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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.

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 (*Parapercis 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-