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Marine reserves increase the abundance and size of blue cod and rock lobster

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ABSTRACT: Size and abundance data were compiled and collated for blue cod *Parapercis colias* and rock lobster *Jasus edwardsii* from New Zealand marine reserve (MR) studies for a meta-analysis to test the null hypotheses that reserve status does not affect the size or abundance of either species. Calculation of meta-analysis effect sizes revealed that significant differences in effect size existed among studies, meaning that the biological response to MR status of both species in terms of their changes in size and/or abundance differed significantly among the MRs. Analysis revealed that blue cod were bigger inside compared with outside MRs in 9 of 10 studies and were more abundant inside MRs in 8 of 11 studies, and that rock lobster were bigger inside the MRs in 12 of 13 studies and more abundant inside the MRs in 11 of 14 studies. These findings indicate that MR protection can result in more and bigger individuals soon after the establishment of the MR (mean of 6.5 yr for blue cod, 8.5 yr for rock lobster) despite small sample sizes of studies (≤10 for blue cod, ≤14 for rock lobster). Focused comparison tests did not reveal any relationship between rock lobster or blue cod size or abundance and either age or area of MRs. Our results demonstrate that no-take MRs are valuable conservation tools for species such as blue cod and rock lobster (and probably also for other exploited species with similar life history characteristics and habitat requirements) and that statistically detectable conservation benefits are apparent after only a few years of protection.

KEY WORDS: Meta-analysis · Focused comparison tests · Marine reserves · Marine conservation · Blue cod · Rock lobster · Mean size and mean abundance · New Zealand

INTRODUCTION

Recent recognition of increased anthropogenic demands and influence on marine resources and ecosystems has led to a strong push for 'active' marine conservation (Hockey & Branch 1997, Lubchenco 1997). The value of marine protected areas, particularly no-take marine reserves, and the fundamental importance of understanding marine environments is now recognised by informed politicians, conservation scientists, and recreational and commercial fishers (Attwood et al. 1997, Kingsford & Battershill 1998, Conover et al.

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2000). Concurrent with this increased recognition is the need to demonstrate and quantify the conservation benefits of such marine protected areas (MPAs), which in many countries are established for multiple purposes, including conservation, fisheries management and research, and for aesthetic reasons.

As of mid-2008 there are 31 no-take marine reserves (MRs) spread throughout New Zealand; these date back to 1975 and protect about 7.6% (an area of 1 273 024.4 ha) of New Zealand's territorial waters. These no-take MRs were established to prevent or minimise human-mediated disturbance by prohibiting all forms of extractive use, including commercial, traditional and recreational fishing. It is anticipated that biological communities in MRs will return to a 'natural' condition, although there is often no recognition of what actually constitutes 'natural.' It is also anticipated that such communities can act as a reference to gauge the extent of human effects in adjacent unprotected areas (Attwood et al. 1997, Davidson 2001). This role for MRs as a control or baseline reference is important because it increases our knowledge of how marine systems are structured and function in the absence of human-mediated disturbance. Ultimately, such knowledge is important for successful conservation and management of the wider exploited area (Creese & Jeffs 1992, Ballantine 1994, Halpern & Warner 2002).

Numerous individual studies have been conducted to determine the effects of MRs on a single species or a small group of species. This includes species that are common, are expected to exhibit large and/or rapid changes in size and/or abundance, have commercial or recreational value, or are culturally important (e.g. Buxton & Smale 1989, Cole et al. 1990, Creese & Jeffs 1992, MacDiarmid & Breen 1992, Russ & Alcala 1996, Edgar & Barrett 1997, 1999, Babcock et al. 1999, Chapman & Kramer 1999, Cole et al. 2000, Willis et al. 2000, Jouvenel & Pollard 2001, and references therein). Studies investigating the effectiveness of a single MR typically involve the comparison of sites in a reserve with sites in a non-reserve (i.e. control) area to determine whether communities inside the reserve differ significantly from those in comparable habitats outside. Individual studies may conclude that the establishment of a reservation results in an increase in species mean size and/or abundance, but this approach, valuable as it is, cannot answer the bigger question of the possible conservation benefits of multiple MRs throughout a region or country. This is because individual studies have limited power to detect change because of low within-site replication, low among-site sampling effort, short study duration and the short sampling period following the establishment of the MR (Arnqvist & Wooster 1995). Although there have been several review papers on the potential conservation benefits of MRs (Creese & Jeffs 1992, Jones et al. 1992, Allison et al. 1998, García Charton & Pérez Ruzafa 1999, Palumbi 2004), formal statistical analyses of composite MR data from a number of studies are small in number and tend to focus on fish taxa (Mosquera et al. 2000, Côté et al. 2001, Halpern & Warner 2002, Halpern 2003, Micheli et al. 2004). To the best of our knowledge, this study is the first to statistically analyse composite data to quantify the conservation benefits of no-take MRs to an ecologically and economically important invertebrate, the red or spiny rock lobster *Jasus edwardsii*, and adds to information about the conservation benefits of no-take MRs for a key fish taxon, the blue cod *Parapercis colias*.

Meta-analysis is a statistical technique used to combine the results from several independent studies all testing the same null hypothesis or hypotheses, in an attempt to detect an 'overall' outcome (Arnqvist & Wooster 1995, Adams et al. 1997, Schafer 1999). As noted by Mosquera et al. (2000), methods such as narrative reviews or 'vote-counting' have traditionally been used as ways of summing up findings from many separate studies. Such methods may produce misleading results because they tend to be subjective and do not take into account relative importance or detail of the studies examined (Arnqvist & Wooster 1995, Adams et al. 1997). Meta-analysis is a quantitative synthesis and analysis of a collection of experimental studies (Osenberg et al. 1999) that allows an objective appraisal of the evidence. Because it is quantitative, the results of meta-analysis provide a set of numbers and probabilities that can be used as reference points for future research (Arnqvist & Wooster 1995, Egger et al. 1997). Meta-analysis as a robust statistical technique to quantify results across a range of studies is used widely in the fields of medicine and the social sciences, but its potential application to ecological data is only now being realised (Adams et al. 1997).

Our analysis combined published and unpublished data from 10 New Zealand MRs sampled at different times over the last 2 decades. Meta-analyses were used to investigate the effects of MRs on the size and abundance of 2 key species, the blue cod and the red rock lobster, both of which are widely distributed and are ecologically, economically and culturally important in New Zealand. As noted elsewhere, MRs are effectively 'multiple human-exclusion experiments replicated in a variety of ecosystem types and geographic locations' (Micheli et al. 2004, p. 1709). As such, our study tests the null hypotheses that there are no differences in the mean size or mean abundance at MR sites relative to control sites to quantify the long-term and geographically widespread effect of reservation status on these 2 species. We also examine the effects that MR area and MR age have on the mean size and abundance of these 2 species. Our meta-analysis is restricted to these 2 species only because (1) not all species occur throughout the geographic range of the country, (2) these 2 species are heavily exploited and are, therefore, expected to respond positively and rapidly to reservation status, and (3) most other species are not monitored at all or are not monitored in a sufficient number of marine reserves.

MATERIALS AND METHODS

Two species were selected for analyses: the blue cod and the rock lobster. Meta-analysis methods followed Rosenthal (1987), Egger et al. (1997) and Schafer (1999). Data collected from a total of 10 MRs in New Zealand (Fig. 1) were collated and analysed (Tables 1 & 2).

The blue cod meta-analysis used data from 5 MRs. Each of these data sets included data from the reserve itself and a corresponding control area to permit a reserve versus control comparison. Two of these MRs were investigated at 2 separate time periods by 2 different investigators, and the long-term unpublished data set for the Long Island–Kokomohua MR was divided into 4 separate time periods of equal duration. These data sets were treated as separate studies giving

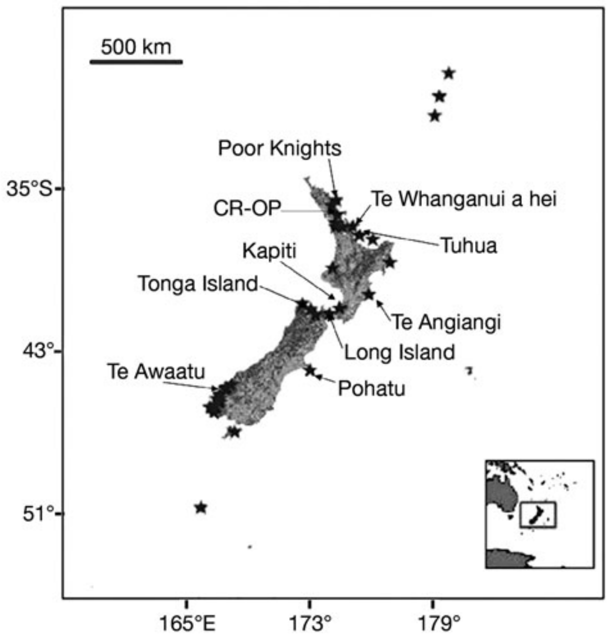

Fig. 1. Location of New Zealand marine reserves from which data were used in this investigation. Inset shows location of New Zealand. Star = marine reserve site. Named site = one of the marine reserves used in this study. CR-OP = Cape Rodney to Okakari Point (Leigh); Te Whanganui a hei = Cathedral Cove; Tuhua = Mayor Island; Long Island = Kokomohua; Pohatu = Flea Bay; Te Awaatu Channel = The Gut

totals of 10 (blue cod size) and 11 (blue cod abundance) studies in this meta-analysis (Table 1). Where the data were collected over a period of years, the average difference in mean size and/or mean abundance estimates between reserve and control per year were tested for a trend. If there was a noticeable trend then the larger data set was divided into smaller time periods. Thus, the unpublished data set collected by R. J. Davidson for the Long Island–Kokomohua MR for the period 1992–2004 was split into 4 separate data sets (1992–1994, 1995–1997, 1998–2000 and 2001–2004) because significant differences in response were observed between the MR and the control (outside MR) sites as a function of time (i.e. the response changed over time). We recognise that such split data sets may not be independent in a statistical sense, but we treat each as being independent because the response differs according to the time period in question (similar problems have been reported in other meta-analyses, e.g. Mosquera et al. 2000). If no noticeable trend was detected then results were treated as one data set. These data sets were tested for differences in mean size and mean abundance of blue cod between MR and neighbouring non-MR sites.

The rock lobster meta-analysis used data from 10 MR studies, 3 of which were monitored at different times by different groups and were, thus, treated as separate studies. As outlined above, testing for trends was carried out that resulted in the recognition of data sets that were formed by splitting some of these into smaller time periods. This brought the total number of rock lobster studies to 13 (rock lobster size) and 14 (rock lobster abundance) (Table 2). These individual data sets included data from a reserve and a corresponding control area. The data sets were tested for differences in rock lobster mean size and mean abundance between MR and neighbouring non-MR sites.

The meta-analyses of both the abundance and size data were performed in 3 stages:

(1) The studies were compared to determine whether there was a significant difference in terms of the 'effect sizes' offered by the different MRs. 'Effect size' is a statistical term defined as the amount of change, or magnitude of the effect, caused by the reserve. This is measured by a standardised mean difference (in size or abundance) between MRs and controls.

(2) Where there was no significant difference in 'effect size' among studies, the studies were combined to give an overall significance and 'effect size.'

(3) Where there was a significant difference in 'effect size' among studies, the studies were investigated for particular patterns that may have resulted in the difference. For both species, 'focused' tests were performed to see if 'effect size' varied according to the area and age at time of study of the MR.

Table 1. Data sets (size and abundance) used in blue cod meta-analysis. MR = marine reserve

Marine reserve (year established)	Year(s) of survey	Source
Kapiti MR (1992)	1998–2000	A. Pande & J. Gardner (unpubl. data)
Kapiti MR (1992)	1999	A. MacDiarmid (unpubl. data)
Long Island–Kokomohua MR (1993)	1992–1994	R. Davidson (unpubl. data)
Long Island–Kokomohua MR (1993)	1995–1997	R. Davidson (unpubl. data)
Long Island–Kokomohua MR (1993)	1998–2000	R. Davidson (unpubl. data)
Long Island–Kokomohua MR (1993)	2001–2004	R. Davidson (unpubl. data)
Long Island–Kokomohua MR (1993)	2001	R. Cole (unpubl. abundance data only)
Tonga MR (1993)	1993 & 1999–2002	R. Davidson (unpubl. data)
Tonga MR (1993)	2001	R. Cole (unpubl. data)
Te Angiangi MR (1997)	1995–2003	D. Freeman & C. Duffy (unpubl. data)
Pohatu (Flea Bay) MR (1999)	2001–2002	R. Davidson (unpubl. data)

Table 2. Data sets (size and abundance) used in rock lobster meta-analysis

Marine reserve (year established)	Year(s) of survey	Source
Cape Rodney–Okakari Point MR (1975)	1985	MacDiarmid & Breen (1992)
Cape Rodney–Okakari Point MR (1975)	1995	A. MacDiarmid (unpubl. data)
Cape Rodney–Okakari Point MR (1975)	1995–2002	S. Kelly (unpubl. data)
Poor Knights MR (1981)	1985	A. MacDiarmid (unpubl. data)
Kapiti MR (1992)	1992–1999	A. MacDiarmid (unpubl. data)
Kapiti MR (1992)	1998–2000	A. Pande & J. Gardner (unpubl. data)
Mayor Island (Tuhua) MR (1992)	1996	S. Kelly (unpubl. data)
Whanganui A Hei (Cathedral Cove, Hahei) MR (1992)	1996	S. Kelly (unpubl. data)
Long Island-Kokomohua MR (1993)	1992–1999	R. Davidson (unpubl. data)
Long Island-Kokomohua MR (1993)	2001–2003	R. Davidson (unpubl. data)
Te Awaatu Channel MR (The Gut) (1993)	1999	S. Kelly (unpubl. data)
Tonga MR (1993) (abundance data only)	1998–2000	Davidson et al. (2002)
Te Angiangi MR (1997)	1998–2002	D. Freeman & C. Duffy (unpubl. data)
Pohatu (Flea Bay) MR (1999)	2001–2002	R. Davidson (unpubl. data)

The calculations used were as follows. For any particular study:

Step 1: Hedge's g was calculated by the formula:

$$g = \frac{\overline{x_1} - \overline{x_2}}{s_p} \quad (1)$$

where

$$s_p^{\,2} = \frac{(n_1 - 1)s_1^{\,2} + (n_2 - 1)s_2^{\,2}}{n_1 + n_2 - 1} \quad (2)$$

For abundance estimates, $\bar{x}$ = mean number of individuals and n = number of transects. For size estimates, $\bar{x}$ = mean size of individuals and n = number of individuals.

In both cases, subscript 1 = marine reserve, subscript 2 = control, s = standard deviation and $s_p^{\,2}$ = pooled variance for the 2 samples (inside and outside the reserve).

Note that Hedge's g computes the number of standard deviations difference between the reserve means and the control means (i.e. the standardised change offered by the reserve). The t-value (not the widely used Student's t-value) is then calculated by the following:

$$t = \frac{g}{\sqrt{1/n_1 + 1/n_2}} \quad (3)$$

This t-value is then used to compute the w-value, to allow the comparison of studies for which the formula is:

$$w = \frac{2n_1 n_2 (n_1 + n_2 - 2)}{(n_1 + n_2)[t^2 + 2(n_1 + n_2 - 2)]} \quad (4)$$

where t, n_1 and n_2 are defined as above. Following this the test statistic T_c is computed to compare the studies:

$$T_c = \sum_{j=1}^{S} w_j (g_j - \overline{g})^2 \quad (5)$$

where S = number of studies, w_j = w-value for study j (from Eq. 4), g_j = g for study j (from Eq. 1), and where S, w_j and g_j are defined as above. The test statistic has an approximate χ^{-2} distribution with S–1 degrees of freedom, under the null hypothesis of no difference in 'effect size' among the MRs.

Step 2: In cases where there is no significant difference in 'effect size', it is reasonable to combine studies to obtain an overall 'effect size' and significance level. This is to find an 'effect size' for all these studies in general (i.e. to define the magnitude of the effect the reserves are having). Defining t_j as the t-value for study j (from Eq. 3) an overall, weighted z-value can be obtained by:

$$z_w = \frac{\sum_{j=1}^{S} w_j t_j}{\sqrt{\sum_{j=1}^{S} w_j^2}} \quad (6)$$

where S is the number of studies and w_j is a weight for study j (we use the number of individuals in study j for size data and the total area sampled [i.e. number of transects × area per transect] for abundance data) to determine the weight. Note the possible confusion between the use of w_j as a weight in Eq. (6) and the w-value of Eq. (4). However, we kept this notation to match standard texts on the subject.

To obtain an overall effect a weighted combination of Hedge's g values is used, i.e.

$$g_w = \frac{\sum_{j=1}^{S} w_j g_j}{\sum_{j=1}^{S} w_j} \quad (7)$$

where g_j is Hedge's g for study j (from Eq. 1) and w_j is the weight discussed previously. The overall significance or p-value is then obtained by comparing z_w to the N(0,1) distribution.

Step 3: In cases where there is a significant difference in effect size, it can be illuminating to investigate these differences further. Hence, we performed focused tests of MR area and MR age. To test for a linear decrease in 'effect size' the studies were ordered from smallest to largest (closest to farthest, youngest to oldest). This was to test the null hypothesis that MRs at one extreme of the scale would have no faster or more pronounced responses to reservation than MRs at the other extreme. A new test statistic for this 'focused' comparison is:

$$T_f = \frac{\sum_{j=1}^{S} \lambda_j g_j}{\sqrt{\sum_{j=1}^{S} \lambda_j^2 / w_j}} \quad (8)$$

where w_j is the w-value for study j (from Eq. 4), g_j is the Hedge's g for study j (from Eq. 1) and S = number of studies. The coefficient λ is calculated according to the following:

$$\lambda = j - \frac{(S+1)}{2} \quad (9)$$

where S = number of studies and is an odd number, and j = number of each study. When S is an even number the formula is:

$$\lambda = 2j - S - 1 \quad (10)$$

Although the actual MR areas and ages could be used to construct the λ coefficients, the simple coefficients as outlined are preferred because they represent the ordering of locations and may be expected to be more robust. The test statistic T_f has an approximate N(0,1) distribution under the null hypothesis of no trend. So, for example, if there are 6 studies being used they would be numbered 1 through 6, 1 being the study of the smallest reserve and 6 the largest. Therefore, as an example, following the λ calculations for an even number of studies, λ for Study 1 would be –5 (i.e. –[6 – 1]), λ for Study 2 would be –3 (i.e. –[6 – 3]) and λ for Study 3 would be –1 (i.e. –[6 – 5]).

In this example, because the smallest reserve would always be Study 1 and the biggest would be Study 6, a positive or a negative test statistic would explain the direction of the trend. A positive test statistic indicates that larger reserves support larger or more individuals. As a secondary test of these data we also carried out least squares linear regression analysis of Hedge's g (weighted by w) as a function of actual MR age or size. These regression analyses do not assume a linear ranked scale (such as λ) for MR age or size, and, therefore, provide a valuable contrast to the above analyses. Table 3 shows the summary values of the data sets used in these meta-analyses.

A pictorial representation of the meta-analysis results was created by plotting the individual Hedge's g values and their confidence interval (CI) against reserve area and reserve age (data in Table 4). In this case, CI was calculated according to the equation:

$$\text{CI} = g \pm 1.96 \times \sqrt{V(g)}$$

where $V(g) = \frac{n_1 + n_2}{n_1 n_2} + \frac{g^2}{2(n_1 + n_2)}$

in Hedges & Olkin (1985).

In Figs. 2 to 5, a positive g value indicates that the MR showed larger mean sizes or greater abundance than the corresponding control area, and a negative g value shows that the control area had a greater mean size or abundance.

RESULTS

The Hedge's g values calculated from the first stage of the meta-analysis were plotted against MR area (ha) and age (yr) (Figs. 2 to 5). In 9 of 10 comparisons the MRs supported larger blue cod than did the control sites, with only the Te Angiangi MR showing a small negative g value (Fig. 2). In 8 of 11 comparisons the MRs supported a greater abundance of blue cod than the control areas (Fig. 3). In 12 of 13 studies of rock lobster size (Fig. 4) and 11 of 14 studies of rock lobster abundance (Fig. 5) the MRs supported larger or more abundant rock lobsters than non-reserve (control) areas.

The second stage in the meta-analysis was a test for differences in 'effect size' among MRs. Our analyses

Table 3. *Parapercis colias* and *Jasus edwardsii*. Mean size and mean abundance values from each reserve and their respective control sites. Data are mean ± SD (n), na = no data available. Note mean size is in cm for *P. colias* and in mm for *J. edwardsii*

Period	Reserve		Control	
	Size (cm)	Abundance (ind. m^{-2})	Size (cm)	Abundance (ind. m^{-2})
Blue cod *P. colias*				
Long Island–Kokomohua MR				
1992–1994	28.3 ± 4.3 (1090)	0.058 ± 3.99 (439)	26.6 ± 4.2 (1342)	0.042 ± 2.7 (245)
1995–1997	30.0 ± 5.6 (817)	0.063 ± 3.25 (669)	25.3 ± 4.0 (1077)	0.038 ± 2.2 (263)
1998–2000	30.6 ± 6.1 (539)	0.096 ± 3.89 (1026)	22.9 ± 4.2 (773)	0.041 ± 3.2 (357)
2001–2004	29.6 ± 6.0 (623)	0.099 ± 4.09 (1359)	24.0 ± 4.1 (773)	0.042 ± 2.9 (513)
2001	28.4 ± 8.1 (194)	0.051 ± 5.50 (197)	22.5 ± 7.2 (197)	0.051 ± 5.2 (194)
Tonga Island MR				
1993 & 1999–2002	27.2 ± 7.5 (104)	0.004 ± 0.97 (116)	20.6 ± 3.0 (48)	0.027 ± 0.6 (55)
2001	na	0.002 ± 0.55 (7)	na	0.003 ± 0.6 (10)
Te Angiangi MR				
1995–2003	22.7 ± 7.5 (169)	0.003 ± 2.61 (132)	23.5 ± 8.5 (124)	0.003 ± 2.4 (121)
Kapiti MR				
1998–2000	24.9 ± 10.8 (149)	0.037 ± 10.80 (920)	24.2 ± 8.9 (63)	0.009 ± 3.5 (214)
1999	28.1 ± 8.0 (119)	0.015 ± 5.13 (120)	22.2 ± 6.1 (101)	0.009 ± 4.5 (104)
Pohatu (Flea Bay) MR				
2001–2002	25.5 ± 6.6 (17)	0.003 ± 0.43 (17)	20.0 ± 0.0 (25)	0.006 ± 0.8 (25)
All	27.4	0.042	23.2	0.024
Rock lobster *J. edwardsii*				
	Size (mm)	Abundance (ind. m^{-2})	Size (mm)	Abundance (ind. m^{-2})
Tonga Island MR				
1998–2000	na	0.025 ± 2.31 (517)	na	0.007 ± 1.34 (122)
Kapiti MR				
1992–1999	105.2 ± 36.1 (95)	0.014 ± 3.39 (100)	93.9 ± 31.5 (74)	0.009 ± 1.73 (83)
1998–2000	56.4 ± 15.0 (9)	0.005 ± 1.04 (31)	36.8 ± 15.2 (5)	0.007 ± 2.59 (46)
Cape Rodney–Okakari Point MR				
1985	109.7 ± 34.5 (1178)	0.091 ± 12.44 (1363)	85.4 ± 28.1 (391)	0.013 ± 4.86 (392)
1995	114.1 ± 26.7 (742)	0.080 ± 22.06 (796)	89.0 ± 21.0 (305)	0.008 ± 7.49 (358)
1995–2002	114.4 ± 25.9 (2022)	0.032 ± 20.03 (2056)	95.1 ± 22.1 (490)	0.007 ± 6.16 (498)
Poor Knights MR				
1985	149 ± 15.0 (15)	0.002 ± 0.54 (15)	85.4 ± 28.1 (391)	0.022 ± 6.50 (330)
Whanganui-a-hei MR				
1996	105.8 ± 27.1 (1484)	0.029 ± 21.72 (1540)	84.0 ± 21.0 (424)	0.009 ± 12.30 (452)
Mayor Island (Tuhua) MR				
1996	89.1 ± 22.6 (107)	0.011 ± 4.89 (110)	81.8 ± 27.1 (100)	0.011 ± 4.73 (117)
Te Angiangi MR				
1998–2002	86.2 ±21.8 (574)	0.020 ± 16.43 (808)	79.3 ± 17.6 (393)	0.020 ± 18.35 (724)
Long Island–Kokomohua MR				
1992–1999	52.4 ± 41.3 (85)	0.023 ± 2.28 (88)	32.1 ± 19.3 (33)	0.022 ± 2.25 (33)
2001–2003	108.2 ± 43.0 (422)	0.056 ± 7.05 (423)	83.9 ± 25.5 (159)	0.011 ± 2.75 (83)
Pohatu (Flea Bay) MR				
2001–2002	79.3 ± 34.6 (84)	0.005 ± 1.21 (19)	81.5 ± 28.9 (62)	0.007 ± 3.35 (25)
Te Awaatu Channel (The Gut) MR				
1999	103.6 ± 19.1 (105)	0.011 ± 14.06 (106)	98.0 ± 14.7 (134)	0.009 ± 17.52 (135)
All	98.0	0.029	78.9	0.012

revealed that there was a significant difference among the effects that individual MRs had on mean size and on mean abundance of both species (Table 5). Because of these statistically significant differences in effect size among MRs it was inappropriate to combine data from the different studies for further formal meta-analysis according to the methods in Eqs. (6) & (7) to provide an overall significance estimate of the effect that all the MRs have had on these species. While the very large and positive T_c-values (Table 5) indicate

Table 4. Marine reserve variables (area and age) used in the analysis of effects on blue cod and rock lobster mean abundance and mean size. Where several ages are indicated, these show the ages, or range of ages, of the MRs at the times of the different studies on that MR

Marine reserve	Reserve area (ha)	Age of reserve at time of study (yr)
Cape Rodney–Okakari Point MR	518	10, 20, 20–27
Kapiti Island MR	2167	7, 5–8
Long Island–Kokomohua MR	619	1–2, 3–10
Mayor Island (Tuhua) MR	1060	4
Pohatu (Flea Bay) MR	215	4
Poor Knights MR	2400	4
Te Angiangi MR	446	2–6, 1–5
Te Awaatu Channel (The Gut) MR	93	3
Tonga Island MR	1835	1, 5–7
Whanganui-a-hei (Cathedral Cove, Hahei) MR	840	4

that large differences exist in the effects of reserves, the plots (Figs. 2 to 5) indicate that these differences are 'positive' in terms of increasing size and/or abundance of these 2 species when compared with areas outside the MRs.

Focused comparisons

Focused comparisons were used to test the null hypothesis that there was no change in effect size with increasing MR age or MR area. Of the 8 different focused comparisons (Table 6), only that for MR age versus rock lobster size was statistically significant ($T_f = 3.777$, df = 12, p = 0.002), indicating that the effect size of older MRs is greater than that of younger MRs. In other words, the older a MR is, the greater the difference in rock lobster size between reserve and non-reserve sites will be (this does not mean that older MRs will necessarily have bigger rock lobsters than younger MRs, because this is a relative measure only of the difference between reserve versus non-reserve rock lobster size). The 4 non-significant results for blue cod abundance and size and the 3 non-significant results for rock lobster abundance and size indicated that the effect size of MRs did not exhibit linear changes in differences

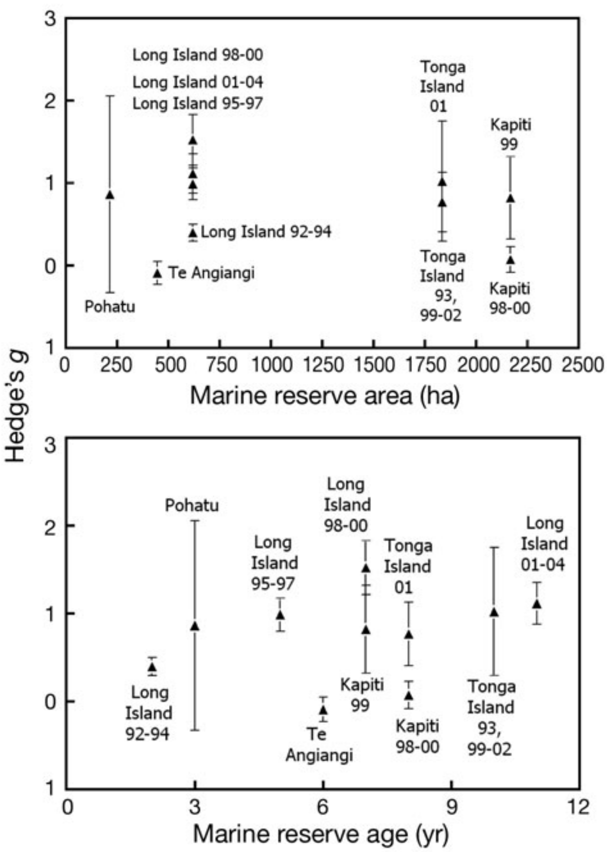

Fig. 2. *Parapercis colias*. Blue cod size: Hedge's *g* (±CI) as a function of marine reserve area (upper panel) and marine reserve age (lower panel). Values annotated with reserve name and years of study

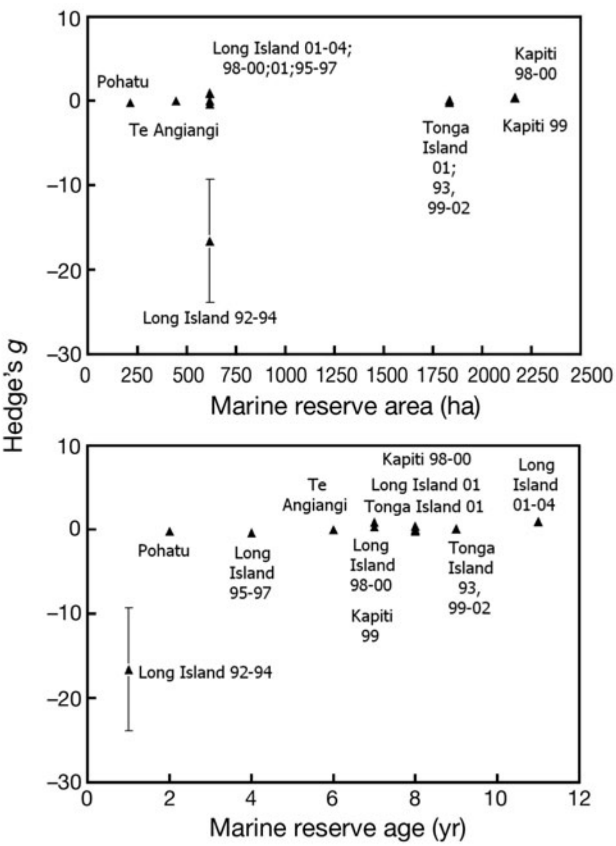

Fig. 3. *Parapercis colias*. Blue cod abundance: Hedge's *g* (±CI) as a function of marine reserve area (upper panel) and marine reserve age (lower panel). Values annotated with reserve name and years of study

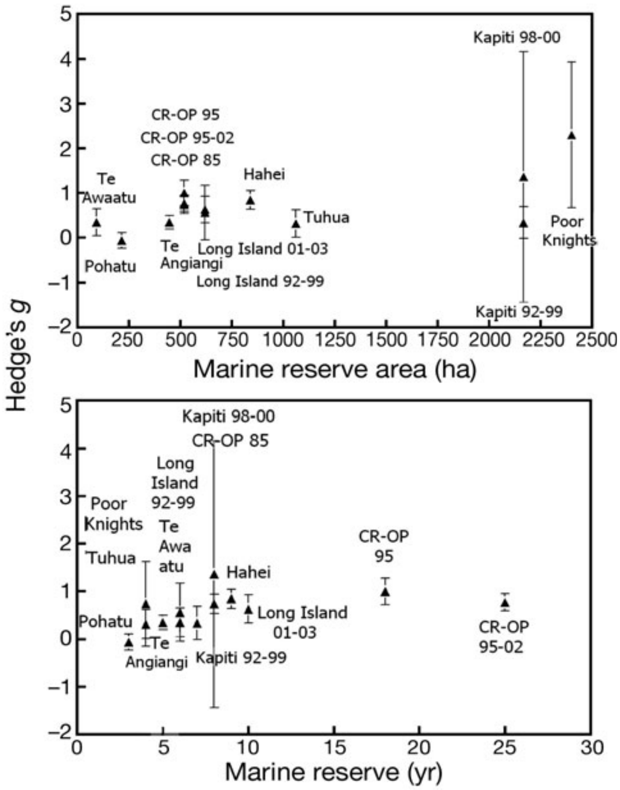

Fig. 4. *Jasus edwardsii*. Rock lobster size: Hedge's *g* (±CI) as a function of marine reserve area (upper panel) and marine reserve age (lower panel). (CR-OP = Cape Rodney to Okakari Point; Hahei = Whanganui-a-hei). Values annotated with reserve name and years of study

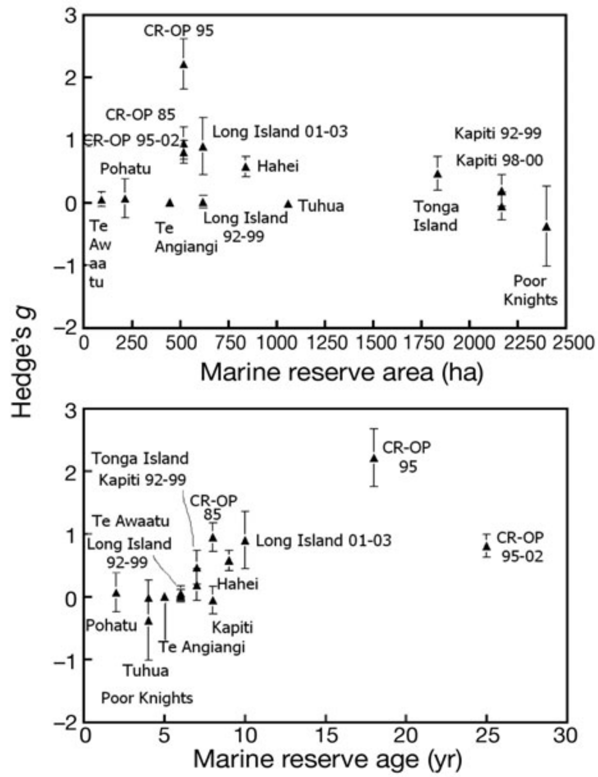

Fig. 5. *Jasus edwardsii*. Rock lobster abundance: Hedge's *g* (±CI) as a function of marine reserve area (upper panel) and marine reserve age (lower panel). (CR-OP = Cape Rodney to Okakari Point; Hahei = Whanganui-a-hei). Values annotated with reserve name and years of study

between reserve and non-reserve estimates as a function of MR age and MR area. Of the 8 linear regression focused comparisons (Table 6), only that for MR size versus rock lobster size was statistically significant ($r = 0.641$, df $= 11$, $p = 0.018$). This indicates that the larger the MR, the greater the difference between rock lobster size inside versus outside the reserve. If these focused tests had shown a simple pattern to similarities between reserve responses, we would have performed a further meta-analysis on a subgroup of the studies to determine the cause of these differences. Overall, both sets of focused comparisons failed to reveal the existence of a consistent relationship between blue cod or rock lobster size or abundance, and MR size or age.

Table 5. Comparison of 'effect size' of marine reserves on blue cod and rock lobster size and abundance

Index	df	T_c	p
Blue cod mean size (cm)	9	351.738	<0.0001
Blue cod mean abundance (m^{-2})	10	150.982	<0.0001
Rock lobster mean size (cm)	12	132.452	<0.0001
Rock lobster mean abundance (m^{-2})	13	137.526	<0.0001

DISCUSSION

In conducting this research our primary aim was to apply the statistically rigorous framework of meta-analysis to the analysis of size and abundance data for blue cod and rock lobster across multiple surveys from New Zealand no-take MRs. We found evidence of a significant positive effect of reservation status on the size and abundance of both blue cod and rock lobster, enough to suggest that New Zealand MRs are achieving the conservation goals implicit in their design.

Meta-analysis revealed significant differences in the 'effect size' among MRs for blue cod and rock lobster size and abundance data. For all indices, with the exception of rock lobster size versus MR age (*t*-test) and rock lobster size versus MR area (linear regression), these findings indicated that the response in the different MRs is independent of MR area and age. Thus, MRs are responding differently to reservation status, such that some have many more and/or bigger individuals at sites inside than outside the

Table 6. Focused comparison test results (ranked *t*-test and linear regression) of blue cod and rock lobster mean size and abundance with respect to marine reserve (MR) age and area. p-values in **bold** are significant

Index	Ranked *t*-test results T_f value	df	p	Linear regression results R	df	p
MR age vs. blue cod size	0.775	9	>0.100	0.272	8	>0.100
MR area vs. blue cod size	0.039	9	>0.100	0.151	8	>0.100
MR age vs. blue cod abundance	0.289	10	>0.100	0.601	9	>0.050
MR area vs. blue cod abundance	1.703	10	>0.100	0.197	9	>0.100
MR age vs. rock lobster size	3.777	12	**0.002**	0.038	11	>0.100
MR area vs. rock lobster size	1.290	12	>0.100	0.641	11	**0.018**
MR age vs. rock lobster abundance	0.716	13	>0.100	0.505	12	>0.050
MR area vs. rock lobster abundance	–0.550	13	>0.100	0.228	12	>0.100

MRs, whereas others do not. In the context of the New Zealand policy for establishment of MRs this differential response is not surprising because MRs are not set up specifically for the preservation or enhancement of blue cod or rock lobster (i.e. there was no special consideration given to MR location, habitat type, area or shape for either blue cod or rock lobster), but are generally established for the preservation of the habitat and all biota in that area. Thus, despite the facts that (1) none of these MRs was specifically established to enhance blue cod or rock lobster populations, (2) we have data from only 10 (blue cod size data) to 14 studies (rock lobster abundance data), (3) the reserves in question are not large (mean area ± SD for blue cod data = 1056 ± 788.9 ha and for rock lobster data = 928.7 ± 776.6 ha), and (4) several of the studies were conducted only a few years after the establishment of the MR (mean time ± SD for blue cod data = 6.5 ± 2.9 yr and for rock lobster data = 8.5 ± 5.8 yr), these findings demonstrate that iconic, ecologically important and heavily fished species such as blue cod and rock lobster are responding positively to protection at MR sites of different areas, ages and locations throughout New Zealand.

Effects of MRs on size and abundance of individuals

Results from meta-analyses of abundance, biomass and size data from independent assessments of MRs in temperate and tropical regions suggest that MRs do indeed achieve the conservation goals implicit in their design in the sense that they do result in bigger and/or more abundant individuals of certain taxa. While most analyses have focused on data for individual fish species or fish assemblages, limited data are available for invertebrate species or assemblages. Meta-analyses by Mosquera et al. (2000), Côté et al. (2001), Halpern & Warner (2002), Halpern (2003) and Micheli et al. (2004) all reported that abundance (numbers of individuals) and/or richness (number of species) was greater inside than outside a range of MRs encompassing temperate, sub-tropical and tropical regions. These studies also noted that not all species responded to protection to the same extent or in the same manner. Species targeted by recreational or commercial fishers tended to exhibit greatest increases in abundance and size in the absence of fishing pressure, whereas non-targeted species often responded negatively to conservation, presumably as a consequence of indirect effects. Other heterogeneous responses were also reported. First, larger fish species tended to exhibit the greatest positive response to protection, regardless of whether they were targeted, presumably because large non-targeted fish inside MRs received increased protection from by-catch mortality (Mosquera et al. 2000). Second, omnivorous and detritivorous species tended to respond poorly, if at all, to protection (Halpern 2003, Micheli et al. 2004). Third, significant heterogeneity was also observed among reserves in their effects on changes in fish abundance (Côté et al. 2001, Micheli et al. 2004), suggesting that different reserves work in different ways or at different rates. Micheli et al. (2004) suggested that some of this differential response may be related to the strength of fishing pressure outside each reserve, but other factors such as habitat structure will also be important (García Charton et al. 2000).

Our analyses clearly show that size and abundance of both species respond positively to MR protection. This effect is more notable for size data (for blue cod, only 2 of the means ± 2 SD overlapped with zero; for rock lobster, only one of the means ± 2 SD overlapped with zero) than for abundance data. For blue cod this difference may result from their territorial behaviour (once established with a territory in a MR they can achieve a large size in the absence of fishing pressure) and also from the fact that blue cod at MR sites move greater distances than blue cod at non-reserve sites (Cole et al. 2000). For rock lobster, the relatively sedentary lifestyle is thought to result in increases in mean size and mean abundance inside MRs, although tagging of lobsters indicates that a proportion of a population will move either into or out of a MR (Kelly & MacDiarmid 2003). The positive response of both species in our study to protection is, therefore, consistent with a body of work which indicates that sedentary species targeted by fishing will benefit very considerably from protection (e.g. Halpern & Warner 2002, Micheli et al. 2004, Palumbi 2004).

Importance of MR age and area in explaining response to protection

Overall, our analyses revealed no consistent significant effect of MR area or age on blue cod or rock lobster size or abundance. In 2 different sets of focused comparisons only 1 of 8 tests was significant in either case (*t*-test, MR age on rock lobster size; linear regression, MR area on rock lobster size). Our findings suggest that neither MR age nor area are particularly important in explaining responses to protection, and are in general agreement with those of recent reviews of data from MPAs for a wide range of vertebrate and invertebrate species, from temperate to tropical regions. Côté et al. (2001), in their meta-analysis of fish abundance data from 19 MRs, concluded that for target and non-target fish combined, and for target fish alone, abundance was not related to MR age or MR area. Halpern & Warner (2002) reviewed 112 independent measurements of 80 reserves, and Halpern (2003) reviewed data from 89 reserve studies (these 2 reviews report on different aspects of what is fundamentally the same data set including both vertebrate and invertebrate species). Despite species density, biomass, size and diversity all being significantly greater inside reserves than outside, overall change among communities or among trophic groups in species density, biomass, size and diversity was independent of MR age (the reserves ranged in age from 1 to 40 yr, with a mean of 11.2 yr; Halpern & Warner 2002). Both studies also noted that biological response was independent of MR area (mean size of 4410 ha, range from 0.2 to 84600 ha; Halpern 2003), the only exception to these findings being for invertebrate mean size, which was significantly smaller in reserves (Halpern 2003), a finding that can result from increased juvenile recruitment and/or survivorship at sites inside versus outside reserves. In their meta-analysis of data from 20 studies carried out at 31 locations looking at multi-species fish assemblages, Micheli et al. (2004) concluded that MR age explains a very small (<3%), but nonetheless significant amount of variation in the response to protection, while MR area does not explain significant variation in fish abundance in response to protection. On balance, these studies, and our own, all indicate that MR area and age do not explain a lot of the conservation success of MRs. Despite this, there is widespread belief that MR area does matter, and clear evidence exists of the importance of area for individual reserves if they are to achieve their conservation roles. For example, despite reporting no significant effect of MR area on conservation outcomes, Halpern (2003) suggested that because absolute differences in biological response variables were most pronounced for larger reserves, this might indicate that larger reserves may be necessary to meet the goals set for reserves (i.e. bigger and more abundant individuals). Parnell et al. (2005) concluded that despite protecting a few sessile or highly residential harvested species, the San Diego–La Jolla Ecological Reserve (established in 1971, area of ca. 216 ha) is too small to achieve its stated conservation aims and for almost all species is too small to be self-sustaining. Elsewhere, modelling simulations of the efficacy of MRs indicate that MR area should be at least half the neighbourhood size of a species, which is effectively a measure of adult mobility (Botsford et al. 2001, 2003). In contrast to this, there is evidence that some small MRs may work for some, but not all species under certain circumstances, e.g. the 2.6 ha Anse Chastanet Reserve in St. Lucia (Roberts & Hawkins 1997). Finally, Sale et al. (2005) noted that larger MRs will hold larger populations of more species that are better buffered from disturbance and extinction because they are larger and because in a larger MR they are better able to be self-sustaining. On balance, the data from several studies indicate that MR area and age do not explain large amounts of variation in changes in size and/or abundance arising from protection. One explanation for this possibly counter-intuitive finding is that when a MR is established and its no-take policy is enforced successfully, the biological response to protection is very rapid (significant results are often reported within 2 yr of MR establishment) and occurs almost regardless of MR area, before the response slows down or stabilises after a few years (e.g. Roberts & Hawkins 1997, Halpern & Warner 2002, Rowe 2002, Halpern 2003, Micheli et al. 2004). Ultimately, perhaps this says more about the high levels of fishing pressure outside the newly created MR than it does about the area of the MR. Studies that have demonstrated a small but significant effect of MR age on protection (e.g. Micheli et al. 2004, present study for rock lobster size) indicate that increases in species size or abundance and changes in community structure may be rapid at first, and then continue to increase much more slowly over long periods of time (decades). Further long-term monitoring of MRs is required to confirm the veracity of this supposition.

Conclusions

Meta-analysis of size and abundance data indicates that New Zealand MRs support larger and more abundant blue cod and rock lobster than control areas. Our findings are consistent with an increasingly large body of evidence that suggests that MRs may play a critical role in the conservation of certain focal species. However, features such as MR age and MR area are not perhaps as statistically important as one might predict *a priori*, but nonetheless may play an important role in promoting more abundant and bigger individuals of certain key species.

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