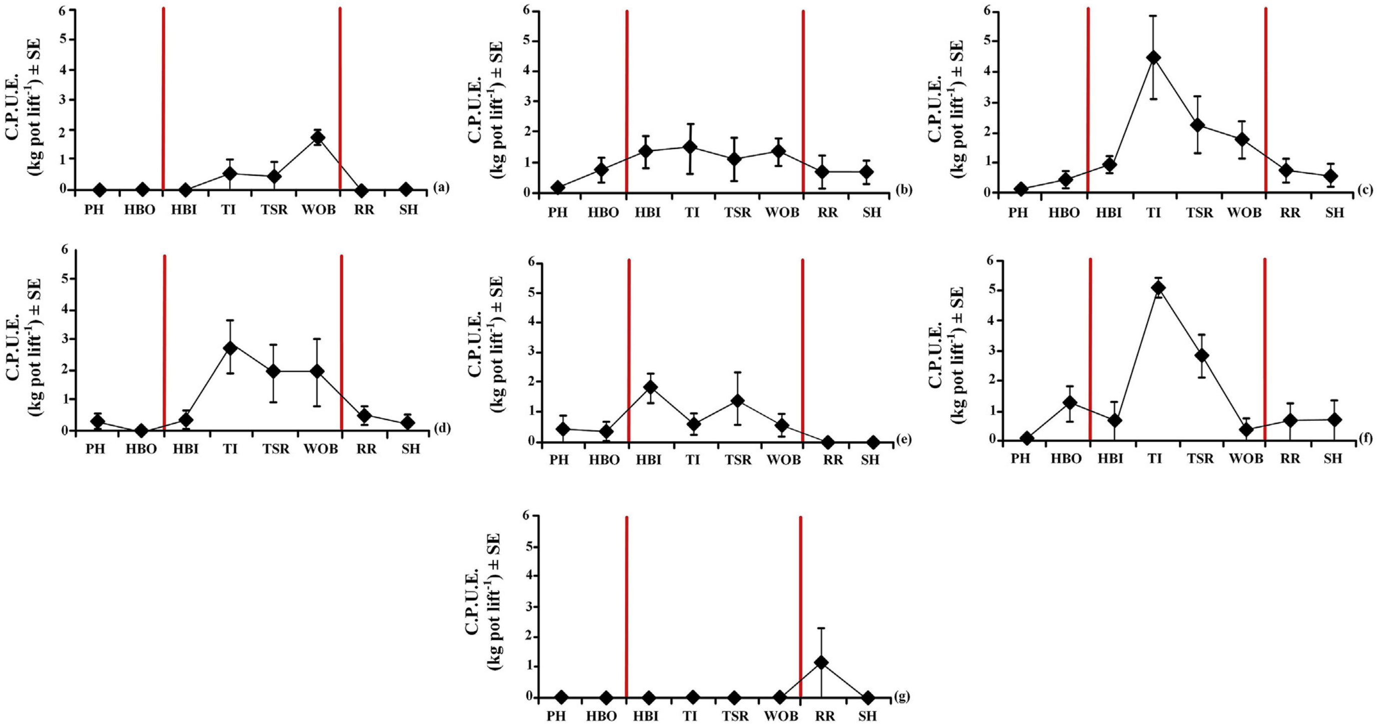

**Fig. 7.** Mean Catch Per Unit Effort (CPUE) at Taputeranga MR expressed as kg per pot lift for different sites from summer 2010 to summer 2012. (a) summer 2010, (b) winter 2010, (c) spring 2010, (d) summer 2011, (e) winter 2011, (f) spring 2011 and (g) summer 2012. The sites outside the reserve were (left to right on x-axis, from east to west) **PH**: Palmer Head, **HBO**: Houghton Bay Outside, **HBI**: Houghton Bay Inside, **TI**: Taputeranga Island, **TSR**: The Sirens Rock, **WOB**: Western side Owhiro Bay, **RR**: Red Rocks and **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.)

CPUE data revealed that CPUE varied significantly among all seasons, both inside and outside the reserve. (Table 3).

In contrast, at KMR the contemporary CPUE was only significantly different inside the MR (PERMANOVA, *pseudo-F* = 3.102, p = 0.049) compared to historical CPUE (Table 2). The average contemporary CPUE (inside) at KMR was 1.93 times higher compared to historical CPUE (1998–2005) (mean historical CPUE was 0.9 kg pot lift$^{-1}$ ± 0.1 SE). For contemporary and historical CPUE variation as a function of season, significant differences were only observed outside KMR (PERMANOVA, *pseudo-F* = 7.294, $p < 0.001$) (Table 2), this difference being recorded for winter inside and outside the reserve (Table 3).

### 3.5. CPUE for reef systems with differing levels of protection

ANOVA revealed a significant difference in mean CPUE amongst the three types of reef system at TMR (protected, partially protected, and unprotected; p = 0.037). The Bonferroni *post-hoc* test revealed that this difference was between the fully protected and unprotected groups. Average CPUE for protected reefs was 1.409 kg pot lift$^{-1}$, while it was 0.971 kg pot lift$^{-1}$ for partially protected reefs and 0.399 kg pot lift$^{-1}$ for unprotected reefs (Fig. 9A).

At KMR, because the majority of the nearshore reef structure inside and outside the reserve was continuous, all reserve sites were considered to be ‘partially protected’. Therefore, it was not possible to

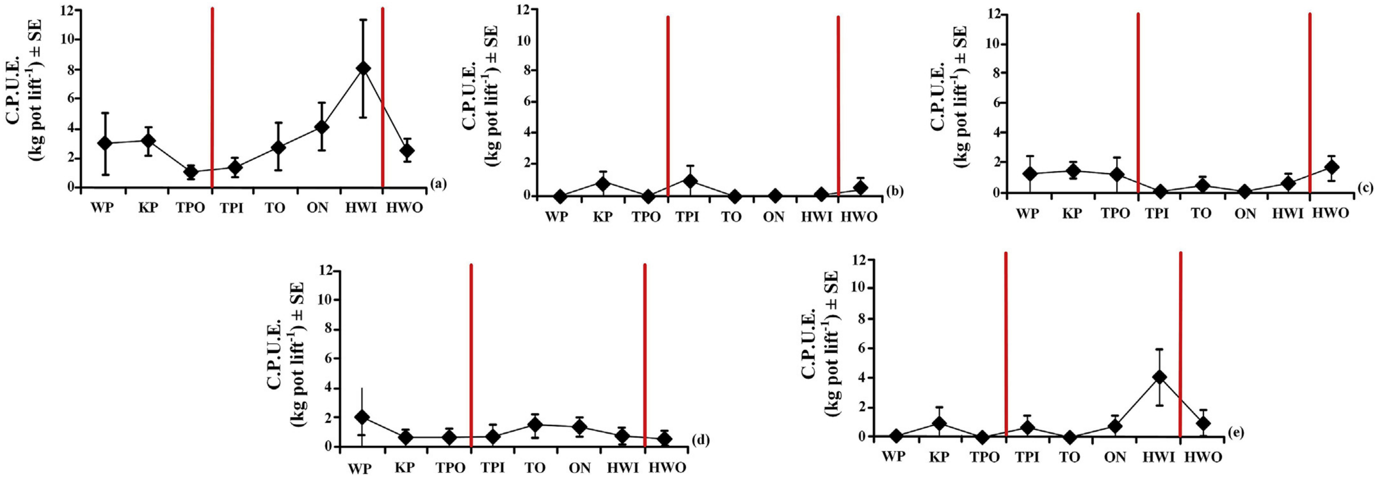

**Fig. 8.** Mean Catch Per Unit Effort (CPUE) at Kapiti MR expressed as kg per pot lift for different sites from winter 2010 to summer 2010. (a) winter 2010, (b) wummer 2011, (c) winter 2011, (d) spring 2011 and (e) summer 2012. The sites outside the reserve were (left to right on x-axis, from south to north), WP: West Point, KP: Kaiwharawhara Point, TPO: Trig Point outside, TPI: Trig Point inside, TO: Te Oneroa, ON: Onepoto, and HWI: Hole in the wall inside, and HWO: Hole in the wall outside.

**Table 2**
PERMANOVA test results of comparison of CPUE data for rock lobsters at Taputeranga and Kapiti marine reserves as a function of time (historical and contemporary data sets) and season (summer, winter, spring).

| INSIDE | Taputeranga MR | | | | | | Kapiti MR | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Source | df | SS | MS | Pseudo-F | p | NP | df | SS | MS | Pseudo-F | p | NP |
| Time | 1 | 9150.9 | 9150.9 | 12.488 | 0.0001* | 9943 | 1 | 3373.9 | 3373.9 | 3.1017 | 0.0490* | 9954 |
| Season | 2 | 10276 | 5138.1 | 7.0116 | 0.0003* | 9962 | 2 | 4519.6 | 2259.8 | 2.0775 | 0.0893 | 9950 |
| Time × Season | 2 | 8974.4 | 4487.2 | 6.1235 | 0.0004* | 9965 | 2 | 5024.7 | 2512.4 | 2.3097 | 0.0567 | 9941 |
| OUTSIDE | Taputeranga MR | | | | | | Kapiti MR | | | | | |
| Source | df | SS | MS | Pseudo-F | p | NP | df | SS | MS | Pseudo-F | p | NP |
| Time | 1 | 29103 | 29103.0 | 40.057 | 0.0001* | 9949 | 1 | 1513 | 1513.0 | 1.6618 | 0.1770 | 9956 |
| Season | 2 | 5443.4 | 2721.7 | 3.7461 | 0.0096* | 9948 | 2 | 13281 | 6640.7 | 7.2936 | 0.0001* | 9954 |
| Time × Season | 2 | 3326.7 | 1663.4 | 2.2894 | 0.0645 | 9935 | 2 | 16071 | 8035.7 | 8.8258 | 0.0001* | 9953 |

NP – number of unique permutations out of 9999.

**Table 3**
Pairwise comparisons of historic CPUE among seasons (summer, winter, spring). Data from inside and outside were run separately.

| | Taputeranga MR | | | | Kapiti MR | | |
|---|---|---|---|---|---|---|---|
| | Season | t | p | NP | t | p | NP |
| Inside | Summer | 2.7173 | 0.0019* | 9948 | 1.7049 | 0.0615 | 9875 |
| | Winter | 2.5489 | 0.0073* | 9940 | 2.5378 | 0.0032* | 9942 |
| | Spring | 3.2655 | 0.0006* | 9939 | 0.5540 | 0.7305 | 9071 |
| Outside | Summer | 5.4463 | 0.0001* | 9948 | 1.7734 | 0.0500 | 9874 |
| | Winter | 3.1121 | 0.0006* | 9951 | 4.0289 | 0.0001* | 9949 |
| | Spring | 2.6833 | 0.0020* | 9948 | 1.8123 | 0.0523 | 9080 |

*$p < 0.05$.
NP – number of unique permutations out of 9999.

perform an analysis for fully, partially, and unprotected categories. However, a *t*-test to compare mean CPUE values at partially protected (mean CPUE = 1.338 kg pot lift$^{-1}$) versus unprotected sites (0.982 kg pot lift$^{-1}$) was not significantly different ($t = 0.705$, df = 38, p = 0.485) (Fig. 9B).

## 4. Discussion

Marine reserves (MRs) in NZ are established primarily for the purposes of habitat and multi-species protection, although legally, they are established first and foremost for scientific research [6]. Both KMR and TMR were selected for reservation status because they constitute representative habitats of the Taranaki Bight and Cook Strait, respectively. Both regions support important local RL fisheries with long histories, with the result that the MRs have had some form of interaction with the local fishery. Trying to understand this interaction, and if MRs may be contributing to local fisheries (e.g. via spill over and/or larval export) is critically important, but also immensely challenging. Using standard industry fishing techniques, our research at two central NZ MRs demonstrates how rock lobster abundance (as quantified using CPUE) can increase inside versus outside MRs, and may be strongly influenced by both the relationship between the proximity of reef habitat to MR boundaries and the extent of protection (fully, partially, unprotected) of reefs.

There is now substantial scientific evidence (including this study) that suggests MRs established directly for biodiversity protection and habitat conservation, may indirectly promote the recovery of previously fished population of some species [69,70]. Recent NZ Government policy on Marine Protected Areas has been guided by the New Zealand Biodiversity Strategy, which reflects NZ's commitments to the Convention on Biological Diversity, to help stem the loss of biodiversity worldwide. In NZ, full no take MRs are recognised as the ‘core tool in the development of a representative network of MPAs’. However, the MPA policy does not include or consider the potential benefits and impacts from MRs to fisheries enhancement. The development of a national network of MRs will inevitably cause conflicts amongst users. To some extent, this conflict may be minimised by the use of spatial management, which is a powerful tool to mitigate and reduce conflicts and can improve marine resource management [71], although the NZ

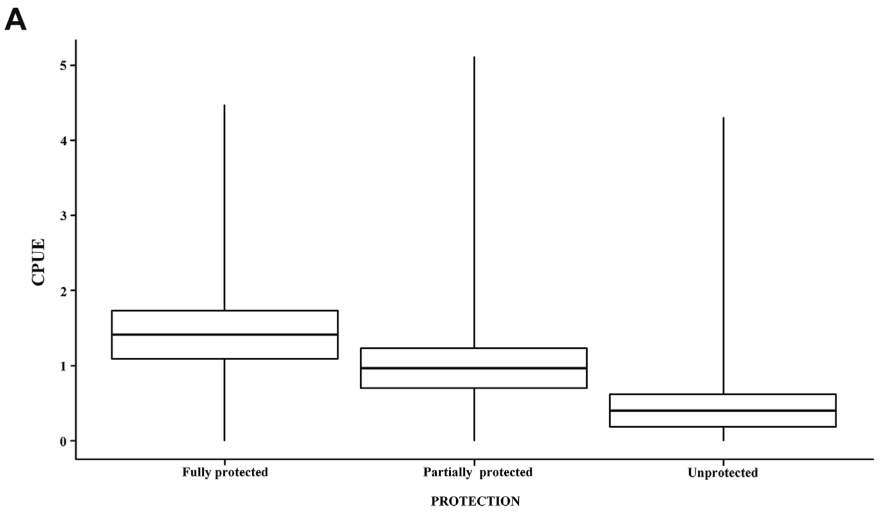

**Fig. 9A.** Box plots of CPUE (kg rock lobster per pot lift) for different reef protection levels at Taputeranga Marine Reserve.

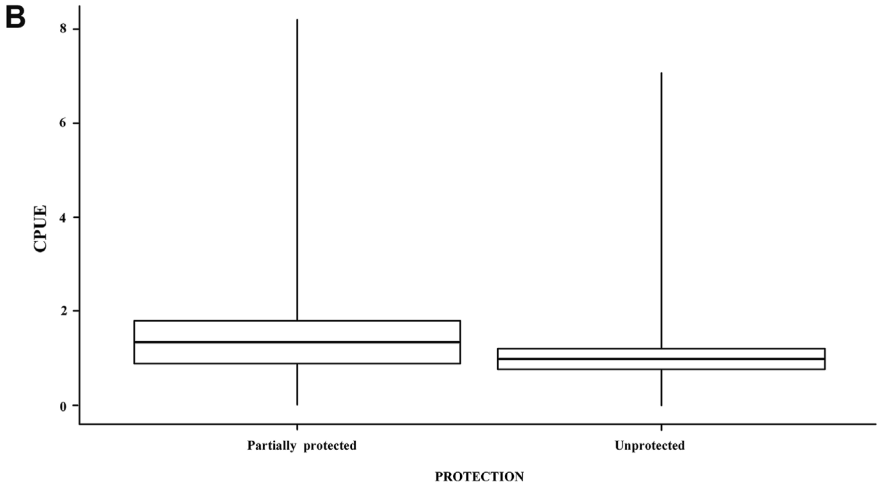

**Fig. 9B.** Box plots of CPUE (kg rock lobster per pot lift) for different reef protection levels at Kapiti Marine Reserve.

experience with spatial management has not always been positive or successful (e.g., the Hauraki Gulf Marine Park Act 2000 [72]). For effective and viable MPA network design, spatial management policies are needed where spatial information such as habitat complexity and extent, species distribution, larval/juvenile/adult and fisheries movement, are given full consideration. Therefore, a well-designed MPA (including MR) network needs design input from, and ongoing consideration of the views of all users, but in particular both conservationists and fisheries managers [69–71]. Our results contribute to the design of MRs with respect to the habitat they protect and provide a better understanding of the interactions between MRs and local fisheries.

### 4.1. Rock lobster population increases

MRs in NZ are not established for the purposes of fisheries management, but may indirectly contribute by way of spill over and larval export. However, research suggests that most coastal MRs in NZ are, in fact, too small (typically about 1000 ha) to provide adequate protection to achieve meaningful fisheries outcomes [e.g. 5,72]. Nonetheless, there is now extensive evidence that MRs in NZ can result in a greater abundance and larger mean size of individuals of highly targeted species [7,14,26,28,55]. Increasingly, international research is demonstrating that multiple interacting factors, including life-history and ecological traits, MR age and size, targeted versus non-targeted status and levels of enforcement all contribute significantly to direct and indirect benefits of MRs [e.g. Refs. [5,18,72–74]].

Consistent with a number of other studies or meta-analyses of data from temperate or subtropical rocky reef regions [e.g. Refs. [7,14,75–78]], RLs at both TMR and KMR showed evidence of recovery (increases in abundance and mean size) once fishing activity ceased, although it was variable between MRs and is temporally variable within the reserves. Where significant differences existed for comparisons of inside versus outside data, all such comparisons favour the RLs inside the reserves. RLs are, on average, bigger, more abundant, and have greater individual mean weight inside the MRs with the result that metrics such as CPUE (here calculated for legal-sized RL only because commercial RL pots were used that allow for the escape of undersized RL) and overall biomass are greater inside than outside the reserves. Generally, these positive responses are greater at TMR than at KMR. This change (or recovery) of the RL population at TMR has occurred very rapidly. When this study began in January, 2010, TMR had been closed to fishing (and all other forms of human disturbance) for less than 2 years since its establishment in August, 2008. While a full population recovery may take much longer [e.g. 9], many studies report similarly rapid increases in marine populations. Elsewhere, it has been suggested that in the years immediately following protection, naturally high levels of variability in settlement patterns may obscure conservation responses, to a point where a MR may appear to be ineffective [78]. This has not been the case in central NZ, where for a slow growing species such as RL, the no-take regime of the MR has given rise to a rapid response in terms of larger and bigger RLs in the absence of fishing pressure.

Changes recorded for RL at KMR are positive, but not of the same magnitude as those at TMR. This may reflect the smaller size of the western KMR (340 ha) compared to TMR (859 ha), but may also reflect ongoing fishing pressure in and around KMR and differential patterns of larval settlement at the two MRs CPUE (kg pot lift$^{-1}$) data inside both MRs were higher than outside, however, significant differences were only observed at TMR. Nonetheless, both CPUE values were lower than those reported from other MRs. For example, Freeman [55] found that in the Te Tapuwae o Rongokako MR (Gisborne, northeastern New Zealand) CPUE was 46 times higher inside than outside the MR four years after establishment. Other RL studies have also reported higher CPUE values inside reserves [e.g. Refs. [11,12,28,37,38,79,80]]. In the case of KMR, the difference in CPUE between inside and outside the reserve was not significant. This lack of contrast in CPUE could because of poaching of lobsters within the MR, movement of lobsters across the marine reserve boundary to fished areas, or because fishing intensity in the unprotected area is low. Other factors potentially affecting the catch data were pot competition (especially outside the MRs where research pots and commercial pots may have competed for the same catch), bait type, soak time, and non-random placement of research pots. These effects remain unstudied.

### 4.2. Rock lobster gradients

At TMR, but not at KMR, the greatest RL biomass was recorded at the centre of the reserve, decreased toward the MR boundaries, and further decreased outside the reserve. Other studies have reported similar results for RLs [28,29,55,80], and also for other species including blue cod (*Parapercis colias*) and snapper (*Pagrus auratus*) [14,55,81]. This pattern is most likely explained by a combination of heavy fishing effort outside the reserve and RL movement from inside to outside the reserve. After establishment of TMR, fishing effort (commercial, recreational, and customary fishing) was displaced outside the boundaries. There is a general perception that MRs can enhance fisheries outside their boundaries through spillover, leading to a ‘fishing the line’ strategy [28]. The loss of fishing grounds due to MR designation, in combination with the location of TMR along Wellington city's coast, has resulted in the TMR boundaries being popular fishing grounds. Cross-boundary behaviour has been described for RLs crossing the offshore boundary of the reserve, making them vulnerable to fishing effort in adjacent areas through their seasonal inshore-offshore migration [34]. Additionally, the largest reef area is mainly located inside the MR and at the boundaries of the reserve [see 9] (Fig. 1), which provides refuge for RLs (adults and juveniles) that do not move, but no protection for RLs that do move outside the reserve.

Other factors possibly affecting RL population distributions in and around TMR and KMR are the size and shape of the MRs, specifically how MR size is related to RL home range [36] and MR shape (i.e. perimeter-to-area ratio) that influences the amount of appropriate shelter areas, habitats (including for reproduction), and food [20,74,82]. For example, the relationship between MR boundaries and local rocky reefs is an important factor for understanding RL population recoveries, whereby fully protected reefs show greater recoveries than partially protected reefs [20,26]: our results confirm this finding at TMR. These results are important when designating MR boundaries with respect to the habitats they protect, as well as for predicting RL recovery potential as a function of MR protection. These factors have been described as important for other lobsters, such as *Panulirus* species like *P. argus*, *P. guttatus, P. homarus, P. marginatus* and also *Homarus gammarus* [83–85]. The high habitat complexity around Kapiti Island may affect RL distribution. For example, Stewart and MacDiarmid [58] found that RLs were more numerous on the western side of the island (at the same sampling sites used in this study), which was explained by the high complexity of reef structures compared to the eastern side of the island. In addition, Kapiti is an area with low puerulus settlement compared to other areas of the North Island of New Zealand, which may lead to a slower recovery of the RL population at Kapiti Island than elsewhere in NZ [58].

### *4.3. Historical versus contemporary catches*

Comparison of historical data (1998–2005) to data collected in this study (2010–2012) inside TMR showed a higher mean CPUE in recent years, with the greatest difference being in winter compared to spring, when the highest catches were recorded. However, catches outside the reserve showed a similar or lower mean CPUE value compared to the historical data. Moreover, the pattern of seasonal variation in CPUE found at TMR is very similar to historical commercial catches. The higher mean CPUE found inside TMR (mean CPUE = 1.409 kg pot lift$^{-1}$) compared to the historical CPUE (less than 1 kg pot lift$^{-1}$) indicates that the RL population is rebuilding inside the reserve.

At KMR, the average contemporary CPUE was higher than historical CPUE, with only summer and winter catches outside the reserve being similar to the historical data pattern. In contrast, CPUE from inside the reserve showed the opposite pattern to the historical data, where the lowest catch was in winter. However, seasonal catches did not show any clear yearly pattern. This may explain, in part, the discrepancies observed between the contemporary data and the historical CPUE data.

### *4.4. Sex ratio effects*

It is important to consider sex ratio when assessing MR effectiveness because fishing may not only impact the biomass and abundance of RLs, but also the sex ratio [55,86]. In NZ and Australia, due to the fishing regulations of no capture of berried (egg bearing) females and the natural pattern of seasonal onshore/offshore movement, the RL fishery may be biased towards catching males [55,62]. In addition, there are different sex-specific minimum legal sizes in NZ (tail width MLS for males is 54 mm, for females it is 60 mm). Therefore, these fishing regulations may have a biasing effect on the sex ratios of fished RL populations. Considering that all fishing activities are banned in MRs (and without denying the importance of other factors such as MPA design, management regime, previous history of harvest, and others), it is expected that the sex ratio inside a reserve will recover to its natural state in the absence of fishing pressure [55]. Both inside and outside TMR, the sex ratio was biased toward more females. This might reflect the fact that the fishery located in the surrounding areas is catching mostly males as a result of the fisheries management regime and associated restrictions (e.g. prohibitions on taking berried females). While similar results were reported by Sullivan [87] and Freeman [55] who found a male-biased fishery in Gisborne (northeast NZ), care needs to be taken with the interpretation of the potting data because, as noted above, potting itself may bias the sex ratio of the caught RLs. In the absence of much published information about RL sex ratios in NZ from non-potting studies, it is relevant that in northern NZ, MacDiarmid (1991) reported seasonally variable sex ratios, with females dominating at certain times and the sex ratio reaching 1:1 at other times. Given that we do not know what the natural sex ratio is for RLs from central NZ (we expect it to be close to 1:1), we suggest that, on balance, our results indicate that potting activity is targeting males, but this needs to be interpreted with care.

Both size and sex ratio are very important for RL group structure, with implications for the reproductive potential of RL populations [20,55,88–90]. For example, a large number of large males makes it is more likely that females will be successfully fertilised, due to females preferentially mating with larger males [12,74,88].: The present study found that RLs inside both MRs were bigger and heavier than in the neighbouring fished areas. Similar results have been reported by other studies [37,91]. Therefore, on average, bigger and more abundant RLs with an even sex ratio are likely to produce more egg output within MRs than outside, which can then potentially be exported to adjacent fisheries [see Refs. [74,88,92]].

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## Appendix A. List of fish species used as bait for rock lobster fishing during this research.

| Common name | Scientific name |
|---|---|
| Blue moki | *Latridopsis ciliaris* |
| Hoki | *Macruronus novaezelandiae* |
| Red gurnard | *Chelidonichthys kumu* |
| Snapper | *Chrysophrys auratus* |
| Tarakihi | *Nemadactylus macropterus* |
| Trevally | *Caranx georgianus* |
| Blue warehou | *Seriolella brama* |

## Appendix B. Location of each sampling site and its distance from the centre the marine reserve.

| Marine reserve | Site name | Latitude | Longitude | Distance from centre of MR (km) |
|---|---|---|---|---|
| TMR | The Sirens Rock (TSR) | −41.350363° | 174.763014° | 0.34 |
| | Western side Owhiro Bay (WOB) | −41.350673° | 174.751375° | 1.31 |
| | Red Rocks (RR) | −41.361008° | 174.725450° | 3.47 |
| | Sinclair Head (SH) | −41.364511° | 174.716047° | 4.09 |
| | Taputeranga Island (TI) | −41.352340° | 174.771733° | 0.39 |
| | Houghton Bay inside (HBI) | −41.349302° | 174.789033° | 1.85 |
| | Houghton Bay outside (HBO) | −41.349205° | 174.793978° | 2.25 |
| | Palmer Head (PH) | −41.350630° | 174.817326° | 4.20 |
| KMR | HWO (out) | −40.819798° | 174.936650° | 2.36 |
| | HWI (in) | −40.821969° | 174.928101° | 1.62 |
| | ON (in) | −40.827548° | 174.917226° | 0.21 |
| | TO (in) | −40.833661° | 174.911865° | 0.62 |
| | TPI (in) | −40.842767° | 174.908563° | 1.65 |
| | TPO (out) | −40.848696° | 174.903477° | 2.43 |
| | KP (out) | −40.856657° | 174.890176° | 3.76 |
| | WP (out) | −40.875091° | 174.868861° | 6.49 |

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## Glossary

*CPUE:* Catch Per Unit Effort
*CRA:* Commercial Rock Lobster Area - Fishery Management Unit
*Kg Pot Lift*$^{-1}$*:* kilogram per pot lift
*KMR:* Kapiti Marine Reserve
*MLS:* Minimum Legal Size
*MPA:* Marine Protected Area
*MR:* Marine Reserve
*NZ:* New Zealand
*QMS:* Quota Management System
*RL:* Rock Lobster
*RLP:* Rock Lobster Pots
*TMR:* Taputeranga Marine Reserve