Demonstrating multiple benefits from periodically harvested fisheries closures

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Abstract

1. Periodically harvested closures (PHCs) are one of the most common forms of fisheries management in Melanesia, demonstrating multiple objectives, including sustaining fish stocks and increasing catch efficiency to support small-scale fisheries. No studies have comprehensively assessed their ability to provide short-term fisheries benefits across the entire harvest regime.
2. We present a novel analytical framework to guide a meta-analysis and assist future research in conceptualizing and assessing the potential of PHCs to deliver benefits for multiple fisheries-related objectives.
3. Ten PHCs met our selection criteria and on average, they provided a 48% greater abundance and 92% greater biomass of targeted fishes compared with areas open to fishing prior to being harvested.
4. This translated into tangible harvest benefits, with fishers removing 21% of the abundance and 49% of the biomass within PHCs, resulting in few post-harvest protection benefits.
5. When PHCs are larger, closed for longer periods or well enforced, short-term fisheries benefits are improved. However, an increased availability of fish within PHCs leads to greater removal during harvests.

Synthesis and applications: Periodically harvested closures (PHCs) can provide short-term fisheries benefits and use of the analytical framework presented here, will assist in determining long term fisheries and conservation benefits. We recommend, PHCs be closed to fishing for as long as possible, be as large as possible, compliance encouraged via community engagement and enforcement and strict deadlines/goals for harvesting set to prevent overfishing.

Keywords: fisheries management, conservation, customary management, meta-analysis, marine reserve, small scale fisheries, analytical framework, locally managed marine areas, periodically harvested closures

Introduction

Inshore fisheries resources that support small-scale coral reef fisheries are in decline (Newton *et al.* 2007; Mora *et al.* 2009), impacting on food security and livelihood for millions of coastal residents (Pauly, Watson & Alder 2005; Bell *et al.* 2009). Various spatial (e.g., no-take marine reserves, NTMRs) and non-spatial (e.g., quotas, gear restrictions) management strategies are being implemented to achieve fisheries management, conservation and socio-cultural objectives with mixed success (Gaines *et al.* 2010; Rassweiler, Costello & Siegel 2012). In small-scale fisheries, these objectives often include maintaining or improving: long-term sustainable yield and profit; catch efficiency; reproductive capacity of fisheries; biodiversity and ecosystem function (Jupiter *et al.* 2014). Because achievement of these objectives requires optimizing different factors, trade-offs may arise in order to achieve multiple objectives simultaneously (Cohen & Steenbergen 2015; Daw *et al.* 2015).

Periodically harvested closures (PHCs) are functionally similar to rotational harvests of fishing grounds (e.g. scallop fisheries; Hart 2003; Valderrama & Anderson 2007) and have opening regimes that can range from mostly closed to mostly open (Cohen & Foale 2013). PHCs are commonly applied in Indo-Pacific coral reef fisheries as a strategy to increase catch efficiency and provide for socioeconomic and cultural needs (Jupiter *et al.* 2012, 2014; Cohen & Foale 2013). The number of PHCs implemented is increasing rapidly with a current estimate of >1000 established across Melanesia (H. Govan, pers. comm.). This rapid increase in PHCs is partially attributed to poor compliance with NTMRs and conventional fisheries management resulting in an increased interest in repurposing customary practice (Johannes 2002; Foale & Manele 2004; Cohen & Foale 2013). The increased reliance on PHCs to manage local fish stocks highlights the importance in understanding the dynamics of this strategy.

Historically, PHCs were implemented to increase catch efficiency through a decrease in fish wariness, as fishers observed that the behaviour of fish changes during closure, making them easier to catch (Cinner *et al.* 2006; Feary *et al.* 2011). More recently an increase in catch efficiency within PHCs has been observed for invertebrates harvested via gleaning (collection during low tide) (Cohen & Alexander 2013) and fish through a reduction in wariness to spearfishers (Januchowski-Hartley, Cinner & Graham 2014; Goetze *et al.* 2017). However, the increased catchability also means that a small amount of fishing effort can effectively remove substantial biomass (Jupiter *et al.* 2012). Consequently, pulse harvests in PHCs benefit fishers in the short-term, but potentially increase the likelihood of overharvesting, compromising long-term conservation and fisheries management objectives (Jupiter *et al.* 2012; Cohen & Foale 2013).

Despite a growing literature on PHCs (Cinner *et al.* 2006; Bartlett *et al.* 2009; Jupiter *et al.* 2012; Cohen & Alexander 2013; Cohen, Cinner & Foale 2013; Januchowski-Hartley, Cinner & Graham 2014; Goetze *et al.* 2015), there has been little quantitative work to understand their ability to achieve these short- and long-term fisheries and conservation objectives.

The complex nature of PHCs with highly variable harvesting regimes (Cohen & Foale 2013) and their use to achieve multiple objectives simultaneously (Jupiter *et al.* 2014) has made it difficult to generalize about their effectiveness. By contrast, drivers of NTMRs performance have been investigated extensively using meta-analytical approaches (e.g., Côté, Mosqueira & Reynolds 2001; Halpern 2003; Claudet *et al.* 2008, 2010; McClanahan *et al.* 2009; Lester *et al.* 2009; Molloy, McLean & Côté 2009; Vandeperre *et al.* 2011). Quantitative analyses of individual PHCs indicate variability in effectiveness (Cinner *et al.* 2006; Bartlett *et al.* 2009; Jupiter & Egli 2011) and suggest pulse harvests may be sustainable where total effort and catch from PHCs are low when compared with continuously fished reefs (Cohen, Cinner & Foale 2013). Meanwhile, theoretical analysis indicates that, under certain harvest regimes, PHCs can generate fisheries yields and in situ biomass levels matching those achievable under optimal non-spatial management or with NTMRs (Carvalho *et al.* 2015). Importantly, these yields may be achieved with greater catch efficiency under a PHC strategy (Januchowski-Hartley, Cinner & Graham 2014).

To assess empirically whether PHC practice matches theory, we developed a framework to assist future research in both conceptualizing and assessing the potential multiple benefits of PHCs for fisheries and conservation management. The aim of this framework is to deconstruct the variety of potential effects of periodically harvested closures (more numerous and complex than NTMRs due to harvesting regimes) and present the associated experimental design and effect sizes that are needed to quantitatively assess their magnitude. We then reviewed the literature and available unpublished data to gather a comprehensive database to quantitatively assess the ability of PHCs to provide short-term fisheries benefits to local communities. We hypothesized that PHCs would provide pre-harvest protection benefits as evidenced by a greater abundance and biomass of targeted fishes within their boundaries, but that these benefits would not be observed post-harvest due to removal during harvests. Finally, we assessed which factors contribute to short-term fisheries and harvest benefits and predicted that PHCs which are larger, closed for longer periods or well enforced would provide increased benefits.

Materials and Methods

Analytical framework

We developed hypotheses, effect sizes and sampling designs to assess eight potential social-ecological benefits (indicated with italicized text) derived from PHCs (Table 1). We use the terminology “PHC” to refer to areas within a periodically harvested closure and “Open” for areas outside of the PHC, in which fishing is always allowed. *Pre-harvest protection* benefits result from increased availability of abundance or biomass within a PHC compared with areas open to fishing prior to a harvest event. PHCs may have experienced historical harvest events depending on the timing of initial surveys making this effect size distinct when compared to assessing the benefits of a NTMR. The pre-harvest protection benefit is comparable to a measurement of *post-harvest recovery*, which is the same effect size measure taken at some defined time following a harvest event. *Post-harvest protection* benefits are shown by an increased level of abundance or biomass remaining after the harvest, while *maintenance of post-harvest protection* indicates that these benefits are retained through a subsequent harvest. *Harvest* benefits to fishing communities occur when a large proportion of the abundance and biomass is efficiently removed from a PHC during a pulse fishing event. *Recovery of pre-harvest protection* assesses the relative state of the fishery to the levels of abundance or biomass prior to the last harvest. The *conservation* benefit evaluates the ability of a PHC to increase fish stocks compared to NTMRs. Finally, the *sustainability of periodic harvest practice* assesses the ability of PHCs to maintain all of these benefits over the long term.

Literature search

We performed a literature search of published information to assess the eight benefits in Table 1. Single and combined terms were used to search all databases of the ISI Web of Knowledge and Google Scholar for literature on PHCs (see search terms in Table S1). A total of 85 publications had information on an area that had been harvested after being closed to fishing. The reference lists of these publications were examined to identify additional studies (mostly grey literature) that were not found in the initial literature search. This identified an additional 40 studies, giving a total of 125 publications with information on PHCs. Of these, 29 studies reported empirical data that could be extracted from tables and/or figures. Additional unpublished data from 5 PHCs was provided by authors, J. Goetze and S. Jupiter.

Selection criteria and data evaluation

Selection criteria were established to ensure that the data could be used to quantify at least one of the potential benefits of PHCs (Table 1): (i) studies must have collected abundance and/or biomass data inside and outside of a PHC; (ii) PHCs needed to be strictly no-take when closed to fishing; (iii) control sites must have been located in areas that were continuously fished; (iv) data collection methods had to be standardized inside and outside of the PHC, before and after the harvest and fisheries independent; and (v) adequate statistical information had to be provided, including number of replicates (transects), means, and error estimates. A total of 11 studies (including the 5 unpublished datasets) met these criteria. All but one presented information on coral reef fishes, thus we restricted analyses to coral reef fish in 10 PHCs (Table 2). Insufficient replication within existing empirical datasets constrained our ability to assess the ability of PHCs to deliver protection benefits, allowing us to address only 3 of 8 questions posed in our analytical framework (Table 1): thus we only assessed the effectiveness of PHCs to deliver pre-harvest protection, harvest and post-harvest protection benefits. We were unable to assess how long the PHC will take to recover to pre-harvest levels, provide benefits after a certain period of recovery, maintain post-harvest protection benefits and conserve abundance/biomass relative to no-take marine reserves; however, our analytical framework outlines methods for conducting these assessments once the data become available. In addition, paired series were not available for benefits 1 to 3, preventing us from assessing the sustainability of these benefits.

The data presented in these ten studies were used following two steps: (i) if there were multiple harvest sampling records, surveys for before/after values were chosen closest to the harvest dates to ensure they provided the most accurate information on PHC protection and harvest impacts;

(ii) observations must have been independent (i.e., when multiple harvests were sampled, we used data before and after the initial harvest and when multiple studies occurred in the same PHC, we chose that which had the most comprehensive data).

A conceptual diagram was created to illustrate the theoretical functioning of a PHC and areas open to fishing and the calculation of effect sizes used to assess pre-harvest protection, post-harvest protection and harvest benefits (Fig. 1). In order to simplify the diagram we assume there is no change in abundance/biomass in open areas, full compliance with the fishing restriction inside the PHC and that abundance and biomass increase during closure periods. During harvest events we also assumed fishing effort is initially intense and decreases towards the end of the harvest, as has been documented empirically (Cohen, Cinner & Foale 2013). Multiple harvests of the same level are shown to indicate a system that is in equilibrium, i.e., the overall biomass/abundance in the system is not increasing or decreasing.

Sampling design and methods (unpublished data)

Surveys were carried out on reefs adjacent to five villages on Koro (Nakodu, Tuatua), Ovalau (Nauouo, Natokalau) and Vanua Levu (Kiobo) islands in Fiji in 2013 and 2014. PHCs had been established for 3-8 years prior to surveys, though the frequency at which they had been previously harvested and level of compliance with management varied (Table 2). Surveys were carried out 1-2 days before and 1-2 days after harvests, which lasted between 1 to 7 days and involved line fishing, spear fishing and/or fish drives into gill nets (Table S3). We sampled between 2 and 5 sites inside each of the five PHCs (depending on PHC size), and 4 to 6 sites in open areas (depending on comparable available habitat, Table S2). At each site, the fish community was sampled by conducting stereo diver operated video (stereo-DOV) surveys along six replicate 5 x 50 m transects separated by 10 m, following (Goetze *et al.* 2015). This matched the transect length used to estimate abundance and biomass from all studies extracted from the PHC literature (Table S2). Stereo-DOVs are one of the most effective methods for detecting harvest impacts on targeted species within PHCs (Goetze *et al.* 2015) and have been shown to be broadly comparable to underwater visual census (Holmes *et al.* 2013). Stereo-DOVs were used to collect abundance and biomass calculated using the standard length-weight equations and values from FishBase (Froese & Pauly 2015), preferentially selected from sites closest to Fiji (Jupiter & Egli 2011). System design and procedures for video analysis followed Goetze *et al.* (2015).

Factors influencing protection benefits

Previous meta-analyses of NTMRs showed that protection effectiveness is a function of enforcement (Guidetti *et al.* 2008), fishing pressure outside of the reserve (Côté, Mosqueira & Reynolds 2001) and the size and age of reserves (Claudet *et al.* 2008). PHCs, however, have complex regimes of opening and closing to fishing and their popularity in small scale fisheries is partially attributed to poor compliance with NTMRs (Foale & Manele 2004; Jupiter *et al.* 2012; Cohen & Foale 2013). Here we assessed how PHC benefits were affected by: (i) compliance with PHC no-take rule (*Compliance*); (ii) fishing pressure outside of the PHC when closed (*Fishing Pressure Outside*); (iii) fishing effort within the PHC when harvested (*PHC Harvest Effort*); (iv) size of PHC in km^2 (*Size*); (v) number of years since the PHC was established when before-harvest sampling took place (*Years Established*); or (vi) number of years the PHC was closed to fishing (following prior harvest or since establishment) when before-harvest sampling took place (*Time Closed*)(Table 2). For published data, information on *Size*, *Time Closed* and *Years Established* was extracted from each manuscript (Table 2). As the same quantitative data collected in this study were not always available in the literature, assessments of *Harvest Effort, Fishing Pressure Outside and Compliance* were converted to categorical two-point scales (High or Low). This was achieved by ranking all PHCs with matching data and then assessing where the remaining PHCs fit on this scale, using information reported in each manuscript and expert knowledge (Table S3) Categorisation occurred at a workshop with all authors present and at least one author had either been directly involved with each study or worked in the same location as the PHC.

To estimate fishing pressure during harvest events for the unpublished data (*Harvest Effort*), we recorded catch per unit effort (CPUE), fishing methods, and harvest duration for each PHC (Table 2, S3). Estimates of *Compliance* were based on surveys with village spokespersons, fishers and other key informants, who were asked to rate compliance as low (frequent breaches of management rules) or high (occasional or infrequent offenses of management rules), based on their direct observations within each village. The extent of fishing in areas outside of PHCs was also collected from key informant surveys, who estimated the number of locally-operated boats within a village; the number of boats from outside the village observed in the fishing area each week and the number of licensed fishers (Table S3). Where available, catch per unit effort data was also reported.

For unpublished data, species were classified as target or non-target based on whether they were caught during the harvest, so that classifications were specific to each PHC (see Table S4 for a full list of targeted/non-targeted species). For published studies targeted/non-targeted species were designated by the authors (see Table S2 for a summary). Variation in the occurrence and target status of species across countries resulted in different groupings of species across studies, limiting analysis to targeted and non-targeted groupings. In all studies, species were combined by summing the targeted and non-targeted abundance/biomass at the transect level.

Statistical analyses

Three effect sizes were developed in order to assess PHC benefits 1 to 3 in the analytical framework (Table 1). Log-ratio effect sizes and confidence intervals were used to quantify proportionate change across all metrics, and account for variation in the sampling methods, focal species and study locations (Hedges, Gurevitch & Curtis 1999). For each PHC *i*, the ability to deliver a pre-harvest protection benefit ($E_{b,i}$), was calculated as the log-ratio of the mean abundance or biomass in the PHC before (*Pb*), $\bar{X}_{Pb,i}$ and the Open before (*Ob*), $\bar{X}_{Ob,i}$, respectively:

$$E_{b,i} = \ln\left(\frac{\bar{X}_{Pb,i}}{\bar{X}_{Ob,i}}\right)$$

Variance of the effect sizes were calculated as:

$$v_{E_{b,i}} = \frac{\sigma^2_{Pb,i}}{n_{Pb,i} \times \bar{X}^2_{Pb,i}} + \frac{\sigma^2_{Ob,i}}{n_{Ob,i} \times \bar{X}^2_{Ob,i}}$$

where $v_{E_{b,i}}$ is the variance associated with the effect size $E_{b,i}$, $\sigma_{Pb,I}$ and $\sigma_{Ob,i}$ are the standard deviations associated with the means $\bar{X}_{Pb,i}$ and $\bar{X}_{Ob,i}$, respectively, and $n_{Pb,i}$ and $n_{Ob,i}$, are the number of transects used to calculate each mean (Hedges, Gurevitch & Curtis 1999).

For each PHC *i*, the ability to deliver a post-harvest protection benefit ($E_{a,i}$), was calculated as the log-ratio of the mean abundance or biomass per transect in the PHC after (*Pa*), $\bar{X}_{Pa,i}$ and the Open after (*Oa*), $\bar{X}_{Oa,i}$:

$$E_{a,i} = \ln\left(\frac{\bar{X}_{Pa,i}}{\bar{X}_{Oa,i}}\right)$$

Variance of the effect sizes were calculated as:

$$v_{E_{a,i}} = \frac{\sigma^2_{Pa,i}}{n_{Pa,i} \times \bar{X}^2_{Pa,i}} + \frac{\sigma^2_{Oa,i}}{n_{Oa,i} \times \bar{X}^2_{Oa,i}}$$

where $v_{E_{a,i}}$ is the variance associated with the effect size $E_{a,i}$, $\sigma_{Pa,I}$ and $\sigma_{Oa,i}$ are the standard deviations associated with the means $\bar{X}_{Pa,i}$ and $\bar{X}_{Oa,i}$, respectively, and $n_{Pa,i}$ and $n_{Oa,i}$, are the number of transects used to calculate each mean.

For each PHC *i*, the harvest benefit ($E_{h,i}$), was defined as the difference in the mean abundance or biomass between the PHC after, $\bar{X}_{Pa,i}$, and before $\bar{X}_{Pb,i}$ the harvest, while controlling for differences in Open areas after $\bar{X}_{Oa,i}$ and before $\bar{X}_{Ob,i}$ the harvest:

$$E_{h,i} = \ln\frac{\left(\bar{X}_{Pa,i}/\bar{X}_{Pb,i}\right)}{\left(\bar{X}_{Oa,i}/\bar{X}_{Ob,i}\right)}$$

Variance of the effect sizes were calculated as:

$$v_{E_{h,i}} = \sum^{Pa,Pb,Oa,Ob} \sigma_i^2/(n_i \times \bar{X}_i^2)$$

where $v_{E_{h,i}}$ is the variance associated with the effect size $E_{h,i}$, σ_i is the standard deviations associated with the mean $\bar{X}_i$, and n_i is the number of transects summed for the PHC after (*Pa*), PHC before (*Pb*), Open after (*Oa*) and Open before (*Ob*).

We then used a mixed effects weighted meta-analysis where weights of each individual effect size incorporate these variances as follows:

$$w_{j,i} = \frac{1}{v_{E_{j,i}} + v_{j,a}}$$

where $w_{j,i}$ is the weight associated to each effect $E_{j,i}$, $v_{Ei,j}$ is the within study variance of each PHC benefit *j* (*pre-harvest*, *post-harvest* or *harvest* as defined above) and $v_{j,a}$ is the among-study variance for each benefit *j*. In a meta-analysis framework, a mixed effect procedure is used when studies are not expected to all share the same true effect (i.e. there is an among-study variation in addition to sampling error; random effect) and where the effect of moderators (covariates) is assessed (mixed-effect). The among study variance was obtained using the generalized equation reported in (Hedges & Pigott 2004). Confidence intervals for group and overall effect sizes were derived from a Student's *t* statistic. Given the possibility of type I error with multiple testing, we recommend a cautious approach when interpreting our results and suggest to use the 95%

confidence intervals to assess confidence in the direction of the result rather than accepting or rejecting each hypothesis.

We assessed the effects of moderators *Compliance, Fishing Pressure Outside, PHC Harvest Effort*, *Size, Time Closed* and *Years Established* on each of the effect sizes described above using comparisons among factors for categorical variables and linear models for quantitative variables. Correlation between moderators were tested using, Pearson's correlations for comparisons between continuous variables, Cramer's V for nominal variables and intra-class correlations (ICC) for continuous vs. nominal moderators. Weak correlations were observed between all moderators, except for *PHC Harvest Effort* and *Time Closed* which was moderate (Table S5). To assess whether a set of effect sizes are heterogeneous (i.e. varied across PHCs), we calculated the total heterogeneity Qt and tested it against a χ^2 distribution with $n - 1$ degrees of freedom (n being the number of studies), as outlined in Hedges and Olkin (1985). We used the package metafor with restricted maximum-likelihood estimator (Viechtbauer 2010) in R language for statistical computing (R Core Team 2014).

Results

Pre-harvest protection benefits

On average PHCs provided pre-harvest protection benefits, with a 48% greater abundance and 92% greater biomass of targeted fishes when compared to open areas; however, these results were heterogeneous, suggesting variation across PHCs (Table 3). Pre-harvest protection benefits for targeted fish abundance varied with compliance, fishing pressure outside, time closed or years since establishment (Fig.2, Table S6). PHCs with high compliance or high fishing pressure outside provided pre-harvest benefits in abundance (Fig. 2). The pre-harvest protection benefit for abundance increased by 6% per year since establishment and 19% per year since previous harvest (*Years Established*: SE = 0.024; $P < 0.01$; *Time Closed*: SE = 0.037; $P < 0.001$). Pre-harvest protection benefits for targeted fish biomass varied with compliance or PHC size. PHCs with high compliance provided pre-harvest protection benefits in targeted biomass (Fig. 2). Pre-harvest protection benefits in targeted biomass increased by 15% per km^2 of PHC (SE = 0.045; P < 0.01). On average PHCs did not provide pre-harvest protection benefits for non-targeted abundance or biomass, although this result was heterogeneous (Table 3). However, none of the co-variates explained this heterogeneity (Table S7; Fig. S1).

Harvest benefits

On average there were harvest benefits with a 21% greater removal of abundance and 49% greater removal of biomass of targeted species within the PHC compared to open areas during harvest events, though results were heterogeneous suggesting variation across PHCs (Table 3). Harvest benefits for targeted fish abundance varied with compliance, fishing pressure outside, PHC harvest effort, size, or the time closed since the previous harvest (Table S6; Fig. 2). PHCs with low compliance, high harvest effort or high fishing pressure outside resulted in greater harvest benefits for targeted abundance (Fig. 2). Harvest benefits in targeted abundance increased by 6% per km^2 of PHC (SE = 0.017; $P = 0.001$) and 11% for each year since the previous harvest (SE = 0.042; $P = 0.01$). Harvest benefits for targeted fish biomass varied with compliance, fishing pressure outside, PHC harvest effort, size or years established (Table S6;

Fig. 2). PHCs with high compliance, high harvest effort or high fishing pressure outside, provided harvest benefits for targeted biomass (Fig. 2). Harvest benefits in targeted biomass increased by 18% per km^2 of PHC (SE = 0.033; $P < 0.001$) and 11% for each year since establishment (SE = 0.046; $P = 0.016$). On average PHCs did not provide harvest benefits for non-targeted abundance or biomass, although biomass results were heterogeneous (Table 3). Harvest benefits in non-targeted species increased by 11% per km^2 of PHC (SE = 0.047; $P = 0.019$; Table S7; Fig. S1).

Post-harvest protection benefits

On average PHCs provided post-harvest protection benefits to targeted fish abundance, with a 14% greater abundance when compared to open areas (Table 3). This result was homogenous, suggesting consistency across PHCs. In contrast, there were no post-harvest protection benefits in the biomass of targeted species within PHCs compared to open areas, however, heterogeneity suggests this varied across PHCs (Table 3). Post-harvest protection benefits for targeted fish biomass varied with fishing pressure outside the PHC (Table S6; Fig. 2). When the fishing pressure outside was high, post-harvest benefits in targeted biomass were greater within open areas; when fishing pressure outside was low, post-harvest benefits in targeted biomass were greater within PHCs (Fig. 2). On average PHCs did not provide post-harvest protection benefits for non-targeted abundance or biomass. Although this result was heterogeneous (Table 3), none of the co-variates explained this heterogeneity (Table S7; Fig. S1).

Discussion

Overall, PHCs provided pre-harvest protection benefits including a 48% greater abundance and 92% greater biomass of targeted species compared with areas open to fishing. This supports our hypothesis that PHCs are capable of providing pre-harvest benefits through an increased abundance and biomass of targeted species, despite historical harvesting. However, we were not able to account for migration/movement of targeted species across PHC boundaries, which differs among target species (Nash *et al.* 2015) and is therefore likely to have contributed to the variability in results across PHCs (Eggleston & Parsons 2008). Regardless of the mechanism, greater abundance and biomass of fish in PHCs translated to harvest benefits where fishers removed an average of 29% of the abundance and 49% of the biomass, a result likely due to greater catch efficiency associated with decreased wariness of targeted fishes within PHCs (Feary *et al.* 2011; Januchowski-Hartley, Cinner & Graham 2014; Goetze *et al.* 2017). Therefore PHCs are a particularly effective fisheries management strategy for increasing short-term fisheries yields from single harvest events. The long-term effectiveness of this strategy will depend on whether there is sufficient recovery time between harvests (Cohen & Foale 2013; Abesamis *et al.* 2014; Goetze *et al.* 2016), and whether increased abundance/biomass can be sustained indefinitely. The high frequency of harvests from many Melanesian PHCs raises concerns about the ability of PHCs to achieve long-term management objectives that relate to maintaining or increasing: sustainable yield and profit; reproductive capacity of fisheries; biodiversity and ecosystem function (Jupiter *et al.* 2014). A complementary suite of fisheries management and conservation strategies (e.g., NTMRs, gear restrictions, catch limits) in conjunction with PHCs will likely be required to achieve these goals (Jupiter *et al.* 2017).

PHCs subject to highly intensive pulse fishing events that reduce more than 50% of standing fish stocks may take between 5-20 years to fully recover (Abesamis *et al.* 2014). Empirical evidence from PHCs in Fiji shows that 1 year of recovery is insufficient and at least 3 years of closure between harvests is recommended to restore fish abundance and biomass to pre-harvest levels (Goetze *et al.* 2016). Given the average closure time of study PHCs here was <2 years, it is unlikely that biomass within PHCs will recover to pre-harvest levels before the next harvest. This suggests that PHCs experiencing high harvest intensity may not be suitable as a long term fisheries management or conservation strategy for large, long lived taxa (Cohen & Foale 2013; Goetze *et al.* 2016). In order to improve the recovery potential within PHCs, harvest benefits may need to be restricted to ≤10% of the standing biomass (Abesamis *et al.* 2014), with harvest effort restricted to low vulnerability (fast growing and abundant) species and/or longer closure times between harvest events (Goetze *et al.* 2016). We observed post-harvest protection benefits for abundance and not biomass, which is likely due to the preferential targeting of larger fishes during harvests, generating a greater impact on biomass levels. The prompt removal of large individuals during harvests may reduce the reproductive output of PHCs and limit benefits of larval or adult spillover that are seen in NTMRs (Abesamis & Russ 2005; Halpern, Lester & Kellner 2009; Harrison *et al.* 2012).

Variability in post-harvest benefits of PHCs was primarily attributable to the size, age, compliance or outside fishing pressure, four key features shown to influence conservation benefits of NTMRs (Guidetti *et al.* 2008; McClanahan *et al.* 2009; Edgar *et al.* 2014). Limited PHC replicates meant we assessed the influence of these variables independently, nonetheless our findings are consistent with the NTMR literature (Claudet *et al.* 2008; Vandeperre *et al.* 2011; Edgar *et al.* 2014), where protection benefits of PHCs generally increased with size, years since establishment, time since the previous harvest and compliance with fishing restrictions. However, unlike NTMRs, PHCs have had a history of harvesting suggesting that periods of closure were providing some cumulative benefit. To assess protection benefits, PHC boundaries need to be large enough to incorporate adequate site replication. This resulted in the average size of PHCs assessed here (2.7 km^2) being larger than the average for the western Pacific (Govan 2009; Cohen & Foale 2013). This limitation coupled with our result of increasing benefits as the size of PHCs increase, suggests that larger PHCs need to be established. PHCs have also been promoted as an alternative to NTMRs due to greater compliance, yet our results suggest that pre-harvest protection and harvest benefits vary due to compliance, suggesting PHCs are not the solution to poor compliance with other management strategies. An increase in the size or age of PHCs also resulted in a greater harvest benefits, suggesting increased availability of fish stocks in larger, older PHCs generates greater yields during harvests. However, increased harvest benefits may also result from a failure to shut down harvests once pre-determined catch targets are achieved (Jupiter *et al.* 2012), emphasising the importance of setting and enforcing strict deadlines for the cessation of fishing within PHCs in order to prevent overfishing.

PHCs with high fishing pressure outside of their boundaries generally performed better in terms of benefits with increased abundance. Similar findings from studies comparing permanent reserves with fished areas suggest closures are most effective in areas where overfishing is occurring (Hart 2003; Hilborn *et al.* 2004; Gaines *et al.* 2010). In contrast, the same result was not evident with the biomass data which may relate to larger-bodied fish moving over larger areas (Nash *et al.* 2015) and being more likely to transcend PHC boundaries where they are susceptible to fishing. High fishing pressure outside of PHCs also resulted in a greater proportion of both the abundance and biomass being removed from the PHC during harvests. This is likely due to an increased reliance of the resources within PHCs in areas where fish stocks in open areas have already been depleted (Cohen, Cinner & Foale 2013). It is therefore important that communities with high levels of fishing or depleted fish stocks do not rely on PHCs as their sole form of management.

The effect of compliance on harvest benefits was inconsistent, with a greater proportion of biomass being removed where compliance was high and a greater proportion of abundance removed where compliance was low. Fishers typically target larger-bodied fish (Graham *et al.* 2005) and depletion of larger species within PHC boundaries where compliance is low reduces the biomass available at harvesting. Consequently, harvests in these PHC rely on catching a large number of smaller fish and have a greater impact on abundance than biomass. Similarly, the removal of larger individuals during harvest in areas where compliance was high would naturally have a greater impact on biomass than abundance. These finding support the theory that PHCs are most suitable for short lived, fast growing species (Cohen & Foale 2013; Goetze *et al.* 2016) and highlights the importance of examining life history traits in conjunction with recovery data (Cheung, Pitcher & Pauly 2005; Abesamis *et al.* 2014).

To adequately assess the conservation benefits of PHCs, a study design with a PHC and NTMR of comparable size, habitat and in the same locality is required. NTMRs are a valuable tool for assessing management strategies (Langlois, Harvey & Meeuwig 2012), and future research should focus on areas where both NTMR and PHCs occur. To assess long-term conservation and fisheries management objectives, temporal data through multiple harvest events and recovery trajectories will be required. Collecting such data is complicated by haphazard harvest schedules designed to meet the needs of communities rather than researchers, requiring considerable liaison with local communities.

We recommend future research focus on collecting data from an array of PHCs with different harvest histories and physical attributes, using the analytical framework outlined here to survey over multiple harvest events. Increasing study locations will improve capacity to assess interactions between covariates and understand their influence on harvest dynamics. Further studies that focus on post-harvest recovery and recovery of pre-harvest protection over standardised time scales such as Goetze *et al.* (2016), will provide valuable insight and recommendations for harvesting regimes. However, in Melanesia where PHCs are common, small-scale fisheries are often essential for livelihood, meaning these communities cannot afford such delays in management advice that may help sustain their fisheries. To overcome this issue, empirical data could be combined with population modelling to assess the potential of PHCs for long term sustainability of fish stocks and conservation (Carvalho *et al.* 2015). This would also allow for the assessment of long-term fisheries benefits and whether effort displacement following PHC implementation may lead to overharvesting in the nearby areas open to fishing, an issue that is currently in debate with rotational fisheries (Game *et al.* 2009; Kaplan, Hart & Botsford 2010; Plagányi *et al.* 2015a; b; Purcell *et al.* 2015).

Our results provide the first comprehensive synthesis of empirical data on the effectiveness of PHCs as a fisheries management and conservation strategy. Despite concerns over the long term value of PHCs, we found that they were capable of increasing fish stocks pre-harvest, indicating that abundance and biomass can accumulate within PHCs. Harvesting of PHCs, however, resulted in rapid decline of the fish stocks, suggesting fisheries and conservation benefits associated with protecting high biomass and abundance will fluctuate and may not be sustainable. To increase the build-up in fish stocks and maximise potential for long term benefits we recommend PHCs be closed to fishing for as long as possible, be as large as possible and compliance encouraged via community engagement and enforcement when necessary. When harvested, overfishing can be prevented by setting and not exceeding strict deadlines or goals.

Authors' contributions: This manuscript was developed during a workshop organised by JSG and TJL and attended by all authors. JSG completed the literature review, data selection/quality analysis. JSG and SDJ collected/analysed data from 5 of the 10 studies included in the meta-analysis. All authors worked on the statistical analysis under the guidance of JC. JSG, SDJ and RW wrote the first draft of the manuscript with all authors contributing to revisions. All authors gave final approval for publication.

Acknowledgments

This study was conducted with funding from the School of Plant Biology at The University of Western Australia (UWA) and grants (2012-38137, 2014-39332) to the Wildlife Conservation

Society (WCS) from the David and Lucile Packard Foundation. This manuscript was conceived during a workshop funded by the University of Western Australia, Oceans Institute as part of an Emerging Leaders Grant. We would like to thank Paul Iskov for his assistance during this workshop. RW acknowledges funding support from the Australian Research Council**.**

Data accessibility

Data associated with this paper is available as the “Fiji Periodically Harvested Closures Project” in the GlobalArchive repository at http://globalarchive.org/geodata/explore/ (Goetze *et al.* 2017).

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1: Single and combined search terms used in the literature review

Table S2: Methods, experimental design and species selection for each PHC study.

Table S3: Fishing pressure, compliance**,** harvest intensity for each PHC.

Table S4: Targeted/non-targeted species for each PHC.

Table S5: Correlations between moderators

Table S6: Results of tests for model heterogeneity for targeted species.

Table S7: Results of tests for model heterogeneity for non-targeted species.

Fig. S1: The influence of categorical co-variates on PHC benefits for non-targeted species.

Table 1: Benefit and assessment of individual or multiple PHCs. Benefits 1 to 3 were assessed in this manuscript.

Potential PHC benefit	Hypothesis	Effect size description	Effect size equation	Sampling
1. Pre-harvest protection	Abundance and biomass are greater inside PHCs compared to outside immediately prior to a harvest.	Ratio of inside to outside before harvests.	$E_b = Pb/Ob$	CI
2. Harvest	Harvests remove a larger proportion of the abundance and biomass within PHCs than outside.	Ratio of after to before in the PHC while controlling for change outside.	$E_h = (Pa/Pb)/(Oa/Ob)$	BACI
3. Post-harvest protection	Abundance and biomass remain greater inside PHCs compared to outside immediately after they are harvested.	Ratio of inside to outside after harvests.	$E_a = Pa/Oa$	CI
4. Post-harvest recovery	Abundance and biomass are greater inside PHCs compared to outside after a certain period of time after the prior harvest.	Ratio of inside to outside after a certain period of recovery.	$E_r = Pr/Or$	CI
5. Recovery of pre-harvest protection	Abundance and biomass within the PHCs after a certain period of time is equal to or greater than prior to the harvest.	Ratio of the PHC after a certain period of recovery to the PHC before the prior harvest while controlling for change outside.	$E_p = (Pr/Pb) / (Or/Ob)$	Multiple CI
6. Maintenance of post-harvest protection	Abundance and biomass within PHCs immediately after the subsequent harvest is equal to or greater than immediately after the prior harvest.	Ratio of the PHC after the subsequent harvest to the PHC after the prior harvest while controlling for change outside.	$E_m = (Pa_{n+1}/Oa_{n+1}) /(Pa_n/Oa_n)$	Multiple CI
7. Conservation	The pre-harvest protection benefit of PHCs is equal to or greater than the protection benefit of no-take marine reserves.	Ratio of inside to outside before harvests, relative to inside outside no-take areas (NTMR) in the same area.	$E_c = (Pb/Ob)/(NTMR/O)$	Beyond CI
8. Sustainability of periodic harvest practice	PHCs benefits are maintained or increased over the long term.	Slope of the above effect sizes over multiple harvest cycles.	$E_s = m$ where $Y = m*E_x + b$	BACIPS

CI: Control Impact; BACI: Before After Control Impact; BACIPS: Before After Control Impact Paired Series; Pb: PHC Before; Ob: Open Before; Pa: PHC after; Oa: Open After; Pr: PHC Recovery; Or: Open Recovery; O: Open; $E_x = E_b$, E_h, E_r, E_c *or* $f(E_{b \ldots c})$.

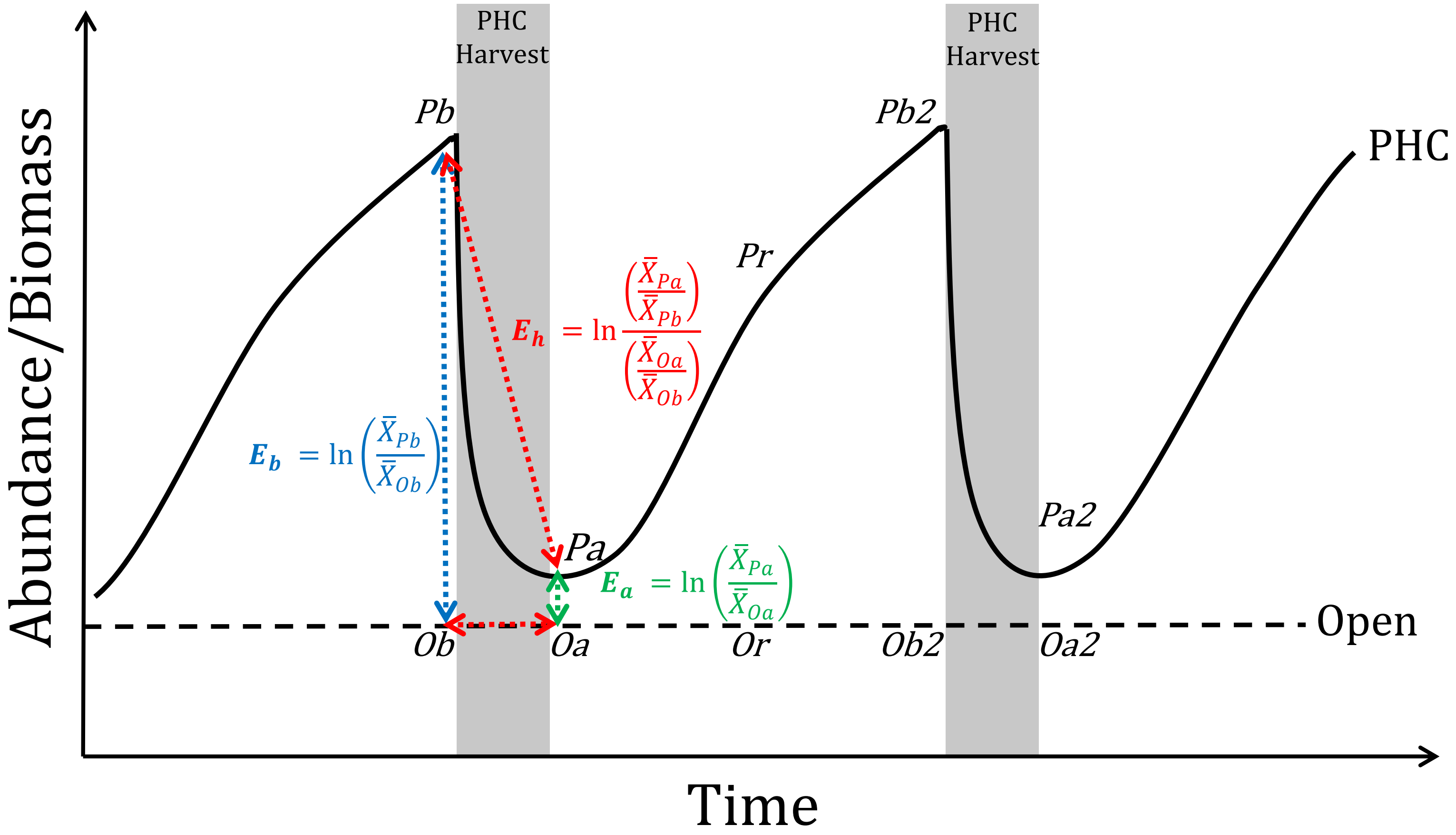
648 **Table 2:** PHC information and data source for each study case. NA = information not available.

PHC Name	**Country**	**PHC Size (km^2)**	**Years established**	**Compliance**	**Fishing pressure**	**Harvest Time (Days)**	**Harvest effort**	**Time closed when sampled (Years)**	**Historical Harvest Regime (at time of sampling)**	**Reference**
Nakodu	Fiji	0.73	3	High	Low	4	High	3	None since establishment	This study
Kia	Fiji	15.5	6	High	High	21	High	1	Once in six years	(Jupiter *et al.* 2012)
Kiobo	Fiji	2.07	3	Low	Low	7	Low	1	Once every year	(Goetze *et al.* 2015)
Tuatua	Fiji	1.34	8	High	Low	1	Low	0.25	Every three months	This study
Sumilon	Philippines	0.23	9.5	High	High	570	High	9.5	None since establishment	(Russ & Alcala 2003; Alcala *et al.* 2005)
Natokalau	Fiji	2.17	7	High	High	2	Low	1	Once a year for the last 2 years only	This study
Nauouo	Fiji	3.69	3	Low	High	3	Low	0.08	Twice in three years	This study
Muluk	Papua New Guinea	0.58	10	High	Low	NA	NA	0.5	Closed 2-3 times for 1-2 years over a	(Cinner *et al.* 2006)

									10 year time span	
Unakap	Vanuatu	0.14	5	High	Low	3	Low	0.5	Once every six months (not always for finfish)	(Januchowski-Hartley, Cinner & Graham 2014)
Laonamoa	Vanuatu	0.16	3	High	Low	3	Low	0.5	Once every 6 months	(Januchowski-Hartley, Cinner & Graham 2014)

Table 3: Quantification of PHC benefits using log-ratio effect size ($E_{b,a,h}$) and tests for total heterogeneity (*Qt*). Effect sizes with confidence intervals that do not overlap zero and/or significant tests for heterogeneity (P(Qt) < 0.05) are shown in bold.

Benefit	Group	Metric	E [95% CI]	Qt	P(Qt)	df
Pre-harvest protection	Targeted	Abundance	**E_b = 0.392 [0.111;0.673]**	**50.17**	**<0.0001**	9
		Biomass	**E_b = 0.654 [0.147;1.161]**	**113.63**	**<0.0001**	9
	Non-targeted	Abundance	E_b =-0.041 [-0.239;0.157]	**15.5891**	**0.029**	7
		Biomass	E_b =-0.0236 [-0.531;0.483]	**29.45**	**<0.001**	7
Harvest	Targeted	Abundance	**E_h = -0.239 [-0.471;-0.007]**	**18.51**	**0.018**	8
		Biomass	**E_h = -0.671 [-1.155;-0.187]**	**30.68**	**<0.001**	8
	Non-targeted	Abundance	E_h = -0.078 [-0.325;0.169]	12.56	0.083	7
		Biomass	E_h = -0.152 [-0.75;0.446]	**27.41**	**<0.001**	7
Post-harvest protection	Targeted	Abundance	**E_a = 0.134 [0.035;0.233]**	12.23	0.1414	8
		Biomass	E_a = 0.012 [-0.387;0.411]	**69.12**	**<0.0001**	8
	Non-targeted	Abundance	E_a = -0.129 [-0.448;0.19]	**45.07**	**<0.0001**	7
		Biomass	E_a = -0.07 [-0.518;0.378]	**52.72**	**<0.0001**	7


PHC Harvest
PHC Harvest
Pb
Pb2
PHC
Pr
$E_h = \ln \frac{\left(\frac{\bar{X}_{Pa}}{\bar{X}_{Pb}}\right)}{\left(\frac{\bar{X}_{Oa}}{\bar{X}_{Ob}}\right)}$
$E_b = \ln\left(\frac{\bar{X}_{Pb}}{\bar{X}_{Ob}}\right)$
Pa2
Pa
$E_a = \ln\left(\frac{\bar{X}_{Pa}}{\bar{X}_{Oa}}\right)$
Open
Ob
Oa
Or
Ob2
Oa2
Abundance/Biomass
Time

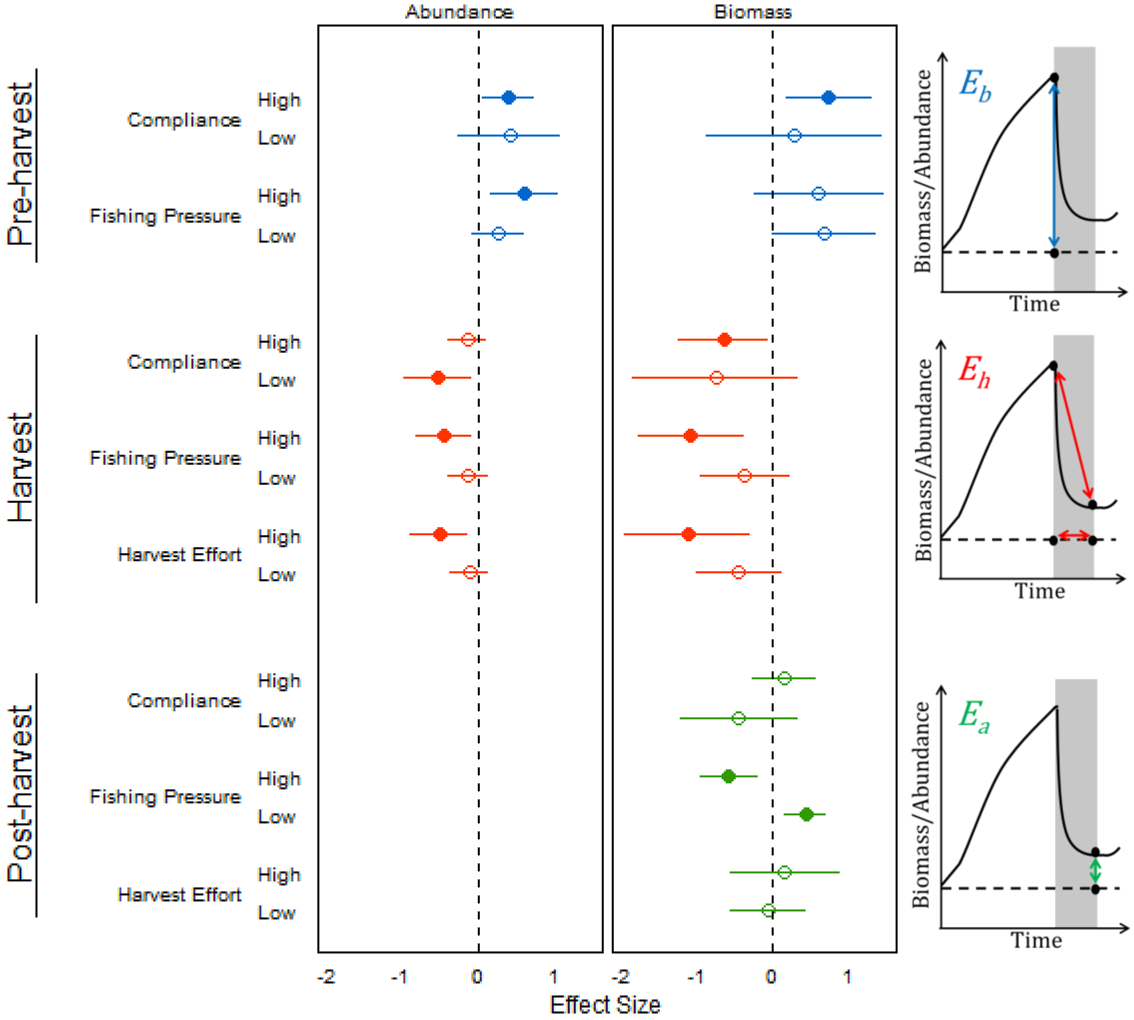

Abundance
Biomass
Pre-harvest
Harvest
Post-harvest
Compliance
Fishing Pressure
Harvest Effort
High
Low
-2
-1
0
1
Effect Size
E_b
E_h
E_a
Biomass/Abundance
Time

Table S1: Single and combined search terms used in the literature review

Single Terms	Combined Terms
Ra'ui	Periodically Harvested Closure
Bul	Customary Closure AND OR Reserve
Sasi	Marine Protected Area
Rahui	Community-based Closure AND OR Reserve
Raui	Rotational Closure
	Seasonal Closure
	Partially Closed
	Temporary Closure OR Reserve
	Periodic Fisheries Reserve
	Periodic Fisheries Closure
	Customary Marine Tenure
	Rotative Closure
	Tabu Area
	Taboo Area
	Tambu Area
	Opening No-take
	Removing No-take

Table S2: Methods, experimental design and species selection used at each PHC for each study.

PHC Name	Observation Method	Transect Dimensions	Depth (m)	Sites (Transects)		Target Species List	Non-Target Species List	Reference
				PHC	Open			
Nakodu	Stereo Diver Operated Video	50 x 5m Belt	1-3	3(6)	6(6)	Species caught during harvest (list below)	Species not caught during harvest (list below)	This study
Kia	UVC	50 x 5m Belt	5-8 and 12^{-1}5	4(10)	4(10)	Acanthuridae, Carangidae, Lethrinidae, Lutjanidae, Scaridae, Serranidae	Balistidae, Chaetodontidae, Pomacanthidae, Zanclidae	(Jupiter et al. 2012)
Kiobo	Stereo Diver Operated Video	50 x 5m Belt	5-8	2(6)	4(6)	Species caught during harvest (list below)	Species not caught during harvest (list below)	(Goetze et al. 2015)
Tuatua	Stereo Diver Operated Video	50 x 5m Belt	5-8	3(6)	6(6)	Species caught during harvest (list below)	Species not caught during harvest (list below)	This study
Sumilon	UVC	50 x 20m Belt	2^{-1}7	1(6)	3(2)	Serranidae, Lutjanidae, Lethrinidae and Carangidae	Not Assessed	(Russ and Alcala 2003, Alcala et al. 2005)
Natokalau	Stereo Diver Operated Video	50 x 5m Belt	5-8	6(6)	6(6)	Species caught during harvest (list below)	Species not caught during harvest (list below)	This study
Nauouo	Stereo Diver Operated Video	50 x 5m Belt	1-3	3(6)	6(6)	Species caught during harvest (list below)	Species not caught during harvest (list below)	This study
Muluk	UVC	50 x 5m Belt	3-7	3(5)	3(5)	Acanthuridae, Balistidae, Chaetodontidae, Haemulidae, Labridae ,Lethrinidae, Lutjanidae, Mullidae, Nemiteridae, Scaridae, Serranidae, Siganidae	Not Assessed	(Cinner et al. 2006b)
Unakap	UVC	50 x 5m Belt	5-8	1(8)	1(8)	All fish families of which more than one individual was caught during harvests	All remaining species (not specified)	(Januchowski-Hartley et al. 2014)
Laonamoa	UVC	50 x 5m Belt	5^{-1}0	1(8)	1(8)	All fish families of which more than one individual was caught during harvests	All remaining species (not specified)	(Januchowski-Hartley et al. 2014)

Table S3: The level of fishing pressure outside, compliance with the fishing restriction and intensity of the harvest within each PHC and the information used to determine each category.

PHC Name	Harvest Effort (CPUE; Duration; Gear)	Harvest Effort (Category)	Compliance (Raw data/Information)	Compliance (Category)	Fishing Pressure Outside (Raw data/Information)	Fishing Pressure Outside (Category)
Nakodu	3.7 fish person^{-1} h^{-1} (1.47 kg person^{-1} h^{-1}); 4 days; Spearfishing, hook/line and fish drive (net)	High	Infrequent offenses of management rules (Key informants)	High	No local boats or external boats sighted and no fishing licenses; 6.66 kg/person*hr	Low
Kia	Fished 24 hours a day for 21 days; Spearfishing and hook/line	High	Infrequent offenses of management rules (pre-harvest) (Key informants)	High	20 local boats across 3 villages, >10 external boats sighted per week and 16 licensed fishers	High
Kiobo	1.95 fish person^{-1} h^{-1} (1.6 kg person^{-1} h^{-1}); 7 days; Spearfishing and handlines	Low	Frequent breaches of management rules	Low	1 local boat, no external boats sighted and 4-5 licensed fishers; 0.46 kg/person*hr	Low
Tuatua	2.93 fish person^{-1} h^{-1} (0.8 kg person^{-1} h^{-1}); 1 day; Spearfishing and fish drive (net)	Low	Infrequent offenses of management rules (Key informants)	High	1 local boat, between 1-2 external boats observed each week and 1 licensed fisher	Low
Sumilon	570 days; Trap, gillnet, hook\line and spearfishing	High	Very good (R. Weeks Pers Comm)	High	~100 municipal fishers and subject to high fishing pressure	High
Natokalau	3.38 fish person^{-1} h^{-1} (1.03 kg person^{-1} h^{-1}); 2 days; Spearfishing, hook/line, gillnet	Low	Infrequent offenses of management rules (Key informants)	High	2 local boats, between 2-10 external boats observed each week and 2 licensed fishers,	High
Nauouo	2.44 fish person^{-1} h^{-1} (0.58 kg person^{-1} h^{-1}); 3 days; Spearfishing and hook/line	Low	Frequent breaches of management rules (Key informants)	Low	No local boats, between 2-10 external boats observed each week and 1 licensed fisher; 5.55 kg/person*hr	High
Muluk	NA	NA	High (91% reported few or no people) (Cinner et al. 2006)	High	2.1 trips/ha/week	Low
Unakap	4.57 fish person^{-1} h^{-1}, 2.5kg person^{-1} h^{-1}); 3 days; Spearfishing and hook/line	Low	Very good (F. Januchowski-Hartley Pers Comm)	High	~ 1.6 trips/ha/week or 6.67 fishers/km reef	Low
Laonamoa	4.8 fish person^{-1} h^{-1}, 4 12kg person^{-1} h^{-1}); 3 days; Spearfishing	Low	Very good F. Januchowski-Hartley Pers Comm	High	~5.6 trips/ha/week or 10.8 fishers/km reef	Low

Table S4: Targeted/non-targeted species (and their families) for each PHC in the unpublished data.

Nakodu Targeted Species	Nakodu Non-Target Species	Kiobo Target Species	Kiobo Non-Target Species	Natokalau Target Species	Natokalau Non-Target Species	Nauouo Target Species	Nauouo Non-Target Species	Tuatua Target Species	Tuatua Non-Target Species
Acanthuridae *Acanthurus auranticavus* *Acanthurus lineatus* *Acanthurus nigricauda* *Acanthurus nigrofuscus* *Acanthurus pyroferus* *Acanthurus triostegus* *Ctenochaetus striatus* *Naso unicornis* *Zebrasoma scopas* Balistidae *Balistapus undulatus* *Sufflamen chrysopterum* Chaetodontidae *Chaetodon auriga* *Chaetodon ephippium* *Chaetodon lunulatus* *Chaetodon plebeius* *Chaetodon trifascialis*	Acanthuridae *Acanthurus thompsoni* *Ctenochaetus binotatus* Chaetodontidae *Chaetodon baronessa* *Chaetodon bennetti* *Chaetodon citrinellus* *Chaetodon lineolatus* *Chaetodon lunula* *Chaetodon melannotus* *Chaetodon pelewensis* *Chaetodon rafflesii* *Chaetodon ulietensis* *Heniochus chrysostomus* *Heniochus varius* Cirrhitidae *Paracirrhites arcatus* Labridae *Anampses melanurus*	Acanthuridae *Acanthurus lineatus* *Acanthurus nigricauda* *Ctenochaetus striatus* *Naso lituratus* *Naso unicornis* Haemulidae *Plectorhinchus chaetodonoides* Labridae *Cheilinus undulatus* Lethrinidae *Lethrinus obsoletus* *Monotaxis grandoculis* Lutjanidae *Lutjanus bohar* *Lutjanus ehrenbergii* *Lutjanus fulvus* *Lutjanus gibbus* *Lutjanus semicinctus*	Acanthuridae *Acanthurus nigrofuscus* *Acanthurus nigroris* *Acanthurus pyroferus* *Ctenochaetus binotatus* *Ctenochaetus tominiensis* *Zebrasoma scopas* Aulostomidae *Aulostomus chinensis* Balistidae *Balistapus undulatus* *Balistoides viridescens* *Sufflamen bursa* *Sufflamen chrysopterum* *Sufflamen fraenatum* Chaetodontidae *Chaetodon baronessa* *Chaetodon bennetti* *Chaetodon citrinellus*	Acanthuridae *Acanthurus nigricauda* *Acanthurus olivaceus* *Ctenochaetus striatus* *Zebrasoma veliferum* Balistidae *Balistapus undulatus* *Rhinecanthus aculeatus* Labridae *Hemigymnus melapterus* Lethrinidae *Lethrinus atkinsoni* *Lethrinus harak* *Lethrinus xanthochilus* *Monotaxis grandoculis* Lutjanidae *Lutjanus ehrenbergii* *Lutjanus fulvus* *Lutjanus gibbus*	Acanthuridae *Acanthurus nigrofuscus* *Acanthurus nigroris* *Acanthurus pyroferus* *Acanthurus triostegus* *Zebrasoma scopas* Balistidae *Rhinecanthus rectangulus* *Sufflamen chrysopterum* *Sufflamen fraenatum* Chaetodontidae *Chaetodon auriga* *Chaetodon citrinellus* *Chaetodon ephippium* *Chaetodon lineolatus* *Chaetodon lunulatus* *Chaetodon melannotus* *Chaetodon plebeius* *Chaetodon ulietensis*	Acanthuridae *Acanthurus nigricauda* *Acanthurus xanthopterus* *Ctenochaetus striatus* *Naso lituratus* Balistidae *Balistapus undulatus* Chaetodontidae *Chaetodon ephippium* *Chaetodon oxycephalus* Labridae *Cheilinus trilobatus* *Epibulus insidiator* *Oxycheilinus digrammus* *Thalassoma lunare* Lethrinidae *Monotaxis grandoculis* Lutjanidae *Lutjanus fulvus*	Acanthuridae *Acanthurus nigrofuscus* *Acanthurus nigroris* *Acanthurus pyroferus* *Acanthurus triostegus* *Zebrasoma scopas* *Aulostomus chinensis* Balistidae *Sufflamen bursa* *Sufflamen chrysopterum* Chaetodontidae *Chaetodon auriga* *Chaetodon baronessa* *Chaetodon bennetti* *Chaetodon citrinellus* *Chaetodon kleinii* *Chaetodon lineolatus* *Chaetodon lunula* *Chaetodon lunulatus*	Acanthuridae *Acanthurus lineatus* *Acanthurus nigricauda* *Acanthurus olivaceus* *Ctenochaetus striatus* *Naso lituratus* *Naso unicornis* *Zebrasoma scopas* *Zebrasoma veliferum* Labridae *Anampses neoguinaicus* Lethrinidae *Monotaxis grandoculis* Mullidae *Mulloidichthys vanicolensis* *Parupeneus crassilabris* *Parupeneus cyclostomus* *Parupeneus multifasciatus* Scaridae	Acanthuridae *Acanthurus nigrofuscus* *Acanthurus nigroris* *Acanthurus pyroferus* Balistidae *Balistapus undulatus* *Sufflamen chrysopterum* Chaetodontidae *Chaetodon auriga* *Chaetodon baronessa* Chaetodon bennetti *Chaetodon citrinellus* *Chaetodon ephippium* Chaetodon lineolatus *Chaetodon lunula* *Chaetodon lunulatus* *Chaetodon melannotus* *Chaetodon mertensii* *Chaetodon pelewensis*

Chaetodon vagabundus
Cirrhitidae
Paracirrhites forsteri
Holocentridae
Neoniphon sammara
Sargocentron spiniferum
Labridae
Anampses caeruleopunctatus
Cheilinus chlorourus
Cheilinus trilobatus
Coris aygula
Coris gaimard
Epibulus insidiator
Gomphosus varius
Halichoeres hortulanus
Hemigymnus fasciatus
Hemigymnus melapterus
Hologymnosus annulatus

Anampses meleagrides
Anampses neoguinaicus
Anampses twistii
Bodianus mesothorax
Halichoeres marginatus
Halichoeres melanochir
Halichoeres melanurus
Halichoeres nigrescens
Halichoeres prosopeion
Halichoeres trimaculatus
Labrichthys unilineatus
Labroides bicolor
Labroides dimidiatus
Labropsis australis
Stethojulis strigiventer
Thalassoma amblycephalum
Thalassoma hardwicke
Thalassoma jansenii

Mullidae
Parupeneus barberinus
Parupeneus cyclostomus
Ostraciidae
Ostracion cubicus
Scaridae
Chlorurus sordidus
Scarus dimidiatus
Scarus frenatus
Scarus ghobban
Scarus oviceps
Scarus psittacus
Scarus rivulatus
Scarus schlegeli
Serranidae
Cephalopholis argus
Epinephelus merra
Epinephelus polyphekadion

Chaetodon ephippium
Chaetodon kleinii
Chaetodon lineolatus
Chaetodon lunula
Chaetodon lunulatus
Chaetodon melannotus
Chaetodon oxycephalus
Chaetodon pelewensis
Chaetodon plebeius
Chaetodon rafflesii
Chaetodon semeion
Chaetodon speculum
Chaetodon ulietensis
Chaetodon unimaculatus
Chaetodon vagabundus
Forcipiger flavissimus
Heniochus chrysostomus
Heniochus monoceros

Lutjanus semicinctus
Mullidae
Mulloidichthys flavolineatus
Parupeneus barberinus
Parupeneus cyclostomus
Parupeneus indicus
Parupeneus multifasciatus
Scaridae
Chlorurus sordidus
Scarus ghobban
Scarus rivulatus
Scarus schlegeli
Serranidae
Epinephelus merra
Epinephelus polyphekadion
Siganus doliatus

Chaetodon unimaculatus
Chaetodon vagabundus
Heniochus chrysostomus
Cirrhitidae
Paracirrhites forsteri
Fistulariidae
Fistularia commersonii
Labridae
Anampses caeruleopunctatus
Anampses neoguinaicus
Cirrhilabrus punctatus
Gomphosus varius
Halichoeres nebulosus
Halichoeres nigrescens
Halichoeres prosopeion
Halichoeres spp
Halichoeres trimaculatus
Labrichthys unilineatus

Lutjanus semicinctus
Mullidae
Parupeneus cyclostomus
Parupeneus multifasciatus
Pomacanthidae
Pygoplites diacanthus
Scaridae
Chlorurus bleekeri
Chlorurus microrhinos
Chlorurus sordidus
Scarus dimidiatus
Scarus prasiognathos
Scarus rivulatus
Scarus schlegeli
Serranidae
Epinephelus merra

Chaetodon melannotus
Chaetodon pelewensis
Chaetodon plebeius
Chaetodon rafflesii
Chaetodon trifascialis
Chaetodon ulietensis
Chaetodon unimaculatus
Chaetodon vagabundus
Heniochus chrysostomus
Heniochus varius
Cirrhitidae
Paracirrhites forsteri
Labridae
Anampses caeruleopunctatus
Anampses neoguinaicus
Bodianus mesothorax
Coris gaimard
Gomphosus varius

Cetoscarus bicolor
Chlorurus bleekeri
Chlorurus sordidus
Scarus chameleon
Scarus frenatus
Scarus niger
Scarus psittacus
Scarus rivulatus
Scarus schlegeli
Siganidae
Siganus argenteus

Chaetodon plebeius
Chaetodon rafflesii
Chaetodon reticulatus
Chaetodon trifascialis
Chaetodon ulietensis
Chaetodon unimaculatus
Chaetodon vagabundus
Forcipiger flavissimus
Forcipiger longirostris
Heniochus chrysostomus
Heniochus monoceros
Heniochus varius
Cirrhitidae
Paracirrhites arcatus
Paracirrhites forsteri
Labridae
Anampses caeruleopunctatus
Anampses meleagrides

Novaculichthys taeniourus

Lethrinidae
Lethrinus atkinsoni

Monotaxis grandoculis

Lutjanidae
Lutjanus ehrenbergii

Lutjanus fulvus
Lutjanus gibbus

Mullidae
Mulloidichthys flavolineatus
Mulloidichthys vanicolensis
Parupeneus barberinus
Parupeneus crassilabris
Parupeneus cyclostomus
Parupeneus indicus
Parupeneus multifasciatus
Parupeneus pleurostigma

Scaridae
Cetoscarus bicolor
Chlorurus microrhinos
Chlorurus sordidus

Thalassoma lunare

Monacanthidae
Cantherhines pardalis
Oxymonacanthus longirostris

Nemipteridae
Scolopsis bilineata

Pomacanthidae
Centropyge bicolor

Centropyge flavissima
Pygoplites diacanthus

Plectropomus laevis
Plectropomus leopardus
Plectropomus pessuliferus

Siganidae
Siganus argenteus
Siganus doliatus

Siganus stellatus

Heniochus singularius
Heniochus varius

Cirrhitidae

Paracirrhites arcatus

Labridae

Anampses caeruleopunctatus
Anampses geographicus
Anampses meleagrides
Anampses neoguinaicus
Bodianus mesothorax
Cirrhilabrus punctatus
Gomphosus varius
Halichoeres prosopeion
Labrichthys unilineatus
Labroides bicolor
Labroides dimidiatus
Labroides pectoralis
Labropsis australis
Pseudocoris yamashiroi
Stethojulis strigiventer
Thalassoma hardwicke

Labroides dimidiatus
Novaculichthys taeniourus
Pseudocheilinus evanidus

Stethojulis bandanensis
Stethojulis strigiventer
Thalassoma hardwicke

Thalassoma lunare

Nemipteridae

Scolopsis bilineata
Scolopsis trilineata

Pomacanthidae
Centropyge bicolor
Centropyge bispinosa
Centropyge flavissima
Pygoplites diacanthus

Tetraodontidae
Canthigaster valentini

Zanclidae
Zanclus cornutus

Halichoeres chrysus
Halichoeres hortulanus
Halichoeres marginatus

Halichoeres melanochir
Halichoeres nigrescens
Halichoeres trimaculatus

Labrichthys unilineatus
Labroides bicolor

Labroides dimidiatus
Macropharyngodon negrosensis
Novaculichthys taeniourus
Stethojulis strigiventer
Stethojulis trilineata
Thalassoma hardwicke
Thalassoma jansenii

Monacanthidae

Amanses scopas
Cantherhines dumerilii
Oxymonacanthus longirostris

Nemipteridae
Scolopsis bilineata

Anampses twistii
Bodianus anthioides
Bodianus mesothorax

Cirrhilabrus punctatus

Coris gaimard
Gomphosus varius

Halichoeres chrysus
Halichoeres marginatus

Halichoeres nigrescens
Halichoeres prosopeion
Halichoeres trimaculatus
Labrichthys unilineatus
Labroides bicolor
Labroides dimidiatus
Labropsis australis
Novaculichthys taeniourus
Pseudodax moluccanus
Stethojulis bandanensis
Stethojulis strigiventer
Thalassoma hardwicke
Thalassoma jansenii

Hipposcarus longiceps *Scarus chameleon* *Scarus dimidiatus* *Scarus forsteni* *Scarus frenatus* *Scarus ghobban* *Scarus globiceps* *Scarus niger* *Scarus oviceps* *Scarus prasiognathos* *Scarus psittacus* *Scarus rivulatus* *Scarus rivulatus* *Scarus schlegeli* *Scarus spinus* Serranidae *Epinephelus merra* Siganidae *Siganus argenteus* *Siganus spinus*	*Thalassoma jansenii* *Thalassoma lunare* Monacanthidae *Cantherhines dumerilii* Nemipteridae *Scolopsis bilineata* Pinguipedidae *Parapercis hexophtalma* Pomacanthidae *Centropyge bicolor* *Centropyge bispinosa* *Centropyge flavissima* *Pygoplites diacanthus* Tetraodontidae *Canthigaster valentini* Zanclidae *Zanclus cornutus*	*Scolopsis trilineata* Pomacanthidae *Centropyge bicolor* *Centropyge bispinosa* *Centropyge flavissima*	*Thalassoma lunare* *Thalassoma lutescens* Monacanthidae *Amanses scopas* Cantherhines dumerilii *Oxymonacanthus longirostris* Nemipteridae *Scolopsis bilineata* Pinguipedidae Parapercis hexophtalma Pomacanthidae *Centropyge bicolor* *Centropyge bispinosa* *Centropyge flavissima* *Pygoplites diacanthus* Zanclidae *Zanclus cornutus*

Table S5: Pearson's (ρ), Cramer's V (*V*) and Intra-class (*IC*) correlations between moderators

	Compliance	Fishing Pressure Outside	PHC Harvest Effort	Size	Time Closed	Years Established
Compliance	-					
Fishing Pressure Outside	0.102 (*V*)	-				
PHC Harvest Effort	0.378 (*V*)	0.316 (*V*)	-			
Size	-0.451 (*IC*)	0.268 (*IC*)	0.076 (*IC*)	-		
Time Closed	-0.226 (*IC*)	0.025 (*IC*)	0.525 (*IC*)	-0.175 ($\boldsymbol{\rho}$)	-	
Years Established	0.382 (*IC*)	-0.168 (*IC*)	-0.13 (*IC*)	-0.046 ($\boldsymbol{\rho}$)	0.376 ($\boldsymbol{\rho}$)	-

Table S6: Results of tests for model heterogeneity for targeted species (* < 0.05, ** < 0.01, *** < 0.001 or "–" = not significant). Results are only shown if tests for total heterogeneity (*Qt*) were significant (see Table 1).

Benefit	Metric	Compliance	Fishing Pressure Outside	PHC Harvest Effort	Size	Time Closed	Years Established
Pre-harvest protection	Abundance	-	-	Not Relevant	-	***	*
	Biomass	-	-	Not Relevant	**	-	-
Harvest	Abundance	-	-	-	**	*	-
	Biomass	-	-	-	***	-	*
Post-harvest protection	Biomass	-	***	-	-	-	-

Table S7: Results of tests for model heterogeneity for non-targeted species (* < 0.05, ** < 0.01, *** < 0.001 or "–" = not significant). Results are only shown if tests for total heterogeneity (*Qt*) were significant (see Table 1).

Benefit	Metric	Compliance	Fishing Pressure Outside	PHC Harvest Effort	Size	Time Closed	Years Established
Pre-harvest protection	Abundance	-	-	Not Relevant	-	-	-
	Biomass	-	-	Not Relevant	-	-	-
Harvest	Biomass	-	-	-	*	-	-
Post-harvest protection	Abundance	-	-	-	-	-	-
	Biomass	-	-	*	-	-	-

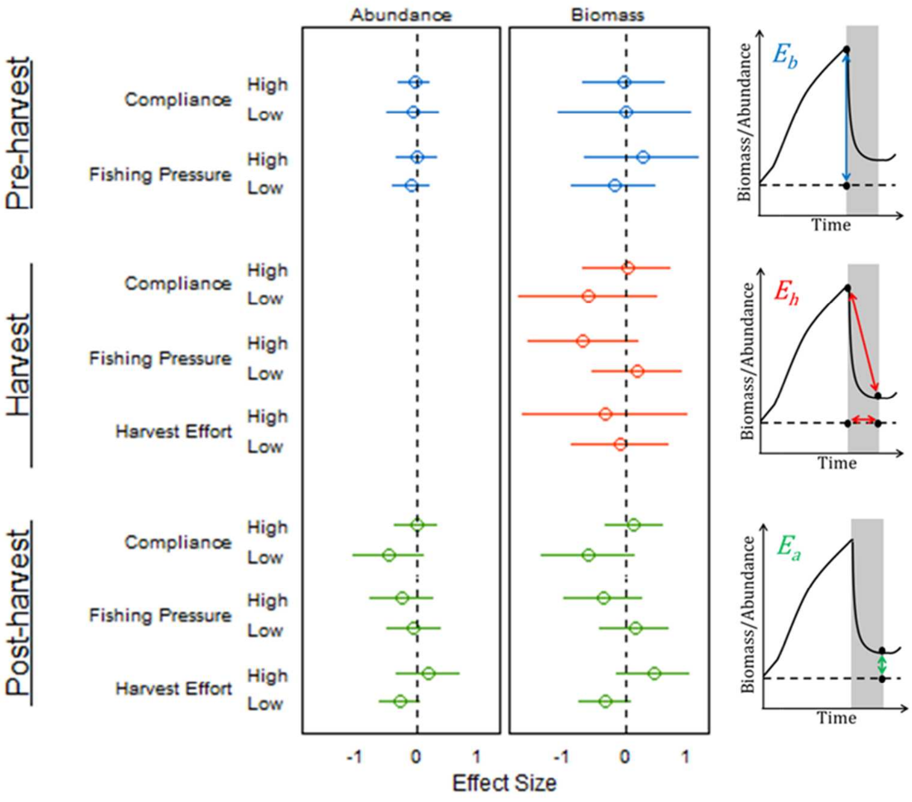


Fig. S1: The influence of categorical co-variates on PHC pre-harvest, harvest and post-harvest benefits for non-targeted species abundance and biomass. Conceptual diagrams showing the effect size calculations are displayed on the left for the pre-harvest E_b (blue), harvest E_h (red) and post-harvest E_a (green). Open circles represent results where the 95% confidence interval of the effect size does not overlap zero.