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Massive differential site-specific and species-specific responses of temperate reef fishes to marine reserve protection

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ABSTRACT

As the field of marine reserve (MR) research matures, individual studies and meta-analyses are now able to answer some of the fundamental questions initially posed regarding timelines and trajectories for biological change (often termed recovery), the effect of reserve size, age, and location, and responses to protection as a function of life-history characteristics. Kapiti MR is New Zealand's fourth oldest MR, established in 1992, and falls into the category of a MR where all sites are not equal in terms of habitat characteristics. We surveyed temperate reef fishes at protected and unprotected sites and compared our data to previous studies at this MR, to quantify changes through time. We employed a before-after-control-impact (BACI) approach and compared our results to the commonly employed control-impact (CI or inside/outside) analysis. The CI analysis revealed greater abundances and biomasses of reef fish species inside the MR that were not revealed by the BACI analysis. The BACI approach revealed that exploited species of reef fishes increased in biomass by 300–400% at protected sites. Butterfish (*Odax pullus*), an exploited herbivorous species, showed pronounced site-specific responses, and increased in abundance by >400% and in biomass by >2 100% in 19 years at protected sites. This study highlights both the importance of site-specific effects and the method of analysis when quantifying MR effects to correctly attribute observed differences among sites to MR effects or to site-specific habitat quality effects.

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1. Introduction

The number of studies documenting the species-specific and/or ecosystem responses derived from the establishment of marine reserves (MRs—full no-take protection) or marine protected areas (MPAs—partial protection) in temperate and tropical regions has increased substantially in recent years, concurrent with an increase in the number of MRs and MPAs established globally (Willis et al., 2003a; Lester et al., 2009; Edgar et al., 2014). General findings indicate that MRs result in significant increases in the abundance, size, and biomass of many, but not necessarily all species, but in particular of exploited species (Pande et al., 2008; Aburto-Oropeza et al., 2011; Molloy et al., 2009; Diaz et al., 2012; Edgar et al., 2014), as well as some unexploited species (Babcock et al., 2010). The magnitude and rates of biological change for individual species are dependent on a number of factors, including non-biological factors such as MR age, size, levels of enforcement and exploitation, and geographic isolation, and also on biological factors such as life history traits (growth rate, age at maturity,

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trophic level), either as independent or as interacting factors (Guidetti and Sala, 2007; Molloy et al., 2009; Pande et al., 2008; Claudet et al., 2010; Diaz et al., 2012; Edgar et al., 2014). In some instances, trajectories of biological response to protection appear to level off reasonably quickly (only a few years), while in other cases, responses can take two or three decades to become apparent (Roberts, 1995; Halpern and Warner, 2002; Babcock et al., 2010). The multi-species comparative approach provides new insights into the conservation outcomes of no-take areas (Lester et al., 2009; Aburto-Oropeza et al., 2011; Edgar and Barrett, 2012; Edgar et al., 2014), and illustrates how such areas may contribute to fisheries management in terms of the individual responses to highly exploited species, both invertebrate and vertebrate, through spillover or increased egg production and recruitment (Roberts et al., 2001; Batista et al., 2011; Eddy et al., 2014).

As scientists seek to quantify the immediate impacts that a MR may have on an ecosystem, and as our longer term (30 years in some cases) understanding of ecological responses continues to mature, it has become clear that both the method of survey (e.g., Colton and Swearer, 2010; Langlois et al., 2010; Dickens et al., 2011; Gardner and Struthers, 2013) and the analytical method employed to quantify the response (Halpern, 2003; Osenberg et al., 2006; Diaz et al., 2012) can strongly influence results and the interpretation of outcomes. Ideally, a multi-year and multi-site survey of an ecosystem should be undertaken prior to MR establishment, providing a baseline against which to measure any future changes (e.g., Pande and Gardner, 2008). This approach is often referred to as “BACI” (Before After Control Impact; Green, 1979), although as usually applied in this context it is a “beyond BACI” approach because it involves multiple control–impact sites (Underwood, 1992, 1994; Benedetti-Cecchi, 2001; Skilleter et al., 2006). However, while a multi-year and multi-site baseline approach to monitoring is preferable, it is generally not possible because, as noted in many studies, a baseline survey has not been undertaken (Battershill et al., 1993; Edgar and Barrett, 1999; Edgar et al., 2004; Pande and Gardner, 2008). Therefore researchers seeking to quantify impacts of a MR on an associated ecosystem are often forced to use alternative methods of analysis. The most commonly used approach to quantify the impacts of a MR on its associated ecosystem in the absence of a baseline survey is the “CI” approach (control–impact, often referred to as the “Inside–Outside” approach). Sometimes this approach is replicated through time, while in some instances it is used as a “snapshot” to capture one point in time (Aburto-Oropeza et al., 2011). In either case, the biological responses at sites that are protected by the MR (impact or “inside” sites) are compared to those at sites that are unprotected (control or “outside” sites), and differences between inside and outside sites (often abundance, size, biomass or diversity comparisons) are attributed to the MR (e.g., Halpern and Warner, 2002; Halpern, 2003; Micheli et al., 2004; Lester et al., 2009; Molloy et al., 2009). The inside–outside approach assumes that the environmental conditions and characteristics of all sites (regardless of whether they are inside or outside) do not contribute to differences in the associated biological community among control and impact sites. That is to say, the inside–outside approach assumes that all sites are equal. However, it has long been recognised that this assumed equality of sites is unlikely to exist for several different reasons, including the fact that MRs are often established at sites with known high conservation value, or because there is limited knowledge of actual differences in ecology (e.g., habitat type or quality) or coastal oceanography between or among sites inside or outside the MR (Halpern and Warner, 2002; Guidetti and Sala, 2007; Freeman et al., 2009).

In New Zealand, marine reserve protection has resulted in increased size and abundance of several commercially and recreationally important fish and shellfish species (MacDiarmid and Breen, 1993; Kelly et al., 2000; Davidson et al., 2002; Willis et al., 2003a; Shears et al., 2006). For example, meta-analyses of responses for blue cod (*Paraperis colias*) and rock lobster (*Jasus edwardsii*) reveal that they are, on average, larger and more abundant inside versus outside reserves at locations throughout the country (Pande et al., 2008; Diaz et al., 2012). However, not all temperate MR studies have documented positive responses for exploited species, and to explain such results it has been suggested that species-specific or community-specific mixed responses may occur (Cole, 1994; Willis et al., 2003b), sampling methodology is inadequate to detect changes (Kelly et al., 2000) or that baseline datasets are inadequate (too poorly replicated) to reveal changes (Pande and Gardner, 2012). While most MR studies have traditionally focused on individual species, more recent research is now quantifying impacts on entire ecosystems (Shears and Babcock, 2002, 2003; Pinkerton et al., 2008; Eddy et al., 2014).

Established in 1992, the full no-take Kapiti MR is the fourth oldest of the 38 MRs in New Zealand (Department of Conservation, 2014). Kapiti Island is a popular recreational fishing and diving destination for tourists and residents of the greater Wellington region. A one-off survey of the biological communities (fishes, macroinvertebrates, and macroalgae) immediately prior to establishment of Kapiti MR was conducted (Battershill et al., 1993), and although this baseline survey was not replicated in time, the qualitative value of the dataset has been highlighted by subsequent monitoring (Pande and Gardner, 2012). To date, the only differences in size and abundance of reef fishes that have been reported at Kapiti MR are inside–outside comparisons (Stewart and MacDiarmid, 2003; Pande and Gardner, 2012; Gardner and Struthers, 2013). Studies that made comparisons to the baseline study have not reported statistically significant differences in species-specific size or abundance, a result that is likely to be due to the low replication and high variability in the baseline dataset (Stewart and MacDiarmid, 2003; Pande and Gardner, 2012). However, three separate studies conducted in different years have reported that blue cod (Stewart and MacDiarmid, 2003; Gardner and Struthers, 2013), blue moki (Pande and Gardner, 2012), and butterfish (Stewart and MacDiarmid, 2003; Pande and Gardner, 2012) were all larger inside than outside the MR.

In this study, we test the biological responses (changes in abundance, size, and biomass) of reef fishes of as a function of exploited versus unexploited status over an 18-year period. In addition, we quantify the possible differential contribution to MR protection response of a single site within the MR that was known to be a “high quality habitat” site at the time of establishment, so that we can test the case of all sites not being equal. For these purposes, we employ and compare results from two different analytical approaches. First, we take advantage of the fact that a multi-site but single time period baseline dataset exists and we employ a BACI analysis. Secondly, we employ the more common inside versus outside analyt-

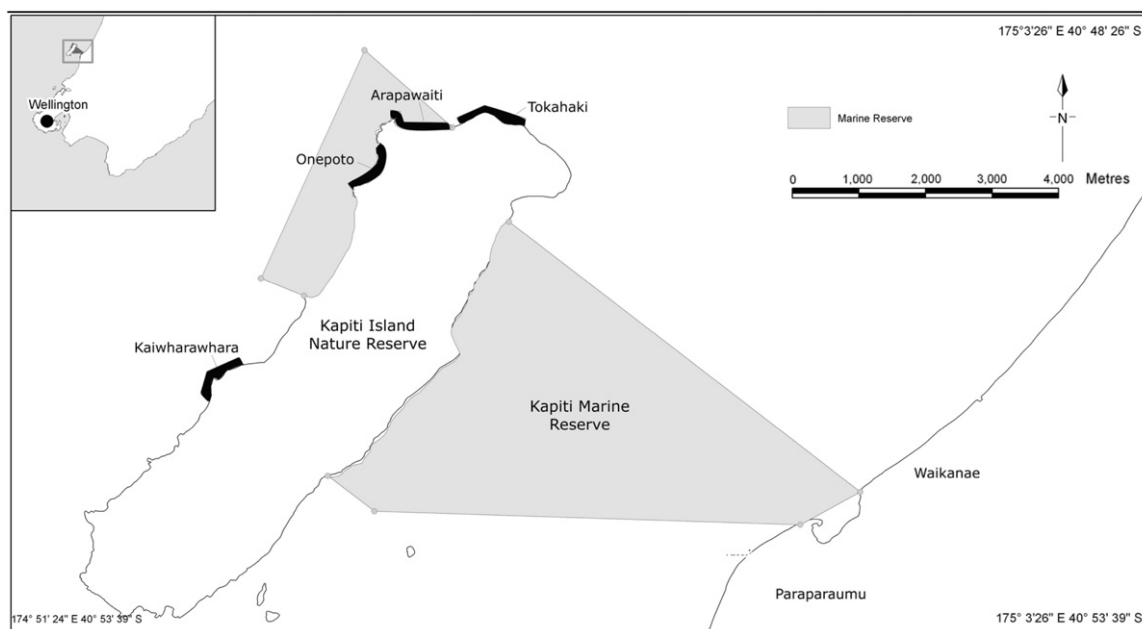


Fig. 1. Map of Kapiti Marine Reserve showing four study sites (shaded in black).

ical approach for comparison. Our findings contribute to a greater understanding of the conservation role of MRs, and they illustrate the importance of understanding site-specific differences in biological responses and the different outcomes and interpretations that widely employed, but contrasting analytical methods, may generate.

2. Methods

2.1. Study area

Kapiti Island is located in the northwestern Cook Strait region of New Zealand, approximately 50 km north of Wellington ($40^{\circ} 51' S$, $174^{\circ} 55' E$; Fig. 1). This region is a convergence zone for the cold Southland Current and the warm d'Urville Current (Pande, 2001). Kapiti MR provides full no-take protection to an area of 2167 ha, divided into two parts—1825 ha on the eastern (landward) and 342 ha on the western (seaward) side of the island (Fig. 1). This study is focused on the western side of the island, which is exposed to high wave and wind energy from the Tasman Sea, as well as strong currents. Subtidal habitat at study sites is characterised by a rocky reef platform that slopes off to sand and gravel substrates at ~ 20 m depth (Battershill et al., 1993; Pande and Gardner, 2012; Gardner and Struthers, 2013).

Kapiti Island is ~ 5 km offshore and a boat is required to access fishing and dive sites. Recreational fishing effort around Kapiti Island is substantial, with many boats “fishing the line” with hook-and-line at the northern boundary of the MR on the west side of the island (*personal observation of authors*), most often targeting blue cod (*Parapercis colias*). The MR is patrolled by the Department of Conservation (DoC) by boat, with a manned ranger station on the island. Compliance has been observed to be high amongst most fishers, although rare occurrences of fishing within the MR boundaries have been observed (*personal observation of the authors*). Spear-fishers are also regularly observed in the waters surrounding the island, targeting benthic-associated reef fishes such as butterfish (*Odax pullus*; Fig. 2), as well as larger pelagic species such as kingfish (*Seriola lalandi*). In addition, each year the New Zealand North Island spear-fishing competition takes place in waters surrounding Kapiti MR. In New Zealand, set-netting and long-lining by recreational fishers is permitted in waters outside a MR, which target species such as blue and red moki (*Latridopsis ciliaris* and *Cheilodactylus spectabilis*, respectively) and snapper (*Chrysophrys auratus*). Arapawaiti, a site within the MR (Fig. 1), was identified by fishers as being a good fishing spot prior to MR implementation (Pande, 2001) and was identified as having habitat differences compared to other sites from the snapshot baseline survey (Battershill et al., 1993). These observations suggest that using inside–outside (or control–impact) comparisons may be problematic for detecting MR effects because varying habitat quality may confound interpretation of results (Pande and Gardner, 2012).

2.2. Underwater visual census

A baseline study that was conducted in 1992 (Battershill et al., 1993), immediately before establishment of the Kapiti MR, surveyed 11 sites on the north, east and west sides of Kapiti Island, employing underwater visual census (UVC) with 25 m (length) by 10 m (width) transects. While this was a one-off study with only three replicate transects of reef fish size



Fig. 2. Butterflyfish (*Odax pullus*) at the protected site Arapawaiti, Kapiti Marine Reserve, New Zealand.

and abundance per site (in two depth strata; six transects per site), it identified site-specific differences in habitat quality based on substrate type and macroalgal and encrusting communities (Battershill et al., 1993). Reef fish surveys at Kapiti MR that were carried out from 1998 to 2000 (Pande and Gardner, 2012) involved seasonal monitoring at four of the original 11 sites surveyed by Battershill et al. (1993) using 25 m (length) by 5 m (width) transects. We employ data from both studies in our analyses, in addition to our more recently collected data.

UVC of reef fish size and abundance were conducted in the austral summers (February) of 2008, 2009, and 2010, with permission from the New Zealand Department of Conservation. For each survey in the present study, four sites were sampled to determine abundance and size of reef fishes (Fig. 1). Eighteen species were surveyed, but due to low abundance of many species, detailed analyses are limited to seven species. Of these, four are exploited by fishers – blue cod (*Parapercis colias*), blue moki (*Latridopsis ciliaris*), butterflyfish (*Odax pullus*), and red moki (*Cheilodactylus spectabilis*) – and may therefore be expected to exhibit direct responses to protection. Three species examined are not exploited by fishers – banded wrasse (*Notolabrus fucicola*), scarlet wrasse (*Pseudolabrus miles*), and spotty (*Notolabrus celidotus*) – and therefore are expected to exhibit indirect responses to protection. For each survey, at each site, nine transects were surveyed between 5 and 15 m depth following the monitoring programme as laid out by previous UVC surveys (Pande and Gardner, 2012; Gardner and Struthers, 2013). All transects were conducted over rocky reef habitat that was dominated by brown macroalgae (*Carpophyllum maschalocarpum*, *Ecklonia radiata*, *Lessonia variegata*, *Macrocystis pyrifera*). Pande and Gardner (2012) had earlier reported that Arapawaiti had significantly less *Ecklonia* than the other three survey sites. Each transect was started 5 m from where the transect tape was set in order to minimise error associated with fishes being attracted to or repelled from the diver disturbance (Cole et al., 1990; Cole, 1994; Dickens et al., 2011). Fishes were counted as the transect tape was being deployed rather than retrieved to avoid counting fishes attracted to the diver (Cole, 1994). Each transect was 5 m wide by 25 m long, resulting in an area of 125 m² surveyed for each transect and a total area of 1125 m² surveyed at each site for each survey. Fish size was estimated to the nearest 5 cm (e.g., Battershill et al., 1993; Pande and Gardner, 2008, 2012) and all observations were made by the same observer (T.D. Eddy). Earlier testing of divers' abilities to estimate accurately the size of plastic cut-out fish shapes along a test transect had shown that estimated length was <5 cm different from actual length (Pande and Gardner, 2008). Thus, despite the fact that different divers provided data across the three different temporal studies described here, we are as confident as we can be that measurement error is low and randomly distributed across the full dataset. Size–frequency data were converted into biomass data using species-specific non-linear length–weight relationships for northeastern New Zealand reef fishes as described by Taylor and Willis (1998) and FishBas (Froese and Pauly, 2005).

2.3. Statistical analyses

2.3.1. BACI—Temporal comparisons for 1992, 1998–2000, and 2008–2010

We tested for statistically significant changes in fish abundance, size, and biomass using the factors 'protection', 'time', and the 'protection × time' interaction. The interaction term indicates whether species at protected versus unprotected sites are responding differently to MR protection as a function of time (Edgar and Barrett, 2012). We employed an ANOVA-type design to partition variation amongst spatial and temporal scales (*sensu* Edgar and Barrett, 2012). Statistical comparisons were carried out using univariate PERMANOVA, as implemented in the software package PRIMER with PERMANOVA+ (Anderson et al., 2008). Species-specific raw abundance and size data were used, while biomass data were $\log(x+1)$ transformed (Edgar and Barrett, 2012). Similarity matrices based on Euclidean distance were constructed for abundance, size, and biomass of each species separately, as well as for exploited and unexploited species and permuted residuals under a reduced Type III (partial) PERMANOVA model (Edgar and Barrett, 2012). Outputs from analyses (sum of squares, mean squares, F-values) were therefore the same as those calculated using mixed-model ANOVA (protection = fixed effect; time = random effect;

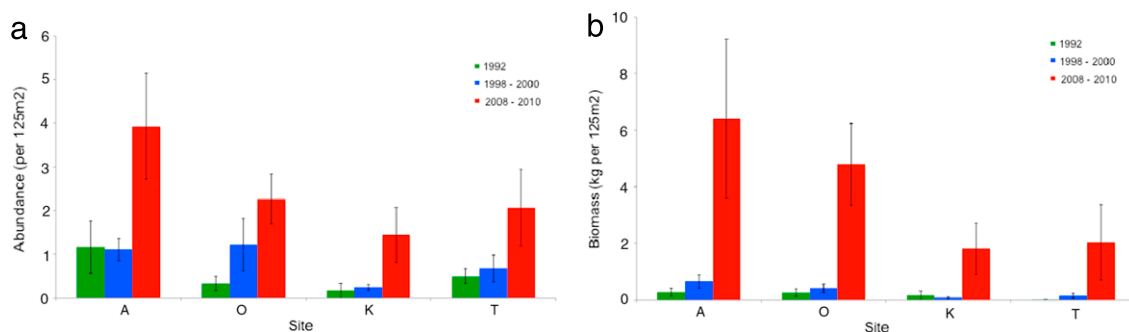


Fig. 3. Abundance (panel A) and biomass (panel B) of butterflyfish (mean \pm SE) at Kapiti Marine Reserve sites for the 1998–2000 survey and the 2008–2010 survey. A = Arapawaiti (MR), O = Onepoto (MR); K = Kaiwharawhara (control); T = Tokahaki (control).

site = random effect) except for the p -values, which were calculated using permutation routines (Anderson et al., 2008; Edgar and Barrett, 2012). A nested mixed-model design was employed with the categorical factor ‘protection’ (two levels: protected or unprotected) being crossed with the fixed factor ‘time’ (three levels: 1992 (the baseline dataset of Battershill et al., 1993); 1998–2000 (the dataset of Pande and Gardner, 2012); 2008–2010 (the dataset of present study)), with the random factor ‘site’ nested hierarchically below ‘protection’ (Edgar and Barrett, 2012). In order to ensure that our results were robust to alternative modelling approaches, we also ran a mixed-effects modelling approach in STATISTICA, which produced very similar results.

2.3.2. Inside–outside comparisons—2008–2010

Univariate pairwise tests were conducted to determine if abundance, size, and biomass of reef fishes showed statistically significant differences between inside–outside sites (pooled according to reserve status) for the present study (2008–2010) using PRIMER with PERMANOVA+ software (Anderson et al., 2008). We controlled for false discovery rate (FDR) using the technique described by Verhoeven et al. (2005). This inside–outside snapshot analysis is typical of the type of analysis often employed in MR monitoring work in the absence of baseline data and/or repeated surveying.

3. Results

3.1. BACI—Temporal comparisons for 1992, 1998–2000, and 2008–2010

Abundance estimates for the time periods 1992, 1998–2000, and 2008–2010 for the seven species at the four study sites revealed substantial temporal and spatial variability (Table 1). BACI PERMANOVA results revealed that ‘site’ was a statistically significant factor in explaining observed abundance variation for banded wrasse (68% of variation explained) and blue cod (36%; Table 4; Fig. 3(a)). The site at Arapawaiti generally had a greater abundance of all species than the other sites, with the exceptions of greater blue cod abundance at Kaiwharawhara and Onepoto in 1992 (Table 1). The factors ‘protection’ and ‘protection \times time’ were statistically significant in explaining observed variation in butterflyfish abundance (14% and 13% of variation explained respectively), from an average of 0.75 per transect in 1992, to 1.2 per transect in 1998–2000, and 3.1 per transect in 2008–2010 at protected sites, an increase of 413% (Tables 1 and 4; Figs. 2 and 3(a)).

BACI PERMANOVA results for size estimates of reef fishes indicated that the factor ‘site’ was statistically significant in explaining observed variation for exploited fishes (25% of variation explained; Tables 2 and 5). The factor ‘protection \times time’ was statistically significant in explaining observed variation in exploited reef fish size (20%; Table 5). Average size of exploited fishes at protected sites increased from 30.1 cm in 1992 to 36.4 cm in 2008–2010, a 21% increase (Tables 2 and 5). The factor ‘date’ was statistically significant in explaining variation in the average size of scarlet wrasse, spotty, exploited, and unexploited fishes (77%, 44%, 33%, and 71% of variation explained, respectively; Tables 2 and 5).

BACI PERMANOVA results for biomass estimates of reef fishes indicated that the factor ‘site’ was statistically significant in explaining observed variation for banded wrasse (38% of variation explained), red moki (35%), spotty (69%), and unexploited fishes (51%; Tables 3 and 6; Figs. 3(a), 4). Generally, there was greater banded wrasse biomass at Arapawaiti over the three time periods, while red moki and spotty were more variable in biomass at sites among time periods (Table 3). There was a greater biomass of unexploited fishes at Arapawaiti during the last two time periods (Table 3; Fig. 4(b)). The factor ‘time’ was statistically significant in explaining observed variation in butterflyfish (32%), red moki (25%), scarlet wrasse (32%), and spotty (10%; Table 6). Butterflyfish and red moki biomasses were greatest at unprotected sites during the 2008–2010 survey, while the biomasses of scarlet wrasse and spotty were notably lower at all sites during the 1998–2000 survey (Table 3). The factor ‘protection \times time’ was statistically significant in explaining observed variation in the biomass of butterflyfish (29%), as average biomass of butterflyfish increased from 0.26 kg per transect in the baseline survey, to 0.53 kg per transect in 1998–2000, to 5.6 kg per transect at protected sites, a 2154% increase (Tables 3 and 6). The factor ‘protection’ was statistically significant in explaining observed variation in the biomass of blue cod (34%) and exploited fishes (34%).

Table 1

Average abundance of reef fish species per transect (125 m²) with standard error (SE) at sites surveyed in 1992; 1998–2000; 2008–2010. A = Arapawaiti; K = Kaiwharawhara; O = Onepoto; T = Tokahaki. For the 1992 data, number of surveys = 1; 5 surveys for the 1998–2000 data, and 3 surveys for 2008–2010 data. #exploited species; *protected site. Data are also pooled for exploited and unexploited species, as well as for inside and outside of the MR.

Site	Year (s)	Species/Group																	
		<i>Banded wrasse</i>		<i>Blue cod#</i>		<i>Blue moki#</i>		<i>Butterfish#</i>		<i>Red moki#</i>		<i>Scarlet wrasse</i>		<i>Spotty</i>		<i>Exploited species</i>		<i>Unexploited species</i>	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
A	1992	0.83	0.60	1.50	1.50	0.50	0.29	1.17	0.60	0.17	0.17	6.67	1.76	3.17	1.17	3.33	2.35	10.67	3.18
*	1998–2000	5.82	0.95	7.14	2.26	0.34	0.15	1.11	0.26	0.32	0.07	3.33	0.78	10.81	2.97	7.18	0.99	16.89	2.73
*	2008–2010	3.07	0.78	3.89	0.96	0.22	0.07	3.93	1.22	0.20	0.07	2.36	0.58	6.84	1.52	10.56	1.58	14.19	2.41
K	1992	0	0	5.50	1.04	0.17	0.17	0.17	0.17	0	0	19.83	3.77	1.50	0.76	5.83	0.93	21.33	4.04
	1998–2000	1.14	0.20	0.47	0.15	0.10	0.05	0.24	0.07	0.19	0.06	0.39	0.23	3.54	1.24	0.98	0.29	2.82	0.40
	2008–2010	0.62	0.46	0	0	0	0	1.44	0.63	0.29	0.13	0.42	0.11	1.64	1.15	1.07	0.34	1.15	0.24
O	1992	0.83	0.17	3.67	1.30	0.50	0.29	0.33	0.17	0	0	12.83	4.42	27.33	1.45	4.50	0.87	41.00	3.06
*	1998–2000	0.89	0.25	1.69	0.40	0.64	0.18	1.22	0.61	0.25	0.05	0.83	0.34	1.88	0.54	5.02	1.33	4.27	1.12
*	2008–2010	1.22	0.23	1.16	0.32	0.16	0.08	2.27	0.57	0.27	0.08	0.84	0.28	1.42	0.49	2.78	0.59	2.15	0.40
T	1992	0.50	0.17	0	0	0	0	0.50	0.17	0	0	2.00	0.44	7.50	1.15	0.17	0.17	3.33	1.20
	1998–2000	0.77	0.19	1.73	0.67	0.18	0.06	0.68	0.30	0.16	0.05	0.44	0.16	13.43	7.62	3.84	0.93	24.73	11.67
	2008–2010	2.04	0.65	0.24	0.09	0.07	0.03	2.07	0.88	0.16	0.06	0.60	0.17	3.93	1.08	1.81	0.66	6.19	1.00
Inside (A&O)*	2008–2010	2.30	0.62	2.54	0.64	0.17	0.06	3.74	0.68	0.22	0.07	1.31	0.23	4.56	1.17	2.30	0.62	2.54	0.64
Outside (K&T)	2008–2010	1.07	0.25	0.17	0.08	0.02	0.03	1.04	0.48	0.22	0.06	0.48	0.14	2.11	0.43	1.07	0.25	0.17	0.08

Table 2

Average size (cm) of reef fish species observed with standard error (SE) at sites surveyed in 1992; 1998–2000; 2008–2010. A = Arapawaiti; K = Kaiwharawhara; O = Onepoto; T = Tokahaki. For the 1992 data, number of surveys = 1; 5 surveys for the 1998–2000 data, and 3 surveys 2008–2010 data. Blank spaces indicate that no data were collected. #exploited species; *protected site. Data are also pooled for exploited and unexploited species, as well as for inside and outside of the MR.

Site	Year(s)	Species/Group																			
		<i>Banded wrasse</i>		<i>Blue cod#</i>		<i>Blue moki#</i>		<i>Butterfish#</i>		<i>Red moki#</i>		<i>Scarlet wrasse</i>		<i>Spotty</i>		<i>Exploited species</i>		<i>Unexploited species</i>			
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE		
A	1992	16.00	1.00	21.11	1.11	25.00	7.64	27.50	6.29	60.00	0	13.63	0.91	12.63	0.59	33.40	8.96	14.09	0.87		
*	1998–2000	23.51	0.75	22.51	0.53	34.44	3.19	31.73	3.17	27.26	2.61	3.60	0.31	8.01	0.95	29.88	2.73	22.62	2.23		
*	2008–2010	24.48	0.85	25.53	0.62	27.19	5.09	41.94	2.51	44.17	3.73	20.66	0.89	10.58	0.92	33.05	2.85	18.54	1.10		
K	1992			17.88	1.04	40.00	0.	40.00	0			20.00	0	10.00	0	32.63	6.39	15.00	3.54		
	1998–2000	20.18	0.98	22.02	1.35	24.96	1.89	24.41	1.50	25.41	4.67	7.50	0.82	7.50	0.54	28.44	1.54	17.78	1.75		
	2008–2010	18.67	0.47					40.99	5.99	42.02	3.13	18.50	1.94	11.01	1.20	43.25	2.67	16.27	1.73		
O	1992	23.00	2.00	20.83	0.60	23.33	3.33	37.50	2.50			20.00	0	20.00	0	27.22	4.49	21.00	0.87		
*	1998–2000	20.18	1.41	26.59	1.63	33.80	2.56	27.97	2.52	33.45	3.26	15.75	3.17	15.75	1.50	32.79	1.83	20.59	3.81		
*	2008–2010	26.93	1.85	32.30	1.58	30.31	3.30	46.22	1.89	47.63	2.13	20.27	1.12	11.60	1.27	39.72	1.82	20.69	1.98		
T	1992	30.00	0					20.00	0			20.00	2.89	15.00	0.67	20.00	0.00	21.67	3.82		
	1998–2000	20.41	1.75	23.93	1.55	17.37	1.26	21.70	2.25	30.49	3.99	10.00	1.27	4.56	0.38	20.81	3.19	19.41	2.99		
	2008–2010	23.52	3.33	21.88	0.72	38.33	4.65	34.35	2.10	45.42	7.31	21.47	1.15	10.57	0.66	34.11	3.66	17.53	0.63		
Inside (A&O)*	2008–2010	26.34	1.66	29.14	2.12	22.81	3.78	44.93	2.41	45.17	1.99	21.08	0.71	11.42	1.19	36.39	2.12	19.61	1.12		
Outside (K&T)	2008–2010	19.73	0.64	21.67	0.78	35.00	0	38.58	5.36	43.89	5.67	19.58	1.77	11.39	0.94	38.68	2.88	16.90	0.87		

Table 3

Average biomass (kg) of reef fish species per transect (125 m²) with standard error (SE) at sites surveyed in 1992; 1998–2000; 2008–2010. A = Arapawaiti; K = Kaiwharawhara; O = Onepoto; T = Tokahaki. For the 1992 data, number of surveys = 1; 5 surveys for the 1998–2000 data, and 3 surveys 2008–2010 data. #exploited species; *protected site. Data are also pooled for exploited and unexploited species, as well as for inside and outside of the MR.

Site	Year(s)	Species/Group																			
		<i>Banded wrasse</i>		<i>Blue cod#</i>		<i>Blue moki#</i>		<i>Butterfish#</i>		<i>Red moki#</i>		<i>Scarlet wrasse</i>		<i>Spotty</i>		<i>Exploited species</i>		<i>Unexploited species</i>			
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE		
A	1992	0.06	0.03	0.26	0.26	0.56	0.36	0.27	0.14	1.08	1.08	0.23	0.06	0.10	0.07	2.16	0.19	0.40	0.052		
*	1998–2000	2.09	0.35	1.61	0.51	0.24	0.09	0.65	0.23	0.11	0.03	0.01	0.01	0.04	0.04	2.61	0.57	2.14	0.35		
*	2008–2010	1.03	0.19	1.30	0.34	0.17	0.10	6.40	2.81	0.31	0.11	0.46	0.17	0.26	0.08	8.18	2.60	1.75	0.33		
K	1992	0	0	1.20	0.30	0.41	0.41	0.15	0.15	0	0	0.99	0.19	0.03	0.01	1.76	0.27	1.02	0.32		
	1998–2000	0.28	0.09	0.14	0.06	0.06	0.04	0.07	0.03	0.12	0.05	0	0	0	0	0.39	0.084	0.28	0.088		
	2008–2010	0.09	0.07	0	0	0	0	1.81	0.90	0.43	0.21	0.04	0.01	0.05	0.03	2.24	0.81	0.18	0.25		
O	1992	0.21	0.10	1.30	0.19	0.31	0.22	0.25	0.14	0	0	0.68	0.10	1.36	0.07	1.87	0.29	2.25	0.33		
*	1998–2000	0.26	0.09	0.62	0.20	0.73	0.33	0.41	0.16	0.21	0.06	0.01	0.01	0	0	1.97	0.34	0.28	0.088		
*	2008–2010	0.61	0.17	0.77	0.23	0.14	0.10	4.79	1.45	0.51	0.17	0.12	0.03	0.07	0.02	6.21	1.45	0.79	0.14		
T	1992	0.09	0.09	0	0	0	0	0.01	0.01	0	0	0.10	0.05	0.20	0.11	0.014	0.0034	0.39	0.035		
	1998–2000	0.34	0.17	0.44	0.14	0.04	0.02	0.14	0.08	0.14	0.09	0	0	0	0	0.77	0.17	0.34	0.22		
	2008–2010	0.48	0.08	0.05	0.02	0.08	0.05	2.03	1.34	0.24	0.11	0.10	0.03	0.15	0.04	2.40	1.35	0.73	0.12		
Inside (A&O)*	2008–2010	1.35	0.21	1.35	0.22	0.16	0.088	10.16	2.30	0.55	0.10	0.33	0.076	0.30	0.080	12.21	2.20	1.98	0.32		
Outside (K&T)	2008–2010	0.29	0.13	0.029	0.018	0.024	0.017	1.72	0.80	0.38	0.13	0.05	0.011	0.071	0.025	2.15	0.76	0.41	0.16		

Table 4

Results of BACI PERMANOVA where total variation in abundance for each fish species, fished species, and unfished species at Kapiti Marine Reserve is partitioned as percentage attributable to the various components, with residual error based on *site* × *time* interaction. Negative components are equated to 0. #exploited species.

Species	Factor				
	Protection	Protection × time	Site	Time	Residual
Banded wrasse	0	5.1	67.6 ^{***}	10.1	17.2
Blue cod#	23.7	0	35.5 [*]	21.7	19.1
Blue moki#	0	0	0	0	100.0
Butterfish#	13.5 [*]	13.4 [*]	59.5	13.6 [*]	0
Red moki#	0	48.8	0	51.2	0
Scarlet wrasse	0	0	26.1	15.5	58.5
Spotty	0	48.8	0	51.2	0
Exploited species	31.5	0	27.4	5.7	35.4
Unexploited species	0	1.8	16.7	0	81.4

^{*} 0.01 < *p* < 0.05.

^{**} 0.001 < *p* < 0.01.

^{***} *p* < 0.001.

Table 5

Results of BACI PERMANOVA where total variation in size of each fish species, fished species, and unfished species at Kapiti Marine Reserve is partitioned as percentage attributable to the various components, with residual error based on *site* × *time* interaction. Negative components are equated to 0. #exploited species.

Species	Factor				
	Protection	Protection × time	Site	Time	Residual
Banded wrasse	54.1 ^{**}	0	5.5	9.1	31.4
Blue cod#	21.2	0	2.4	0	76.4
Blue moki#	11.2	41.4	21.9	13.2	12.2
Butterfish#	9.3	0	0	29.7	61.1
Red moki#	0	0	0	26.3	73.7
Scarlet wrasse	0	8.6	4.8	76.8 ^{***}	9.8
Spotty	0	0.8	22.0	44.1 [*]	33.2
Exploited species	0	19.8 [*]	25.0 ^{**}	32.9 ^{**}	22.2
Unexploited species	3.8	0	1.1	71.2 ^{***}	23.8

^{*} 0.01 < *p* < 0.05.

^{**} 0.001 < *p* < 0.01.

^{***} *p* < 0.001.

Table 6

Results of BACI PERMANOVA where total variation in biomass for each fish species, fished species, and unfished species at Kapiti Marine Reserve is partitioned as percentage attributable to the various components, with residual error based on *site* × *times* interaction. Negative components are equated to 0. #exploited species.

Species	Factor				
	Protection	Protection × time	Site	Time	Residual
Banded wrasse	8.6	0	38.3 ^{**}	13.7	39.3
Blue cod#	34.3 [*]	0	10.3	8.3	47.0
Blue moki#	0	0	0	0	100.0
Butterfish#	17.0	28.9 [*]	3.5	31.6 ^{**}	19.1
Red moki#	0	0	35.2 [*]	25.2 [*]	39.6
Scarlet wrasse	0	0	2.5	31.6 [*]	65.9
Spotty	0	0	69.4 ^{**}	10.1 [*]	20.5
Exploited species	33.6 [*]	5.5	0	16.7	44.2
Unexploited species	0	0	51.1 ^{**}	12.6	36.3

^{*} 0.01 < *p* < 0.05.

^{**} 0.001 < *p* < 0.01.

^{***} *p* < 0.001.

3.2. Inside–outside comparisons—2008–2010

Average abundances of reef fishes at sites inside the MR were significantly greater than outside for blue cod (inside average = 2.52 per transect ± 0.66 SE; outside average = 0.12 per transect ± 0.058; *p* = 0.001) and scarlet wrasse (inside average = 1.60 per transect ± 0.40; outside average = 0.51 per transect ± 0.10; *p* = 0.011). Average abundance of exploited reef fishes was also significantly greater at sites inside than outside Kapiti MR (inside average = 6.04 per transect ± 1.22; outside average = 2.13 per transect ± 0.53; *p* = 0.012 Fig. 3(a)).

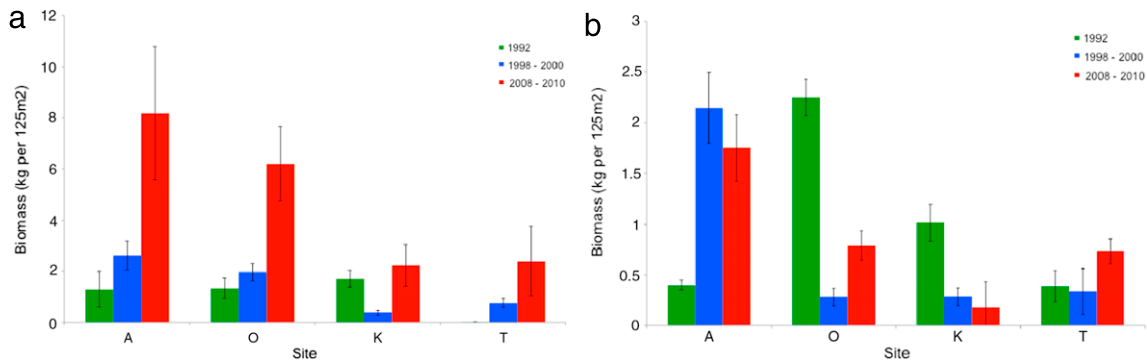


Fig. 4. Biomass of exploited (panel A) and unexploited (panel B) reef fishes (mean \pm SE) at Kapiti Marine Reserve for the 1998–2000 survey and the 2008–2010 survey. A = Arapawaiti (MR), O = Onepoto (MR); K = Kaiwharawhara (control); T = Tokahaki (control).

Average sizes of blue cod and banded wrasse were significantly greater inside than outside the MR (blue cod—inside average = $28.9 \text{ cm} \pm 1.02$; outside average = $21.9 \text{ cm} \pm 1.27$; $p = 0.0069$; banded wrasse—inside average = 25.7 ± 1.24 ; outside average = 19.2 ± 1.22 ; $p = 0.0082$).

Average biomass was significantly greater at sites inside than at outside for blue cod and for exploited reef fishes (blue cod—inside average = $1.03 \text{ kg per transect} \pm 0.21$; outside average = $0.027 \text{ kg per transect} \pm 0.014$; $p = 0.001$; exploited reef fishes—inside average = $7.19 \text{ kg per transect} \pm 1.44$; outside average = $2.32 \text{ kg per transect} \pm 0.74$; $p = 0.0051$; Fig. 4(b)).

4. Discussion

Quantifying change in biological responses over time is an important component of monitoring at MR and/or MPA sites at locations throughout the world, in temperate and tropical waters. However, being able to interpret such changes and understand why they occur has, at times, proved to be difficult, at least in part because multiple factors appear to contribute to MR success (e.g., Edgar et al., 2014). An improved understanding of which factors (non-biological as well as biological) contribute to conservation success, across which species and over what time frames, is critical for the future establishment of MRs as biodiversity protection tools (Lester et al., 2009; Babcock et al., 2010; Claudet et al., 2010). This applies to the success of individual MRs, as well as the contribution that MRs make to a network (Russ et al., 2008; Christie et al., 2010). Our results highlight how exploited reef fishes may recover from fishing pressure, that recovery is still ongoing after 20 years, and that individual highly targeted species may exhibit profound positive changes far in excess of what might have been predicted at the time that the MR was established.

4.1. Reef fish response to marine protection

This is the first study that has been able to detect statistically significant changes in abundance, size, and biomass of reef fishes at Kapiti MR. Previous studies at this location have made comparisons to the baseline study, which has proved to be valuable but has low power to detect change (Stewart and MacDiarmid, 2003; Pande and Gardner, 2012). By comparing the 1992 baseline survey to the highly replicated 1998–2000 dataset and our well-replicated 2008–2010 study, we had greater power to detect temporal changes. Our statistically significant findings that abundance and biomass of butterflyfish have increased 413% and 2154% respectively in less than 20 years, are the greatest documented responses for this species, as well as being among the largest changes for any temperate species.

Our findings that the average size of all exploited reef fishes (i.e., blue cod, blue moki, butterflyfish, and red moki) has increased during 19 years of protection at Kapiti MR indicate that direct effects (recoveries of these exploited species) may take place on decadal rather than annual time scales. This is in contrast to a body of work which suggests that direct effects occur rapidly, often within the first 1–3 years of MR implementation, after which the response slows down or stops (e.g., Halpern, 2003; Halpern and Warner, 2002; Micheli et al., 2004). However, other studies have shown that MRs may continue to produce biological responses (increased size and/or abundance of exploited species) many years (10–20) after establishment (e.g., Molloy et al., 2009; Pande et al., 2009; Diaz et al., 2012). Elsewhere, it has been shown that direct effects on exploited species take, on average, only 5 years to be recognised, whereas indirect effects such as trophic cascades take considerably longer to be recognised, on average 13 years (Babcock et al., 2010). We suggest that a similar set of rapid direct responses probably occurred at the Kapiti MR but that these were not detected (or detectable) due to high variation in the dataset of the baseline study. Nonetheless, the value of the baseline dataset has again been illustrated by the outcomes of the analyses reported in the present study. We cannot say yet if this recovery of exploited fishes has started to slow down or even reached some sort of asymptote. Inspection of the response plots, in particular for butterflyfish, suggests that further positive change is likely into the future, but for how long and at what rate such changes will continue can only be determined by further monitoring.

The site-specific changes in abundance and biomass of butterfish over time at Kapiti MR are extraordinary. These changes suggest that the very large butterfish response observed at Kapiti MR is indicative of an environment that can support a high biomass of this species in the absence of fishing pressure, and that when the MR was implemented in 1992, butterfish biomass had already been substantially depleted by fishing exploitation. Butterfish (*Odax pullus*) is an herbivorous, protogynous hermaphrodite, endemic to New Zealand. It is distributed throughout the country, from Cape Reinga, on the northern tip of the North Island (34.4° S) to the subantarctic Antipodes Island (49.5° S), spanning 15° of latitude (Francis, 2001). Life history traits of butterfish vary widely throughout this range, with slower growth rates, later age and size at maturity (1–5 years and 22–27 cm fork length, respectively) and sex change (3–7 years and 34–39 cm fork length, respectively), and greater maximum age (10–20 years) and size (45–50 cm fork length) associated with colder, more southerly, waters (Trip, 2009). At New Zealand's first MR, the Cape Rodney to Okakari Point MR (commonly referred to as Leigh or Goat Island), butterfish abundance was similar at protected and unprotected sites as determined by UVC surveys in 2000, 25 years after protection (Haggitt, 2011). However, since then, protected sites have three to four-fold higher butterfish abundances in 2005, 2008 and 2011, 30–36 years after protection (Haggitt, 2011). These observations, along with our results from Kapiti MR, suggest that butterfish recovery from fisheries exploitation may take place on longer time scales than other species such as blue cod (e.g., Pande et al. 2009, Diaz et al., 2012). The protogynous hermaphrodite life history of butterfish may make it susceptible to fishery exploitation, as the present minimum size of capture for recreational fishers is 35 cm fork length, indicating that the majority of male butterfish do not receive any protection by this regulation (sex change occurs at 34–39 cm fork length). This biological factor may play a key role in the slower recoveries observed for butterfish compared to other species.

The biological responses reported from MRs all over the world typically point to more and bigger exploited species within MRs (Pande et al., 2008; Lester et al., 2009; Molloy et al., 2009; Diaz et al., 2012; Edgar et al., 2014). Moving beyond size and abundance, models of reef fish response to MR implementation have shown that biomass is slower to recover than abundance because abundance responds in the form of an sigmoidal (S) curve, whereas biomass responds with an exponential curve given that individuals continue to increase in size with age (Stockwell et al., 2009). While the overall response is generally consistent across MRs, there is increasing evidence of site-specific and species-specific responses, both in terms of magnitude and rate of response. Our results for different species of temperate reef fish at Kapiti MR confirmed this variability in response to protection.

The 21-fold increase in biomass of butterfish at protected sites has most likely had an impact on the biomass of macroalgae at these sites because adult butterfish graze exclusively on brown algal species and have been shown to play a major role in the structure of macroalgal canopies in New Zealand (Taylor and Schiel, 2010). This phenomenon is largely influenced by wave energy, whereby sites exposed to high wave energy are less impacted by butterfish grazing (Taylor and Schiel, 2010). Given the moderate wave exposure at Arapawaiti, the effects of grazing on macroalgae are likely to have a substantial effect on macroalgal community structure. This top-down grazing pressure may influence the flow of energy through the food web and also may modify habitat, thereby indirectly affecting other species in the ecosystem (Shears and Babcock, 2002, 2003; Pérez-Matus and Shima, 2010). Such indirect effects may help explain some of the responses of the unexploited fish species that we observed.

The biomass of butterfish at unprotected sites was greatest during the most recent 2008–2010 survey and 'time' was a statistically significant factor explaining variation in butterfish biomass. Taken together, these results suggest that butterfish recovery at protected sites in the Kapiti MR contributed to greater biomass at neighbouring unprotected sites. Potential mechanisms explaining this response are both spillover of butterfish from protected to unprotected sites and enhanced larval settlement and recruitment due to an overall greater abundance and biomass at the island as a result of marine protection (Almany et al., 2007; Christie et al., 2010; Salinas de León et al., 2012). The detection of larval export has been observed at Kapiti MR (Salinas de León et al., 2012), and we suggest that this mechanism may be contributing to greater observed butterfish biomass at unprotected sites.

4.2. The importance of "Site"

At the time of establishment of Kapiti MR, the subtidal habitat structure was different at Arapawaiti compared to other sites. It was composed of large *Ecklonia radiata* (kelp) stands and boulder barrens, rather than the more homogeneous habitat structure found elsewhere (Battershill et al., 1993). In addition, Arapawaiti was identified by fishers as a good fishing location prior to MR establishment, and there was resistance to closing it to fishing (Pande, 2001). These site-specific differences were confirmed by the 2008–2010 survey, in which the abundance of both exploited and unexploited reef fishes was markedly higher at Arapawaiti in comparison to all other sites, including the other protected site at Onepoto. Detecting the effects of MR implementation on size, abundance, and biomass of reef fishes or macroinvertebrates is challenging when inside–outside comparisons are confounded by the site-specific effects of habitat quality (Anderson and Millar, 2004; Claudet et al., 2010; Huntington et al., 2010). This particular scenario is likely to be common, because it is often the case that MRs or MPAs are set-up to specifically include "high quality" sites, given that they are viewed as having greater biodiversity and/or biomass, and are therefore particularly worthy of protection (e.g., Chapman and Kramer, 1999; Roberts, 2000; Pande and Gardner, 2012).

The absence of a baseline dataset hinders the identification of sites of special significance, whether they be inside or outside the MR (Pande and Gardner, 2008; Huntington et al., 2010). Above and beyond the simple and widely employed inside–outside (control–impact) assessment that may respond poorly in an analytical sense to special sites, various approaches now exist to help address this assessment problem. The earlier identification of Arapawaiti as a site of special

significance highlights the potential role of fishers' ecological knowledge (FEK) in identifying areas of high habitat quality or areas of high abundance of reef fishes (Johannes et al., 2000). While FEK is not always represented in traditional scientific quantitative information sources, the field of historical ecology aims to use non-traditional and often multi-disciplinary data to inform baselines for modern science (Jackson et al., 2001; Pandolfi et al., 2003; Rosenberg et al., 2005; Lotze et al., 2006; Eddy et al., 2010; Taylor et al., 2011). More recently, in response to the problem of detecting changes in populations, communities or ecosystems associated with a MR at sites of varying environmental characteristics or habitat quality, and in the absence of a baseline dataset, a "landscape" approach and a GIS approach have shown promise (Friedlander et al., 2007; Huntington et al., 2010). This method quantifies seascape heterogeneity using different approaches such as remote sensing, image analysis and *in situ* classifications across multiple spatial scales to explain variation in biological data that may blur impacts caused by a MR itself (Huntington et al., 2010). These new and different approaches should now play a key role in helping to disentangle the effect of individual site characteristics from the effects of management impacts and confounding temporal and spatial variability.

4.3. BACI approach vs. inside–outside approach

Our results provide two very different pictures of MR effects on reef fishes at Kapiti MR, depending on the method that was used for analysis. The BACI approach revealed statistically significant changes in the abundance of butterflyfish due to the factor "protection \times time", indicating a four-fold increase in abundance. In contrast, the inside–outside approach for the 2008–2010 dataset revealed that the abundances of blue cod and scarlet wrasse are greater by ten-fold and three-fold respectively inside the MR (two sites pooled) in comparison to outside (two sites pooled). The inside–outside approach also indicates a three-fold statistically significant greater abundance of exploited reef fishes. The two analytical approaches reveal differences in the average size of reef fishes, with blue cod identified as being larger at protected sites using the inside–outside approach, while the BACI approach identifies exploited species as having increased in average size as a result of protection through time. When comparing biomass estimates of reef fishes, the BACI approach indicates a statistically significant twenty-fold increase in butterflyfish biomass at the site Arapawaiti, while the inside–outside approach indicates a thirty-fold statistically significant difference in biomass of blue cod inside the MR compared to outside. The inside–outside approach also indicates a three-fold greater biomass of exploited reef fishes inside the reserve compared to outside. These findings highlight the need for researchers who are quantifying MR impacts to consider the assumptions of the approach that they are employing, to understand the potential pitfalls of pooling data (e.g., pooled inside versus pooled outside sites) and to consider employing more than one analytical approach to better understand biological responses.

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