AN ABSTRACT OF THE THESIS of Steven M. Johnson for the Master of Science in Biology presented, July 14, 2017

Title: Marine protected areas as linked social-ecological systems

Approved: Peter Houk

Peter C. Houk, Chair, Thesis Committee

Marine ecosystems have become increasingly impacted and the coastal communities that rely upon them are continuously adapting to these changes. A key to understanding these social-ecological systems is identifying the components of social structure that support desirable feedback loops, and are most responsible for conservation success. Using the island of Yap, Micronesia as a case study, we implemented a paired social-ecological design to assess the social structure of villages with marine protected areas (MPAs). Structured surveys and open-ended questionnaires were conducted with community representatives from MPAs that had a corresponding ecological monitoring station to characterize the underlying social structure. Surveys of fish assemblages were conducted to measure the ecological outcomes in MPAs; a suite of non-MPA reefs were surveyed as reference sites and used to measure the footprint of human resource use. We report that villages with indicators for social cohesion were linked to MPAs with greater positive ecological outcomes compared to villages that were structured solely around strong leadership and enforcement. Sites with the poorest performing MPAs lacked strong leadership and physical MPA features (e.g., boundary markers and signboards). The site with high levels of social cohesion contained greater total fish biomass, herbivore biomass, and mean fish length relative to reference sites compared with other clusters. We found that fish assemblages in non-MPAs and low-performing MPAs were described by a human footprint. Channel and inner-reef fish assemblages decreased with increased village and commercial fishing pressure, while outer reef fish assemblages decreased with increasing village fishing pressure and decreasing wave energy. Altogether, human proximity was a strong predictor of fish assemblage condition. Successful ecological outcomes in Yap were linked to an underlying social structure characterized by positive attributes for governance and social cohesion. Local management groups, key individuals, and high levels of enforcement were the most important aspects of governance. In turn, these positive governance features were associated with beneficial MPA infrastructure, such as public signboards and boundary markers. While strong governance has previously been linked with successful management and conservation, the present results suggested that social cohesion could play an equal or even greater role. Addressing management in areas where leadership or social cohesion was lacking may be an important next step in advancing conservation. Ultimately, supporting policies that account for these key social structure features will lead to improved fisheries management and greater social-ecological resilience.

TO THE OFFICE OF GRADUATE STUDIES

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# MARINE PROTECTED AREAS AS LINKED SOCIAL-ECOLOGICAL SYSTEMS

BY

**Steven M. Johnson**

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Lastly, I dedicate this thesis in memory of Jesse Googdow, a champion of conservation in Micronesia. May his spirit perpetuate through all of us who call these islands home.

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## Introduction

Human communities and ecosystems are inexorably linked. These social-ecological systems are linked; human actions alter the ecosystem state, which in turn modifies the goods and services communities may receive (Berkes et al. 2000). Marine ecosystems have become increasingly impacted, with an estimated 20% of coral reef area (50,000 km$^2$) already lost, with the remainder likely to be threatened or lost by 2050 (Halpern et al. 2008, Wilkinson 2008, Burke et al. 2011). Coastal communities are adapting to these changes by implementing and reviving management practices that support social-ecological resilience (Marshall et al. 2010, Kittinger et al. 2014, Anthony et al. 2015). Social-ecological resilience is the capacity of a system to absorb ecological changes that arise from socioeconomic utilization, while retaining essential ecosystem function and services (Walker et al. 2004). Social-ecological resilience is integral to many forms of traditional management where societal wellbeing is linked with sustainable resource use (Johannes 1981, Foale et al. 2011). Modern examples of social-ecological resilience often blend “traditional” and “western” management polices (Berkes et al. 1991). However, a key to building social-ecological resilience is understanding which components of social systems support desirable feedback loops between society and ecosystems, and are most responsible for conservation success (Norström et al. 2016).

### *Coral reefs as social-ecological systems*

Biophysical environments and social systems have typically been viewed as disparate drivers of ecosystem dynamics (Colgan 1987, Hughes 1989, Edinger et al. 1998). Conversely, a social-ecological systems (SES) framework appreciates feedback loops between environmental and social factors (Redman et al. 2004). The prevailing SES framework  emphasizes that humans are central participants in the system, making conscious decisions with tangible environmental outcomes (Ostrom 2007, 2009). These environmental outcomes then serve as feedback to the society, and used to inform management actions (Cinner et al. 2006, Heber Dunning 2014).

Coral reefs and coastal societies typify a social-ecological system (Johannes 1978, 2002, Kittinger et al. 2012). High ranking chiefs throughout Melanesia manage fishing grounds by restricting harvesting to increase yields for cultural and socio-political needs (Ruddle et al. 1992). On the atoll of Satawal in Micronesia, socio-political management responsibilities are divvied among chiefs, with one chief assuming the role of "chief of the sea" (Tafileichig and Inoue 2001). This chief manages special areas (seamounts, uninhabited atolls) that are set aside for special feasts, such as the death of an important member of the community. Furthermore, the Palauan *bul* system was traditionally implemented to prohibit fishing during grouper (Serranidae) spawning aggregations (Johannes 1978). Restricting fishing during this biologically sensitive event sustained grouper populations for generations. The *bul* system remains a component of modern co-management strategies to increase support for ongoing conservation by fostering cultural and national pride (Kleiber and Koshiba 2014).

Longer-term stability of these practices is dependent on both the social and ecological outcomes. Cinner et al. (2006) showed that periodic closures in Papua New Guinea provided not only increased fish biomass in closures, but also increased catch success outside of closures. These positive biological and social responses resulted in a stable SES. Elsewhere, periodically harvested MPAs provided minimal benefits to communities where open-access, market driven economies existed and high levels of enforcement are needed (Williams et al. 2006). These results suggest that social-ecological outcomes are context dependent and not specific to any particular management action. Thus, the success or failure of a SES depends greatly on the level of connectivity within social systems (Aswani and Hamilton 2004, Gutiérrez et al. 2011).

### ***Marine protected areas as linked SES***

Marine protected areas (MPAs) are spatially defined areas that are set aside for fisheries management, conservation of biodiversity, or the preservation of cultural and historical features (Gubbay 1995, Graham et al. 2011). MPAs remain a key component of fisheries management globally (Russ et al. 2004, Christie and White 2007, Ban et al. 2011). Restricting or limiting fishing activities has been employed by many cultures for centuries through traditional forms of management and tenure (Ruddle et al. 1992, Johannes 2002b). The benefits of successful fisheries management go beyond food security (McClanahan et al. 2015), they also serve to strengthen cultural identity (Cinner 2014). However, tractable fishery benefits require adequate time (Roberts et al. 2001, Gell and Roberts 2003). Long-term benefits such as spillover from MPA to fished areas (Stobart et al. 2009) and increased breeding stocks (Taylor et al. 2012) are documented from functioning MPAs, but require longer term protection (16 – 20 years). The success or failure of MPAs is highly dependent on socioeconomic conditions (Arias et al. 2015, Gallacher et al. 2016) such as community participation in decision-making and a perceived reduction in fish populations (Pollnac et al. 2001). Because MPAs are ubiquitous and have a rich history of documentation, they serve as ideal models to evaluate which attributes of social-ecological systems facilitate success. In turn, identifying these attributes can help advance our understanding of conservation success.

### ***Ecological outcomes of marine protected areas***

Increased fish density, size, biomass, and reproductive output of target species are ecological outcomes linked to improving the social value of resources (Bohnsack 1990). Numeric density and biomass of fishes within reserves increase quickly after MPA establishment (as little as two years), but the mean size of fishes increases at a slower rate (Halpern and Warner 2002). Williams et al. (2016) documented the biological response of parrotfishes and surgeonfishes to protection in a fish reserve in Hawaii and found biomass increases of 139% and 28%, respectively, over a six-year period. However, large-bodied individuals were scarce before and during the study, suggesting minimal, but continuous, levels of poaching of individuals with the highest market value and slowest growth rates. In Kenya, McClanahan et al. (2007) documented the ecological succession of fish community recovery over 37 years. Young MPAs (<15 years), were most beneficial to labrid fishes, while older MPAs, or longer protection, yielded the greatest returns for surgeonfishes. Similarly, Russ and Alcala (2004) found that biomass of large predatory fishes took from 15 – 40 years to recover in the Philippines. In summary, both biological constraints such as growth rates and social factors such as market demand are correlated with the ecological outcomes of MPAs.

Successful MPAs eventually produce a spillover effect where individuals from within MPA boundaries move to adjacent fishable waters. Russ and Alcala (1996) found significant increases in the number of fishes 200 – 300 m outside of MPA borders at Apo Island, Philippines. These increases, however, took 8 – 10 years to develop and were most pronounced near the reserve. Furthermore, in continued monitoring of the MPA at Apo Island, Russ et al. (2004) documented a tripling of fish biomass within the reserve boundaries. While a significant biomass increase was absent in fished areas, total catch (biomass) and catch-per-unit-effort both increased. This suggests that spillover of individuals from the reserve provided fishermen with socioeconomic benefits.

### ***Linked social-ecological systems in Yap, Micronesia***

This study will use the social-cultural setting of Yap Island, Federated States of Micronesia, as a lens to observe a coral reef SES. Yap presents an ideal setting for SES research because customary marine tenure is still the paramount form of marine resource management. Yap is undergoing a socio-cultural renaissance by integrating Western design principles for MPAs into the traditional management system. Most importantly, the customary marine tenure system dictates that each village owns and manages its resources, granting access solely to members of the village. This allows for a controlled evaluation of the SES at the village-level, where resource use and management occur. Lessons learned from Yap can therefore provide valuable insight to management solutions for MPAs and social-ecological systems at large.

### *Study aims and scope of work*

The present thesis: 1) created management groups based upon MPA characteristics and social factors; 2) provided a quantitative evaluation of MPAs; 3) determined which management and social characteristics were related to MPA performance; 4) determined which management characteristics and social factors were associated with successful MPAs; and 5) holistically assessed reefs outside the local network of MPAs to determine the extent to which social perception predicted ecological trends. The following hypotheses were tested to fulfill these goals:

$H0_1$: Social-ecological indicators for governance, livelihoods and cultural norms do not differ among marine conservation areas based upon interviews of key informants.

$H0_2$: Food-fish assemblage metrics do not differ between MPA clusters based upon standardized ecological fish survey data (contingent on $H0_1$).

$H0_3$: MPA performance measures of food-fish assemblage metrics do not correlate with social clustering (conditional on $H0_1$).

$H0_4$: MPA characteristics or social factors act similarly to predict MPA performance measures of food-fish assemblage metrics within respondent clusters (conditional on $H0_1$).

$H0_5$: Social perception of food-fish abundance outside of MPAs is correlated with ecological trends in food fish biomass along gradients of human footprints (i.e., proxies to fishing and pollution).

## Methods:

### *Study Area*

The islands of the Federated States of Micronesia (FSM) have highly diverse coral reefs that support the economic and cultural well-being of over 100,000 people (The Nature Conservancy 2003). Coral reef resources are an integral aspect of the day-to-day life and cultural identity of these people. Yap State is the westernmost state in the FSM. It is located approximately 800 km southwest of Guam, 480 km northeast of Palau, and 1300 km due east of the Philippines (Fig. 1). The state is comprised of four closely associated high islands, collectively known as *Wa'ab*, or "Yap proper", and 134 low-lying atolls, referred to as the outer islands or *Remethau*. In all, Yap State covers a land area of only 128 $km^2$ but a total area of approximately 600,000 $km^2$. The population of Yap State is 11,377, with a majority of those people living on Yap proper. Yap proper has 10 municipalities, which contain 134 villages, with varying degrees of fishing activity and gear use. Within these municipalities and villages, there are nine MPAs; this study uses data from five MPAs where both social and ecological data were collected (Table 1).

The islands of Yap State have some of the most intact customary marine tenure across Micronesia (Goldman 1994), making it the focus of several academic inquiries (Smith 1991, Dodson and Intoh 1999). The Constitution of Yap State considers chiefs to be the upholders of Yapese custom. With respect to marine resources, the Constitution states, "The State recognizes traditional rights and ownership of natural resources and areas within the marine space of the State, within and beyond 12 miles from the island baselines.

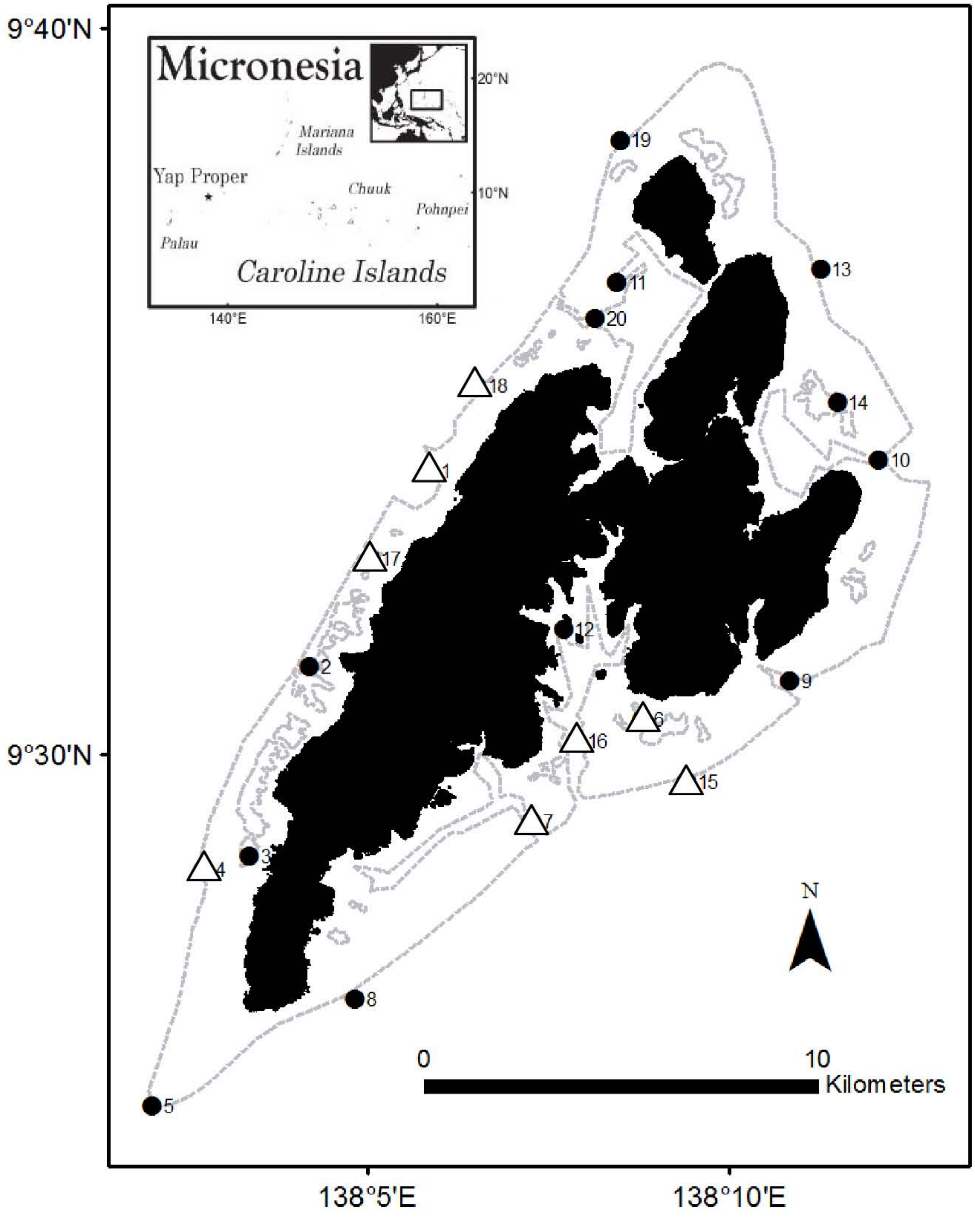
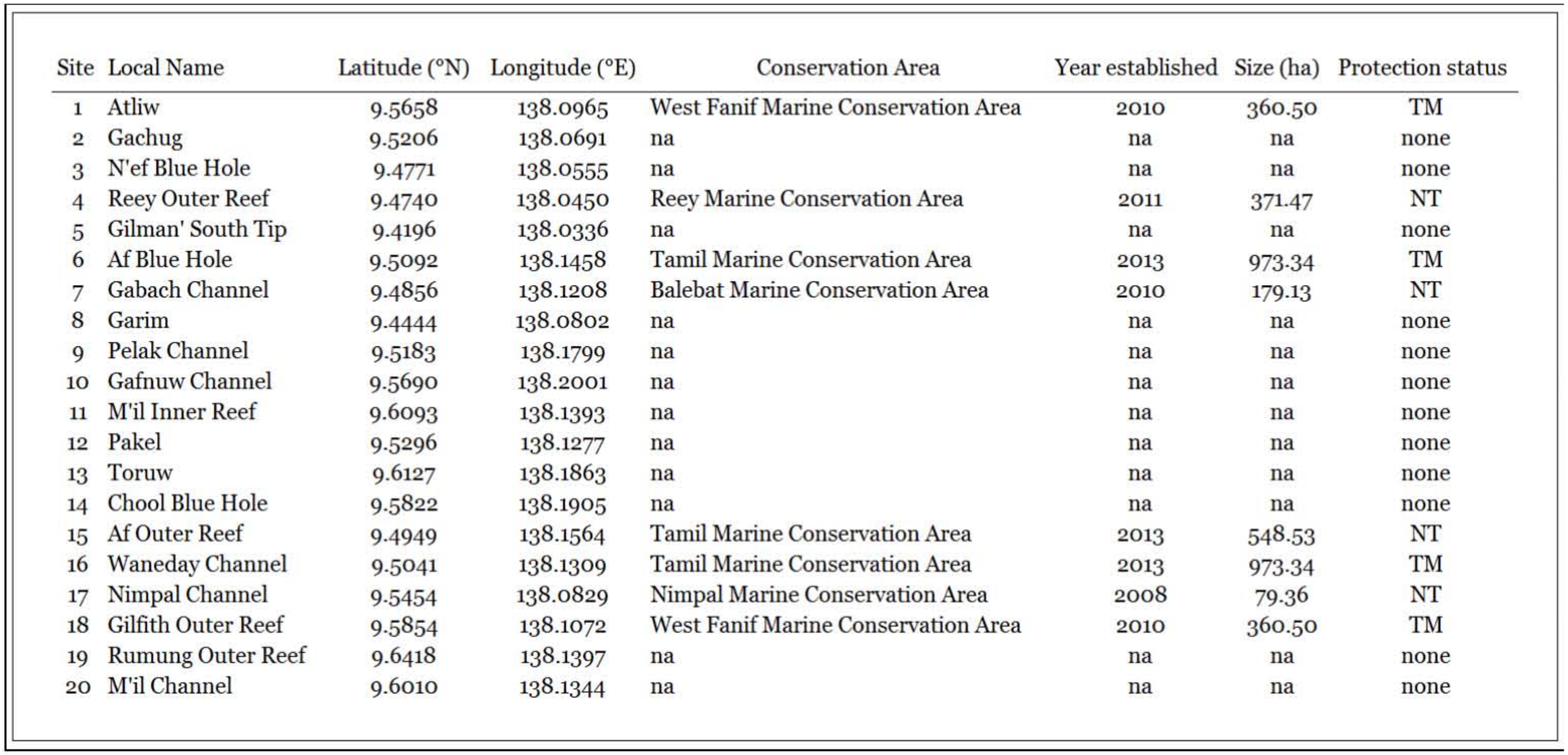


*Figure 1: Map of survey sites on Yap proper (Micronesia inset). MPA sites denoted by triangle.*

Table 1: Monitoring site details. na: not applicable; NT: no-take area; TM: traditionally managed area.



| Site | Local Name | Latitude (°N) | Longitude (°E) | Conservation Area | Year established | Size (ha) | Protection status |
|---|---|---|---|---|---|---|---|
| 1 | Atliw | 9.5658 | 138.0965 | West Fanif Marine Conservation Area | 2010 | 360.50 | TM |
| 2 | Gachug | 9.5206 | 138.0691 | na | na | na | none |
| 3 | N'ef Blue Hole | 9.4771 | 138.0555 | na | na | na | none |
| 4 | Reey Outer Reef | 9.4740 | 138.0450 | Reey Marine Conservation Area | 2011 | 371.47 | NT |
| 5 | Gilman' South Tip | 9.4196 | 138.0336 | na | na | na | none |
| 6 | Af Blue Hole | 9.5092 | 138.1458 | Tamil Marine Conservation Area | 2013 | 973.34 | TM |
| 7 | Gabach Channel | 9.4856 | 138.1208 | Balebat Marine Conservation Area | 2010 | 179.13 | NT |
| 8 | Garim | 9.4444 | 138.0802 | na | na | na | none |
| 9 | Pelak Channel | 9.5183 | 138.1799 | na | na | na | none |
| 10 | Gafnuw Channel | 9.5690 | 138.2001 | na | na | na | none |
| 11 | M'il Inner Reef | 9.6093 | 138.1393 | na | na | na | none |
| 12 | Pakel | 9.5296 | 138.1277 | na | na | na | none |
| 13 | Toruw | 9.6127 | 138.1863 | na | na | na | none |
| 14 | Chool Blue Hole | 9.5822 | 138.1905 | na | na | na | none |
| 15 | Af Outer Reef | 9.4949 | 138.1564 | Tamil Marine Conservation Area | 2013 | 548.53 | NT |
| 16 | Waneday Channel | 9.5041 | 138.1309 | Tamil Marine Conservation Area | 2013 | 973.34 | TM |
| 17 | Nimpal Channel | 9.5454 | 138.0829 | Nimpal Marine Conservation Area | 2008 | 79.36 | NT |
| 18 | Gilfith Outer Reef | 9.5854 | 138.1072 | West Fanif Marine Conservation Area | 2010 | 360.50 | TM |
| 19 | Rumung Outer Reef | 9.6418 | 138.1397 | na | na | na | none |
| 20 | M'il Channel | 9.6010 | 138.1344 | na | na | na | none |

No action may be taken to impair these traditional rights and ownership, except the State Government may provide for the conservation and protection of natural resources within the marine space of the State within 12 miles from the island baselines" (Yap State Constitution, Article XIII, Section 5).

The nearshore coral reef resources of Yap are described in detail by Houk and Starmer (2007), and further characterized by Houk et al. (2012). Coral communities at the 8 – 10 m depth range are best characterized by location and underlying geology (Houk and Starmer 2007). Three distinct reef types occur on Yap: outer reefs, which are located along the surrounding barrier reef; channel reefs, which experience largest tidal flux; and inner reefs, or "Blue Holes", which are isolated deep-water zones within the lagoon. A recent analysis of coral reefs across Micronesia shows that Yap proper reefs are relatively healthy (Houk et al. 2015).

### *MPA social structure*

Structured surveys and open-ended interview questionnaires were conducted with community representatives from MPAs that had corresponding ecological monitoring station (n = 17 individuals, all male, ages 20-76). Informants were selected based on their knowledge of the marine protected area, social system structure, and the local context of natural resource management. Key informants were selected over other survey methods (e.g., broad-scale surveys of community members) due to time restrictions on the project.

Questionnaires were developed based on guidance from Pollnac (1998). Socioeconomic indicators were selected, and a series of questions were developed for each indicator. Thus, indicators were represented by sets of questions, which were further categorized into latent variables for analyses (Table 2).

### ***Food-fish assemblage metrics***

Food-fish assemblage data have been collected from 20 monitoring sites around Yap Proper since 2011. Sites are part of Yap's long-term monitoring program, implemented by the Yap Community Action Program (Yap CAP) and the University of Guam Marine Lab. Surveys were conducted at the 8 m depth contour for outer reef slope sites and at the 5 m depth contour for channel and inner reef sites. This depth represents the optimal zone for coral growth, balancing light attenuation and wave energy. Food-fish assemblage metrics were: assemblage biomass (total biomass; herbivore biomass; predator biomass), assemblage size (mean total fish length (cm), TL; size-class distribution), and trophic structure (ratio of small:large herbivores). Ecological data were derived from a standardized stationary point count protocol established for Micronesia.

Food-fish assemblages were assessed using stationary point counts (SPC) (Bohnsack and Bannerot 1986). Twelve replicate SPCs were spaced equally along five 50-m transects. During each SPC the observer recorded the species and estimated the fork length (cm) of all food fish within a 5-m radius, for three minutes. Food fish are fish families that are regionally targeted for consumption (Acanthuridae, Carangidae, Labridae, Lethrinidae, Lutjanidae, Balistidae, Kyphosidae, Mullidae, Holocentridae, and sharks). The sizes of fishes were categorized in 5-cm bins for demographic analysis.

*Table 2: Questions and responses from social survey administered to respondents. Questions grouped into a priori latent variables.*

| | Question | Responses |
|---|---|---|
| Livelihoods | What percentage of your community fishes (all forms)? | None; A few; Some; Most; Nearly All |
| | What percentage of your community farms (all forms)? | None; A few; Some; Most; Nearly All |
| | Do community members perceive any social or financial benefits from your MPA? | No; Social only; Financial only; Both social and financial |
| | Do community members feel that the MPA limits fishing access? | Mostly no; Somewhat; Mostly yes |
| | What is the status of the fish in your MPA compared to non-MPA reefs? | Worse; No difference; Better |
| | What is the trend in fish population outside of your MPA? | Declining; No change; Increasing |
| | How many commercial fishermen are in your village? | None; A few; Some; Most; Nearly All |
| | Are there commercial betelnut operations or other main businesses in your community? | No; Yes |
| Management features & support | Does your MPA have a management plan? | No; Yes, in draft form; Yes, but not updated; Yes, updated |
| | Do your community members participate in biological monitoring? | No; Sometimes; Yes |
| | Does your community receive regular updates on the status of your MPA? | No; Sometimes; Yes |
| | Does your MPA receive advisement from outside your village? | No; Yes, local peers; Yes, scientific advisors |
| | Has monitoring data resulted in management changes? | No, no action taken; Yes, MPA created/mgmt improved; Yes, an alternative action taken |
| | Has monitoring data changed people's opinions about MPAs? | No; Yes, negatively; Yes, positively |
| | Is your MPA a member of the Local Managed Area Network (LMAN)? | No; No, but used to; No, but planning to join; Yes |
| | Has your community received MPA-related training in the past? | No; No, but it was offered; Yes |
| | Does your MPA have boundary markers present? | No; No, but it used to; Yes |
| | Does your MPA have a signboard notifying the public? | No; No, but it used to; Yes |
| Governance | Is there a key individual responsible for managing and implementing MPA rules? | No, never; No, but there used to; Yes |
| | Is there a management group dedicated to your MPA? | No, never had one; No, but we used to; Yes, but rarely meets; Yes, meets often |
| | Is the management group a traditional one? | No; Yes |
| | Does the key individual/management group consult with the community? | No; Yes |
| | What level of involvement do community members have in community deciision making? | None; Very little; Most decision making; All decision making |
| | Is there surveillance/enforcement of the MPA? | No; No, but used to; Yes, but limited; Yes |
| | When violations occur, how often are penalties handed down? | Never; Sometimes; Often; Always |
| Cultural norms | Do community members participate in work/projects/events? | None; A few; Some; Most; Nearly All |
| | What percent of your village is not Yapese? | None; A few; Some; Most; Nearly All |
| | How often is the Men's House used? | Never; Special occassions; Annually; Monthly; Daily-weekly |
| | What condition is the Men's House in? | Poor; Okay; Fair; High |
| | Dominant form of fishing? | Spearfishing; Fish traps; Net fishing; Gleaning; Other |
| | Most utilized fishing habitat? | Shore/intertidal; Seagrass; Mangrove; Inner reefs (reef flat, blue hole); Deep reefs (outer reefs, channels) |
| | What do fishermen do with their catch? | Keep for houshold; Sell to local market; Ship off-island; Share with community; Other |

Size estimates were converted to biomass (g) using length-weight regressions from FishBase (www.fishbase.org) and fishery-dependent data collected across Micronesia (Cuetos-Bueno and Hernandez-Ortiz unpublished). Comparisons were assessed using biomass per unit area (g $m^{-2}$).

Three, calibrated observers collected fish data across the study period (2011 – 2016), representing four sampling years (2011, 2014, 2015, and 2016). Data from 2011 and 2016 were used for this analysis, as both datasets contain all 20 monitoring stations and observers were consistent during each survey year. Species which were abundant, but seen only during 2016 when target fish lists were expanded, were removed prior to data analysis (Table 3).

## *Data Analysis*

### MPA social structure and clustering

Analysis of socio-cultural interview data were conducted using Multiple Correspondence Analysis (MCA) with the *FactoMineR* package (Husson et al. 2017). MCA simplified multivariate categorical data by first assessing similarity between each pair of interviewees using the Chi-square distance. The resultant similarity matrix was plotted in a principle components ordination (PCO) that provided a two-dimensional interpretation of interviewee similarity, based upon their responses to the questionnaire, and helped to visualize clusters of similar respondents. Vectors describing which interview questions were strongest contributors to the ordination plot structure were derived from correlations between each question and the two PCO axes, and described by their correlation coefficients with each axes using the *dimdesc* function in *FactoMineR* (Husson et al. 2017).

*Table 3. Fish species observed in each sampling period (2011 and 2016).*

| Species | 2011 | 2016 |
|---|---|---|
| *Acanthurus blochii* | | X |
| *Acanthurus lineatus* | X | X |
| *Acanthurus maculiceps* | X | |
| *Acanthurus nigricans* | | X |
| *Acanthurus nigricauda* | X | X |
| *Acanthurus pyroferus* | | X |
| *Acanthurus xanthopterus* | X | X |
| *Aethaloperca rogaa* | | X |
| *Aphareus furca* | X | X |
| *Aprion virescens* | | X |
| *Balistoides viridescens* | | X |
| *Bolbometopon muricatum* | X | X |
| *Caesio caerulaurea* | | X |
| *Carangoides ferdau* | | X |
| *Carangoides orthogrammus* | | X |
| *Carangoides plagiotaenia* | | X |
| *Caranx ignobilis* | | X |
| *Caranx melampygus* | X | X |
| *Caranx papuensis* | | X |
| *Cephalopholis argus* | X | X |
| *Cephalopholis miniata* | | X |
| *Cephalopholis urodeta* | | X |
| *Cetoscarus bicolor* | X | X |
| *Cheilinus fasciatus* | | X |
| *Cheilinus trilobatus* | | X |
| *Cheilinus undulatus* | X | X |
| *Chlorurus bleekeri* | | X |
| *Chlorurus frontalis* | | X |
| *Chlorurus japanensis* | X | |
| *Chlorurus microrhinos* | X | X |
| *Chlorurus sordidus* | | X |
| *Choerodon anchorago* | | X |
| *Coris aygula* | | X |
| *Ctenochaetus striatus* | X | X |
| *Elagatis bipinnulata* | | X |
| *Epibulus insidiator* | | X |
| *Epinephelus merra* | X | X |
| *Epinephelus polyphekadion* | X | |
| *Gnathodentex aureolineatus* | | X |
| *Gracila albomarginata* | X | X |

| | | |
|---|---|---|
| *Hemigymnus fasciatus* | | X |
| *Hipposcarus longiceps* | X | X |
| *Kyphosus cinerascens* | X | X |
| *Kyphosus vaigiensis* | X | X |
| *Lethrinus harak* | X | X |
| *Lethrinus xanthochilus* | X | X |
| *Lutjanus argentimaculatus* | X | |
| *Lutjanus bohar* | X | X |
| *Lutjanus fulvus* | X | X |
| *Lutjanus gibbus* | X | X |
| *Lutjanus monostigma* | X | X |
| *Lutjanus semicinctus* | | X |
| *Macolor macularis* | X | X |
| *Macolor niger* | X | X |
| *Monotaxis grandoculis* | X | X |
| *Mulloidichthys flavolineatus* | X | X |
| *Mulloidichthys vanicolensis* | | X |
| *Myripristis sp (*Holocentridae*)* | | X |
| *Naso brevirostris* | | X |
| *Naso caesius* | X | |
| *Naso lituratus* | X | X |
| *Naso unicornis* | X | X |
| *Naso vlamingii* | X | X |
| *Neoniphon sp (*Holocentridae*)* | | X |
| *Oxycheilinus celebicus* | | X |
| *Parupeneus barberinus* | X | X |
| *Parupeneus bifasciatus* | | X |
| *Parupeneus cyclostomus* | X | X |
| *Parupeneus insularis* | X | |
| *Parupeneus multifasciatus* | X | X |
| *Plectorhinchus chaetodonoides* | | X |
| *Plectorhinchus albovittatus* | | X |
| *Plectorhinchus chaetodonoides* | | X |
| *Plectorhinchus lineatus* | X | X |
| *Plectorhinchus picus* | X | |
| *Plectropomus laevis* | X | X |
| *Plectropomus leopardus* | | X |
| *Pomacanthus sexstriatus* | | X |
| *Pseudobalistes flavimarginatus* | | X |
| *Pterocaesio tile* | | X |
| *Pygoplites diacanthus* | | X |
| *Sargocentron caudimaculatum* | | X |
| *Sargocentron spiniferum* | | X |

|  |  |  |
|---|---|---|
| *Sargocentron tiere* |  | X |
| *Scarus altipinnis* | X | X |
| *Scarus dimidiatus* | X | X |
| *Scarus flavipectoralis* |  | X |
| *Scarus forsteni* |  | X |
| *Scarus frenatus* |  | X |
| *Scarus ghobban* |  | X |
| *Scarus globiceps* |  | X |
| *Scarus niger* |  | X |
| *Scarus oviceps* | X | X |
| *Scarus psittacus* |  | X |
| *Scarus rubroviolaceus* | X | X |
| *Scarus schlegeli* |  | X |
| *Scarus spinus* |  | X |
| *Scarus tricolor* |  | X |
| *Scolopsis ciliata* |  | X |
| *Scolopsis trilineata* |  | X |
| *Scomberomorus commerson* |  | X |
| *Siganus argenteus* | X | X |
| *Siganus doliatus* | X | X |
| *Siganus guttatus* | X |  |
| *Siganus lineatus* | X | X |
| *Siganus puellus* | X | X |
| *Siganus punctatus* |  | X |
| *Siganus randalli* | X |  |
| *Siganus spinus* |  | X |
| *Siganus virgatus* | X |  |
| *Siganus vulpinus* |  | X |
| *Triaenodon obesus* | X | X |
| Unidentified small-bodied Acanthuridae |  |  |
| Unidentified small-bodied Scaridae |  |  |
| *Variola louti* | X | X |
| *Zebrasoma scopas* |  | X |
| *Zebrasoma veliferum* |  | X |

The suite of interview questions regarding physical management features and infrastructure (i.e., MPA boundary markers, signboard, or management plan) were not included in the main multivariate analyses described above, but were instead introduced as supplementary variables. While physical features are often used as predictors of MPA performance (see Edgar et al. 2014, Di Franco et al. 2016), we considered physical features as outcomes of a deeper social process. In sum, the multivariate analyses were centered on questions describing social structure and not physical features. Questions where all respondents answered identically were removed prior to analysis (i.e., questions lacked variation).

Respondent clusters were also assessed using hierarchical clustering on principal components using the *HCPC* function (Husson et al. 2017). This function utilizes the same similarity matrix described above and suggests clusters based on thresholds, via Ward's criterion. Ward's criterion seeks to find the optimal number of clusters by which the growth of within-cluster variation is minimized. Visual inspection and results from the *HCPC* function produced three clusters, with an 80% CI. Given the number of interviewees and corresponding biological monitoring stations, this number was considered to be optimal for our analysis.

## Quantitative analysis of MPA performance

MPA performance was assessed by calculating the difference between several dependent biomass variables in MPAs and their respective reference sites. Dependent variables included total fish biomass, herbivorous fish biomass, predator fish biomass, and mean fish size. Calculating difference between MPA and reference sites made dependent variables less sensitive to changes in habitat, such as differing reef types, and more indicative of MPA performance. Standard pairwise comparisons of dependent variables were conducted between *a priori* defined social clusters, for both 2011 and 2016 data (one-way ANOVA, Kruskal-Wallis rank sum tests if assumptions of normality or heterogeneity were not met following transformations; Tukey's LSD test used for *post-hoc* pairwise comparisons). In addition to the noted dependent variables, fish assemblage size-class distributions were compared as a final indicator of MPA performance using Kolmogorov-Smirnov (K-S) tests, as they explicitly test for differences in cumulative frequency data. Statistical modelling was performed using the *lme4* package in R (Bates et al. 2016).

Results from the quantitative analysis were next used to determine if social clusters aligned with trends in MPA performance. A site was coded as positive if fish assemblage metrics were significantly greater than those in the reference site. If fish assemblage metrics were similar or significantly less than the reference, the site was coded as negative. Individual questions and clusters were tested for correlation, using the *dimdesc* function in the FactoMineR package (Husson et al. 2017).

### Social perception of fisheries trends

This study last assessed whether social perception could be used as a useful indicator of fisheries trends for reefs outside of MPA management. Social perception was quantified based upon responses to the question: "what are the trends in fish biomass outside of your MPA"? First, regression models were built to describe the relationship between a defined metric of fish assemblage condition and proxies to pollution and fishing pressure. The strength of these relationships were then assessed in both 2011 and 2016 as an indicator of fisheries trends. In addition, comparisons of biomass between 2011 and 2016 were also calculated for all non-MPA and low-performing MPA sites.

Proxies for fishing pressure and land-based pollution were derived from wave-energy values, land-use data, census data, and distances from fishing access and pollution discharge. Wave energy values were calculated for each site using a 10-year record of wind-speed, fetch distance, and angle of exposure (Quicksat wind data sets from 1999 to 2009; https://winds.jpl.nasa.gov, wave energy in $J/m^3$; Houk et al. 2015). Land-based sources of pollution (terrestrial nutrient and freshwater input) from adjacent watersheds were calculated for each site by measuring watershed size ($km^2$) in ArcGIS using United States Geological Survey topographic base layer maps. Further, a pollution proxy was developed using the summed area of disturbed land (barren land, urbanized vegetation, and developed infrastructure within each watershed). Human population data was derived from the 2010 FSM census (2010 FSM Census, http://www.sboc.fm/).

Two forms of fishing access were calculated: local and commercial. Local fishing access was calculated by multiplying the standardized values for: 1) the linear distance from main boat access point in community adjacent to a site and 2) wave energy values for the site. Commercial fishing access was calculated in the same manner, but substituted distance to Colonia (main port on Yap) for distance to local access point. Distances were inversely scaled so that larger values for village based access represented shorter distance.

Pollution proxies were generated by calculating values for: 1) total area of altered land in the adjacent watershed (barren urban, urbanized vegetation, developed infrastructure) and 2) the distance from study site to the nearest discharge point (Houk et al. 2015). Altered land area was derived using United States Forest Service land-use data (United States Forest Service, http://www.fs.usda.gov/r5). Distances were inversely scaled so that greater distances from discharge point yielded lower pollution scores.

A forward, stepwise regression modeling processes was used for both 2011 and 2016 timeframes. Fish assemblage condition scores were used as the dependent variables, representing standardized, averaged values of fish assemblage size, biomass, herbivorous fish biomass, and predator biomass (following the previously defined process in Houk et al. 2015). All independent variables, or predictor terms, were first tested individually to determine the main driver of assemblage condition. Additional terms were added and retained only if they improved the explanatory power of the model, and the model stability ($R^2$ and AIC values, respectively). Regression modelling was conducted using the *lme4* package in R (Bates et al. 2016).

Outer reef fish assemblages were not tested against pollution proxies because watershed discharge on Yap flows through the main channels and distances from the discharge points to outer reefs were between 1.45 and 4 km.

## Results

### *MPA social analysis and clustering*

The multiple correspondence analysis (MCA) plot depicted the similarity between respondents and explained 38.41% of the variation in the categorical social survey data (15.15% Dim 1 and 13.26% Dim 2). Interestingly, the suite of responses that best described the underlying social structure in villages with MPAs were derived from questions nested within differing latent variables. Governance questions regarding MPA enforcement ($R^2$ = 0.77, $p$ < 0.001), community consultation ($R^2$ = 0.63, $p$ < 0.001), management groups ($R^2$ = 0.61, $p$ = 0.001), and participation in biological monitoring ($R^2$ = 0.61, $p$ = 0.001) were most correlated to the first dimension of the MCA plot (Figure 2). Fishing-related cultural norms were also influential in structuring of the first dimension (catch sharing: $R^2$ = 0.54, $p$ = 0.03; fishing methods: $R^2$ = 0.49, $p$ = 0.002). Last, perceived benefits from MPAs was highly correlated with the first dimension ($R^2$ = 0.75; $p$ < 0.001). The first dimension is a gradient describing the governance structure of communities and the perception of fisheries outside MPA borders.

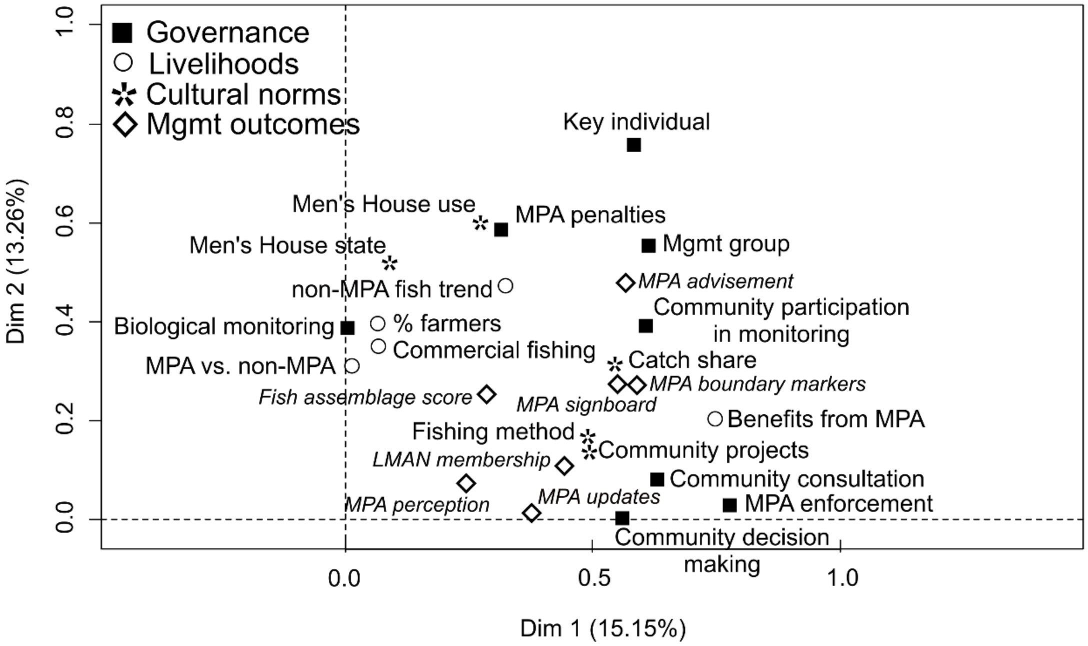
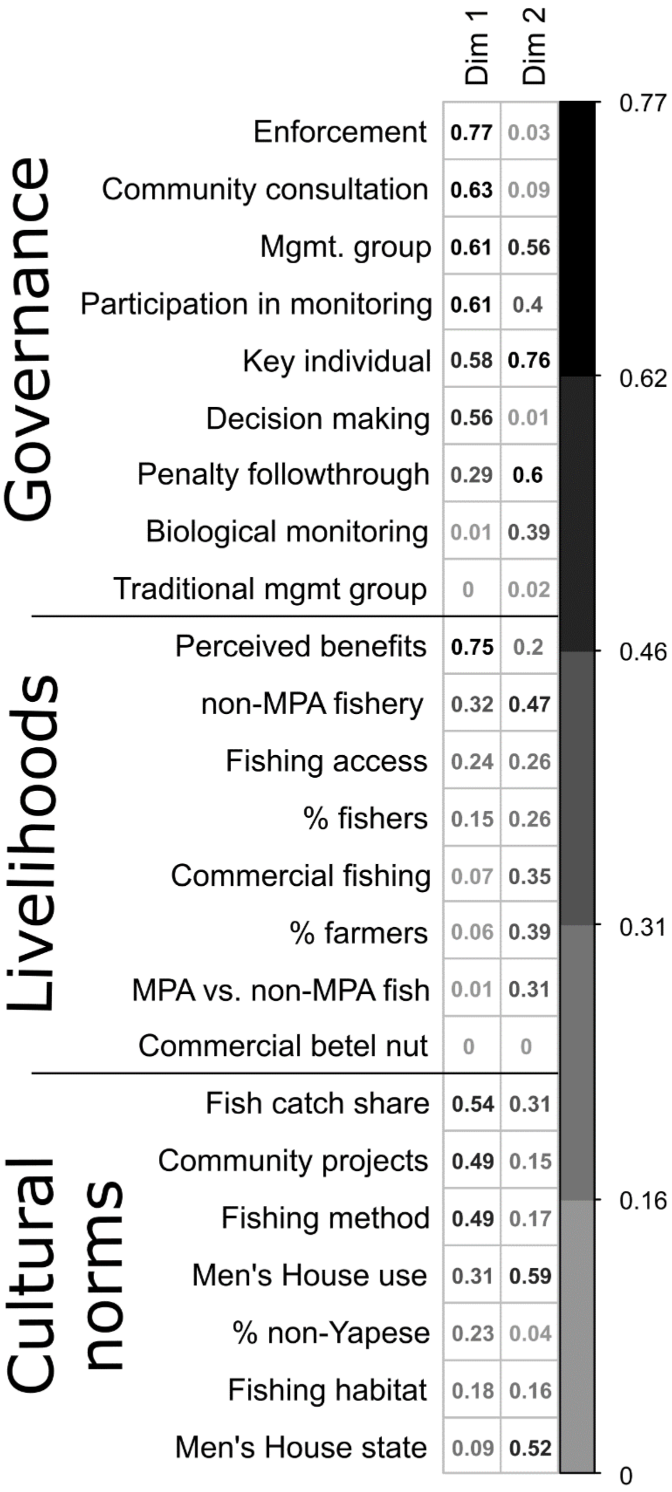


*Figure 2: Biplot of variables from social surveys. Shapes correspond to latent variables and management outcomes (supplementary variables; show in italics). Variables with p values > 0.05 are omitted from plot.*

The second dimension of the MCA plot was mainly driven by the absence of key individuals to drive management success and corresponding management groups ($R^2 = 0.76$, $p < 0.001$). Cultural norms regarding the Yapese Men's House were also correlated with the second dimension (usage: $R^2 = 0.59$, $p = 0.007$; state: $R^2 = 0.52$, $p = 0.019$; Figure 3).

Clustering analysis on respondents were structured primarily by governance and livelihood features, resulting in three clusters (Figure 4). Specific questions with strongest influence on the MCA plot and social clustering were related to MPA leadership and perception of MPAs (Table 4). Positive responses to these questions characterized social cluster 1, which encompassed sites 6, 7, 15, 16, and 17 (Table 4). Respondents in cluster 2, all associated with site 4, indicated that the Yapese Men's House in their village was in poor condition and rarely utilized by community members. Although this key Yapese cultural feature was absent, respondents indicated that net fishing, a communal form of fishing, was the preferred method of this community. Further, they also indicated the presence of other community-centric features, such as community consultation in decision making and implementation processes. Decision-making and conservation management likely takes a "bottom-up" approach as respondents also indicated a key individual was never present and the local management group meets infrequently. Cluster 3 represented sites 1 and 18, both located in the West Fanif Marine Conservation Area. Respondents indicated a lack of strong governance, no key individuals or active management groups, and a lack of beneficial MPA outcomes.



| | | Dim 1 | Dim 2 |
|---|---|---|---|
| Governance | Enforcement | 0.77 | 0.03 |
| | Community consultation | 0.63 | 0.09 |
| | Mgmt. group | 0.61 | 0.56 |
| | Participation in monitoring | 0.61 | 0.4 |
| | Key individual | 0.58 | 0.76 |
| | Decision making | 0.56 | 0.01 |
| | Penalty followthrough | 0.29 | 0.6 |
| | Biological monitoring | 0.01 | 0.39 |
| | Traditional mgmt group | 0 | 0.02 |
| Livelihoods | Perceived benefits | 0.75 | 0.2 |
| | non-MPA fishery | 0.32 | 0.47 |
| | Fishing access | 0.24 | 0.26 |
| | % fishers | 0.15 | 0.26 |
| | Commercial fishing | 0.07 | 0.35 |
| | % farmers | 0.06 | 0.39 |
| | MPA vs. non-MPA fish | 0.01 | 0.31 |
| | Commercial betel nut | 0 | 0 |
| Cultural norms | Fish catch share | 0.54 | 0.31 |
| | Community projects | 0.49 | 0.15 |
| | Fishing method | 0.49 | 0.17 |
| | Men's House use | 0.31 | 0.59 |
| | % non-Yapese | 0.23 | 0.04 |
| | Fishing habitat | 0.18 | 0.16 |
| | Men's House state | 0.09 | 0.52 |

*Figure 3: Correlation coefficients ($R^2$) of social variables. Variables grouped by a priori assigned latent variables, sorted in decreasing correlation with dimensions 1 and 2, respectively.*

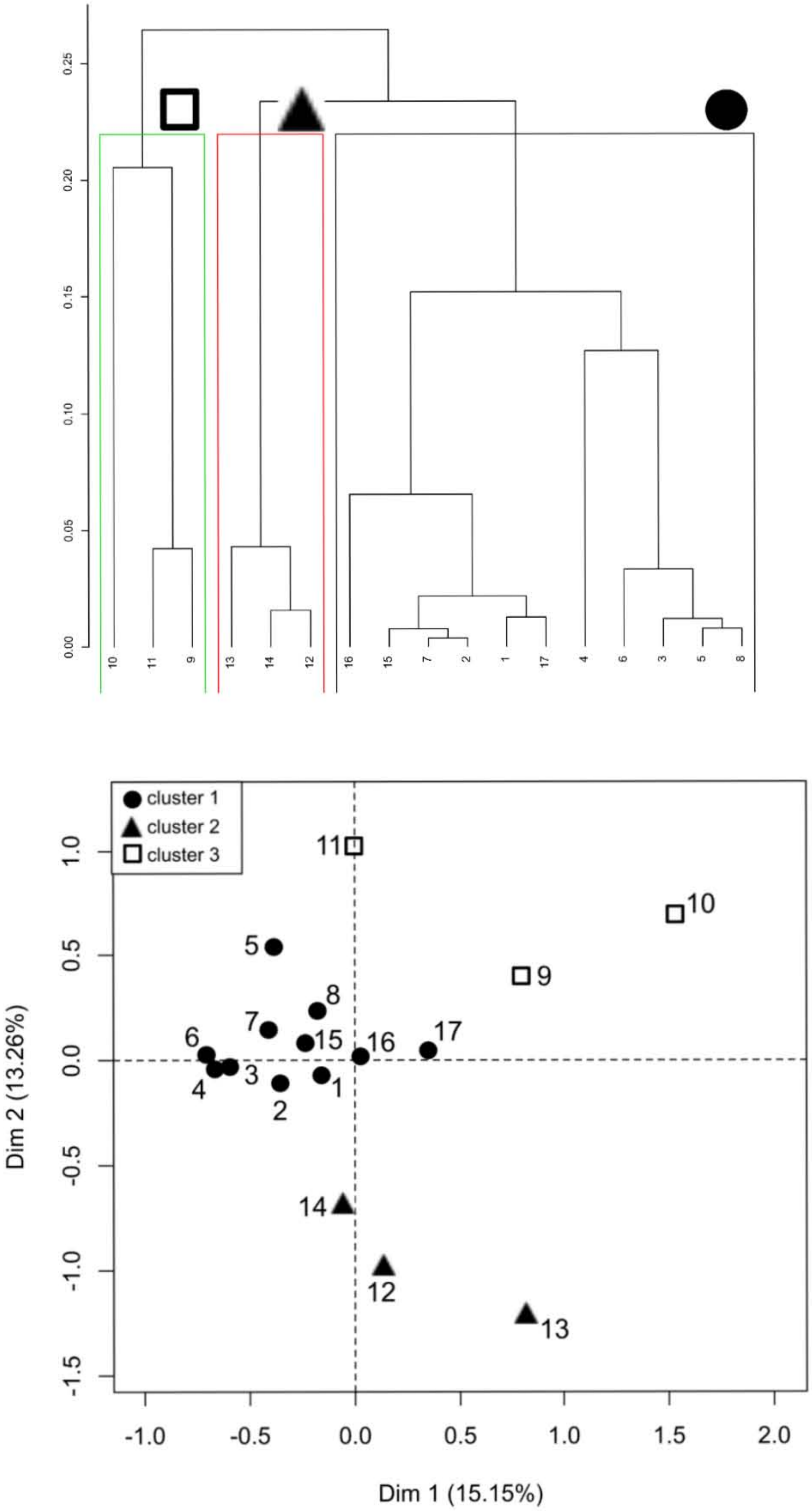


*Figure 4: (A) Dendrogram of individuals based on hierarchical clustering of principle components. Shapes correspond to cluster groups. (B) Orientation of individuals in Euclidean space.*

*Table 4: Chi$^2$ test results for categories that define MPA clusters. Negative v test values indicate a negative correlation between the variable and the cluster. Shapes correspond to latent variable group: squares - governance; circles - livelihoods; asterisks - cultural norms; diamonds – management outcomes. Categories with non-significant values ($p > 0.05$) omitted.*

| **Cluster 1** | | | Cla/Mod | Mod/Cla | Global | *p* value | v test |
|---|---|---|---|---|---|---|---|
| **YAP-06, 07, 15, 16, and 17** | ✲ | Fishing method - *Spearfishing* | 90.91 | 90.91 | 65 | 0.005 | 2.777 |
| | ■ | Community consultation - *Yes* | 84.62 | 100.00 | 76 | 0.006 | 2.732 |
| | ■ | Key individual - *Yes* | 100.00 | 72.73 | 47 | 0.007 | 2.707 |
| | ■ | Management group - *Yes, and meet often* | 100.00 | 72.73 | 47 | 0.007 | 2.707 |
| | ◊ | Update to MPA mgmt - *Yes* | 100.00 | 63.64 | 41 | 0.017 | 2.387 |
| | ■ | MPA enforcement - *Yes* | 100.00 | 63.64 | 41 | 0.017 | 2.387 |
| | ■ | Community decision making - *All* | 90.00 | 81.82 | 59 | 0.018 | 2.364 |
| | ■ | Key individual - *No, never* | 0.00 | 0.00 | 18 | 0.029 | -2.178 |
| | ■ | Management group - *No, but we used to* | 0.00 | 0.00 | 18 | 0.029 | -2.178 |
| | ■ | Community consultation - *No* | 0.00 | 0.00 | 24 | 0.006 | -2.732 |
| | ✲ | Fishing method - *Netfishing* | 16.67 | 9.09 | 35 | 0.005 | -2.777 |

| **Cluster 2** | | | Cla/Mod | Mod/Cla | Global | *p* value | v test |
|---|---|---|---|---|---|---|---|
| **Cluster 2** | ■ | Key individual - *No, never* | 100.00 | 100.00 | 18 | 0.001 | 3.180 |
| | ◊ | Mgmt. assistance - *Yes, from local peers* | 100.00 | 66.67 | 12 | 0.022 | 2.289 |
| | ✲ | Men's House use - *Never* | 100.00 | 66.67 | 12 | 0.022 | 2.289 |
| | ■ | MPA penalties - *Often* | 100.00 | 66.67 | 12 | 0.022 | 2.289 |
| | ✲ | Men's House state - *Bad* | 50.00 | 100.00 | 35 | 0.029 | 2.178 |
| | ✲ | Fishing method - *Netfishing* | 50.00 | 100.00 | 35 | 0.029 | 2.178 |
| | ■ | Management group - *Yes, but rarely meets* | 50.00 | 100.00 | 35 | 0.029 | 2.178 |
| | ✲ | Fishing method - *Spearfishing* | 0.00 | 0.00 | 65 | 0.029 | 2.178 |

| **Cluster 3** | | | Cla/Mod | Mod/Cla | Global | *p* value | v test |
|---|---|---|---|---|---|---|---|
| **YAP-01, 18** | ■ | Management group - *No, but used to* | 100.00 | 100.00 | 18 | 0.001 | 3.180 |
| | ○ | non-MPA trend in fish - *No change* | 75.00 | 100.00 | 24 | 0.006 | 2.754 |
| | ■ | Key individual - *No, but used to* | 60.00 | 100.00 | 29 | 0.015 | 2.440 |
| | ■ | MPA penalties - *Never* | 100.00 | 66.67 | 12 | 0.022 | 2.289 |
| | ◊ | MPA signboard - *Yes* | 0.00 | 0.00 | 65 | 0.029 | -2.178 |
| | ○ | non-MPA trend in fish - *Increasing* | 0.00 | 0.00 | 65 | 0.029 | -2.178 |
| | ◊ | MPA boundary markers - *Yes* | 0.00 | 0.00 | 71 | 0.015 | -2.440 |

Additionally, respondents in this cluster indicated poor perception of fish in both MPAs and non-MPAs. In sum, cluster 3 respondents indicated negative responses to most governance and livelihood questions, while the differences between clusters 1 and 2 provided an opportunity for further investigation.

### *Social clusters and ecological outcomes*

### MPA – reference comparisons

Ecological outcomes differed between MPA clusters. Clusters were best delineated by total fish biomass (46.7, 114.01, and 28.19 g $m^2$, clusters 1, 2, and 3, respectively), herbivore biomass (17.92, 94.37, and -5.49 g $m^2$; clusters 1, 2, and 3, respectively), and mean fish length (3.0, 4.6, and 0.9 cm; cluster 1, 2, and 3, respectively; Figure 5). Total fish biomass within cluster 2 was greater than clusters 1 and 3 (one-way ANOVA: $F = 8.693$, $p < 0.001$; Tukey HSD: c2-c1, c2-c3 $p < 0.001$, c1-c3 $p = 0.805$). Similarly, herbivore biomass within cluster 2 was also greater than clusters 1 and 3 (one-way ANOVA: $F = 9.592$, $p < 0.001$; Tukey HSD: c2-c1 $p = 0.001$, c2-c3 $p < 0.001$, c1-c3 $p = 0.341$). Cluster 3 sites supported smaller mean fish sizes than others (one-way ANOVA: $F = 4.928$, $p = 0.009$; Tukey HSD: c1-c2 $p = 0.342$, c1-c3 $p = 0.044$, c2-c3 $p = 0.012$) and lower predator biomass (one-way ANOVA: $F = 15.117$, $p < 0.001$; Tukey HSD: c1-c2 $p = 0.643$, c1-c3 $p < 0.001$, c2-c3 $p = 0.005$). KS test revealed clusters 1 and 2 contained a greater proportion of fishes > 25 cm in length than cluster 3 ($p < 0.001$; Figure 6). Last, the random term included for site-based variation within each cluster was only significant for predator biomass and mean assemblage size ($\chi^2$ test: $p = 0.01, < 0.001$, respectively), confirming that clusters were indicative of consistent ecological trends for most biological metrics. In sum, cluster 3 exhibited no improvement in fish assemblage condition relative to reference sites, while higher condition scores were found for clusters 1 and 2, with cluster 2 performing the best overall.

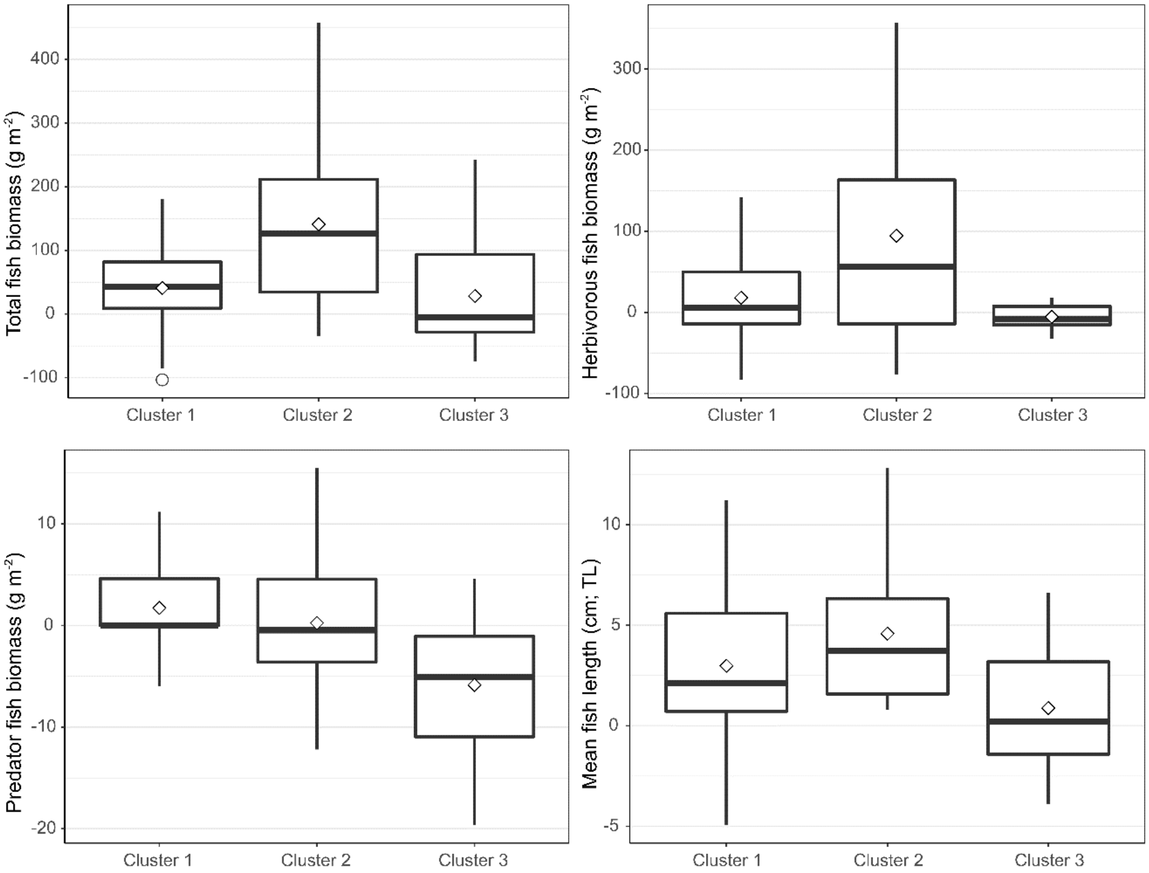


*Figure 5: Differences in total biomass, mean fish length, herbivore fish biomass, and predator biomass relative to reference sites by MPA clusters. Horizontal lines: medians; diamonds: means; boxes: 25th-75th percentiles (interquartile range, IQR); Lower/upper whiskers: extend to min./max. values within 1.5 x IQR above/below 25th/75th percentile; circles: outliers.*

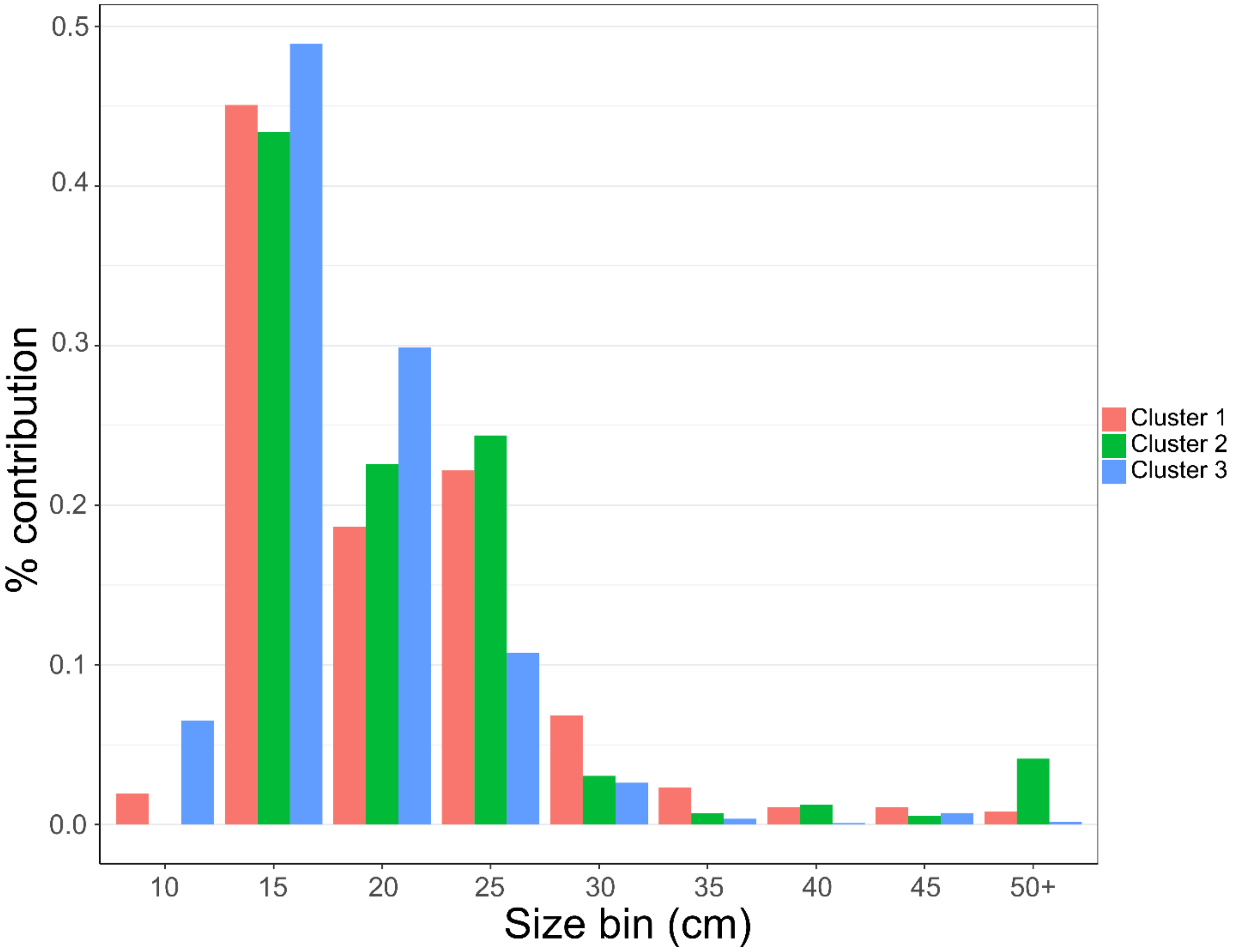


*Figure 6: Size frequency distribution of fishes between MPA clusters. Large individuals were more abundant in clusters 1 & 2 (KS test:* p *<0.001).*

Pairwise comparisons with reference sites also revealed that social clusters generally corresponded with the fish assemblage condition metrics that were developed (Figure 7). Similar to the above findings, cluster 2 had the most notable increases in fish assemblage condition compared to reference locations, while sites in cluster 3 exhibited no difference to reference sites. Cluster 1 contained a combination of sites that improved (6, 16, and 17) and site that underperformed (7 and 15). However, no sites showed improvements in predator biomass compared to reference sites, but shifts from smaller to larger individuals were seen at all sites except (1) (K-S test: $p$ <0.001).

## Temporal comparisons

Temporal analysis agreed with MPA-reference comparisons (Figure 8). Total biomass improved the most in cluster 2, which was significantly greater than those observed in clusters 1 and 3 (one-way ANOVA: $F = 11.974$, $p < 0.001$; Tukey HSD: c2-c1, c2-c3 $p < 0.001$, c1-c3 $p = 0.761$). Changes in herbivore biomass followed a similar trend (one-way ANOVA: $F = 10.510$, $p < 0.001$; Tukey HSD: c2-c1 $p < 0.001$, c2-c3 $p = 0.001$, c1-c3 $p = 0.916$).

*Figure 7: Site assemblage biomass comparisons by MPA clusters. Points represent site means. Whiskers: SE of the mean.*

*Table 4: Pairwise comparisons of fish assemblage metrics. Results of Welch's* t *test. MPA and Ref. are mean values.*

| Fish assemblage metric | MPA | Ref | *t* stat | *p* |
|---|---|---|---|---|
| **Total biomass ($g\ m^{-2}$)** | | | | |
| *Cluster 1* | | | | |
| 6 | 85.84 | 32.69 | 4.784 | < 0.001 |
| 7 | 45.79 | 47.41 | 0.152 | 0.441 |
| 15 | 88.12 | 102.86 | 0.89 | 0.192 |
| 16 | 100.96 | 16.98 | 6.052 | < 0.001 |
| 17 | 79.88 | 34.19 | 3.387 | 0.003 |
| *Cluster 2* | | | | |
| 4 | 217.42 | 76.42 | 3.636 | 0.002 |
| *Cluster 3* | | | | |
| 1 | 61.97 | 76.42 | 1.477 | 0.080 |
| 18 | 135.46 | 76.42 | 1.992 | 0.034 |
| **Herbivore biomass ($g\ m^{-2}$)** | | | | |
| *Cluster 1* | | | | |
| 6 | 32.28 | 20.27 | 1.341 | 0.100 |
| 7 | 37.80 | 60.08 | 1.408 | 0.088 |
| 15 | 83.40 | 73.85 | 0.467 | 0.323 |
| 16 | 96.15 | 12.63 | 5.587 | < 0.001 |
| 17 | 59.13 | 25.30 | 2.352 | 0.020 |
| *Cluster 2* | | | | |
| 4 | 147.63 | 53.26 | 2.452 | 0.015 |
| *Cluster 3* | | | | |
| 1 | 46.48 | 53.26 | 0.812 | 0.214 |
| 18 | 38.42 | 46.44 | 1.571 | 0.066 |
| **Predator biomass ($g\ m^{-2}$)** | | | | |
| *Cluster 1* | | | | |
| 6 | -- | -- | -- | -- |
| 7 | 0.96 | 2.96 | 1.149 | 0.136 |
| 15 | 2.99 | 10.39 | 2.063 | 0.029 |
| 16 | -- | -- | -- | -- |
| 17 | 6.72 | 1.29 | 2.057 | 0.029 |
| *Cluster 2* | | | | |
| 4 | 12.06 | 11.80 | 0.055 | 0.478 |
| *Cluster 3* | | | | |
| 1 | 1.41 | 11.80 | 2.873 | 0.008 |
| 18 | 12.94 | 11.80 | 0.141 | 0.445 |
| **Assemblage size (cm)** | | | | |
| *Cluster 1* | | | | |
| 6 | 20.83 | 18.33 | 2.705 | 0.006 |
| 7 | 20.09 | 18.20 | 2.779 | 0.006 |
| 15 | 18.73 | 18.37 | 0.368 | 0.358 |
| 16 | 21.96 | 14.41 | 9.191 | < 0.001 |
| 17 | 19.70 | 15.05 | 2.592 | 0.011 |
| *Cluster 2* | | | | |
| 4 | 21.21 | 16.62 | 4.551 | < 0.001 |
| *Cluster 3* | | | | |
| 1 | 16.32 | 16.62 | 0.606 | 0.275 |
| 18 | 18.68 | 16.62 | 2.511 | 0.012 |

These changes in cluster 2 were mainly attributed to a consistent presence of Napoleon wrasse (*Cheilinus undulatus*) and bumphead parrotfish (*Bolbometopon muricatum*) during the 2016 surveys. Despite no significant differences from reference locations, predator biomass did increase through time in cluster 1 (one-way ANOVA: $F = 3.122$, $p < 0.001$; Tukey HSD: c2-c1 $p = 0.003$, c2-c3 $p < 0.001$, c1-c3 $p = 0.032$), but predator biomass in cluster 3 declined through time. Site 6 was the only site with a substantial, yet non-significant, increase in predator biomass due to the unique presence of a whitetip reef shark (*Triaenodon obesus*; 2011 – 0.00 g $m^2$, 2016 – 268.46 g $m^2$). Mean fish length increased in clusters 1 and 2, but no change was observed in cluster 3 (one-way ANOVA: $F = 3.331$, $p < 0.001$; Tukey HSD: c2-c1 $p = 0.978$, c2-c3 $p = 0.094$, c1-c3 $p = 0.04$).

In summary, temporal trends reveal positive trajectories for most sites (Table 5). Total biomass doubled and quadrupled in cluster 1 and cluster 2, respectively, while remaining relatively unchanged in cluster 3. Similarly, biomass increases at other sites were concentrated in herbivore and secondary consumer trophic levels (Figure 9). Thus, the trends supported the null hypothesis that predator biomass would not differ between MPA and reference sites or through time.

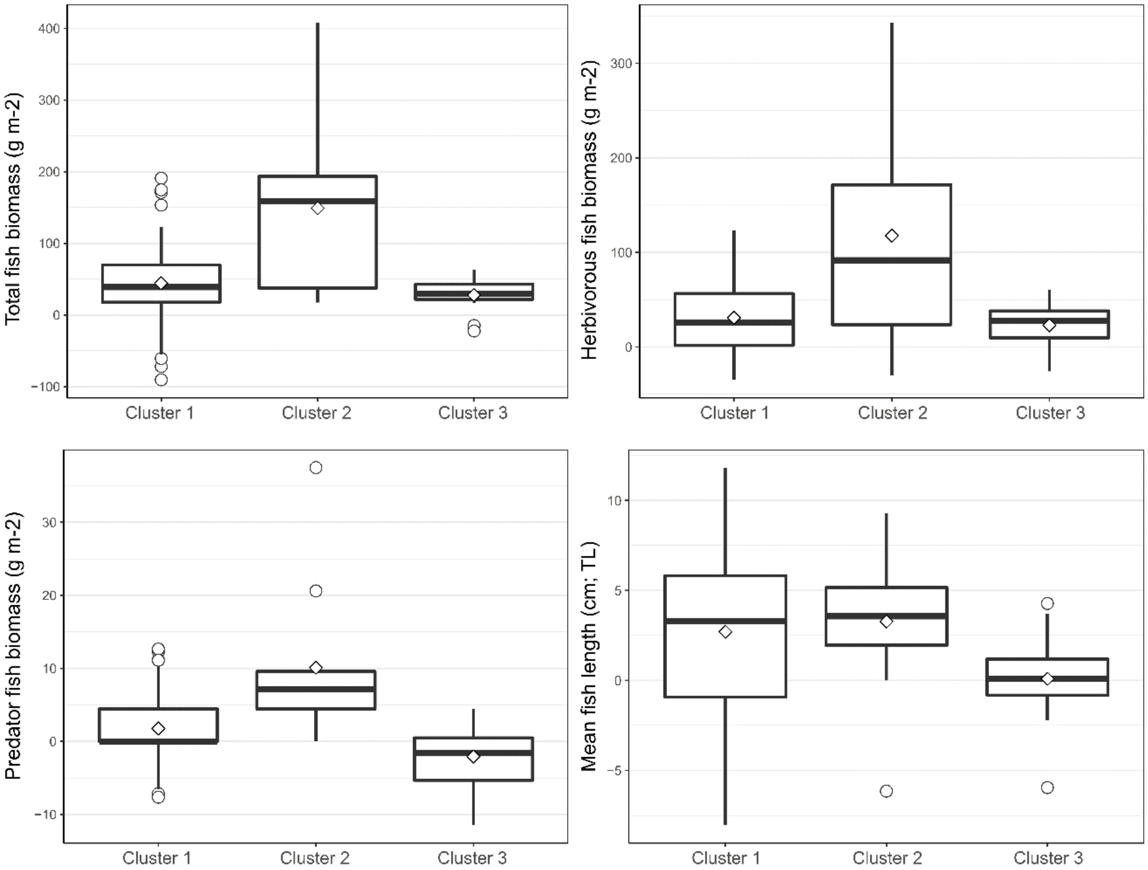


*Figure 8: Comparison of temporal changes in total biomass, mean fish length, herbivore fish biomass, and predator biomass by MPA clusters. Horizontal lines: medians; diamonds: means; boxes: 25th-75th percentiles (interquartile range, IQR); Lower/upper whiskers: extend to min./max. values within 1.5 x IQR above/below 25th/75th percentile; circles: outliers.*

*Table 5: Temporal comparisons of fish assemblage metrics (2011 - 2016). Welch's t test results. Site 18 omitted (not surveyed in 2011).*

| Fish assemblage metric | 2011 | 2016 | *t* stat | *p* |
|---|---|---|---|---|
| **Total biomass (g m$^{-2}$)** | | | | |
| *Cluster 1* | *34.28* | *71.43* | *3.681* | *< 0.001* |
| 6 | 16.93 | 67.35 | 1.117 | 0.144 |
| 7 | 78.43 | 64.68 | 0.468 | 0.322 |
| 15 | 82.00 | 110.50 | 0.915 | 0.185 |
| 16 | 15.98 | 113.40 | 4.492 | < 0.001 |
| 17 | 42.65 | 111.30 | 1.938 | 0.035 |
| *Cluster 2* | | | | |
| 4 | 38.96 | 188.10 | 3.825 | 0.001 |
| *Cluster 3* | | | | |
| 1 | 49.78 | 58.19 | 0.434 | 0.343 |
| 18 | -- | -- | -- | -- |
| **Herbivore biomass (g m$^{-2}$)** | | | | |
| *Cluster 1* | *22.79* | *59.33* | *5.669* | *< 0.001* |
| 6 | 14.64 | 29.79 | 2.149 | 0.026 |
| 7 | 55.51 | 59.97 | 0.16 | 0.437 |
| 15 | 38.07 | 83.40 | 2.464 | 0.015 |
| 16 | 12.10 | 96.13 | 5.596 | < 0.001 |
| 17 | 36.92 | 101.90 | 1.843 | 0.041 |
| *Cluster 2* | | | | |
| 4 | 29.92 | 147.70 | 3.079 | 0.004 |
| *Cluster 3* | | | | |
| 1 | 43.16 | 46.47 | 0.176 | 0.434 |
| 18 | -- | -- | -- | -- |
| **Predator biomass (g m$^{-2}$)** | | | | |
| *Cluster 1* | *1.21* | *2.84* | *2.781* | *0.003* |
| 6 | 1.02 | 28.65 | 1.117 | 0.144 |
| 7 | 6.11 | 3.95 | 1.357 | 0.101 |
| 15 | 5.09 | 2.67 | 0.597 | 0.280 |
| 16 | 2.29 | 2.80 | 0.345 | 0.367 |
| 17 | 13.50 | 6.49 | 0.729 | 0.240 |
| *Cluster 2* | | | | |
| 4 | 7.39 | 11.46 | 0.606 | 0.276 |
| *Cluster 3* | | | | |
| 1 | 3.44 | 1.40 | 1.586 | 0.067 |
| 18 | -- | -- | -- | -- |
| **Assemblage size (cm)** | | | | |
| *Cluster 1* | *17.70* | *20.30* | *4.639* | *< 0.001* |
| 6 | 14.70 | 20.80 | 6.709 | < 0.001 |
| 7 | 17.50 | 20.50 | 2.142 | 0.023 |
| 15 | 18.30 | 18.60 | 0.337 | 0.370 |
| 16 | 19.40 | 22.10 | 2.577 | 0.009 |
| 17 | 19.50 | 19.70 | 0.092 | 0.463 |
| *Cluster 2* | | | | |
| 4 | 17.90 | 21.20 | 2.591 | 0.009 |
| *Cluster 3* | | | | |
| 1 | 16.10 | 16.20 | 0.113 | 0.456 |
| 18 | -- | -- | -- | -- |

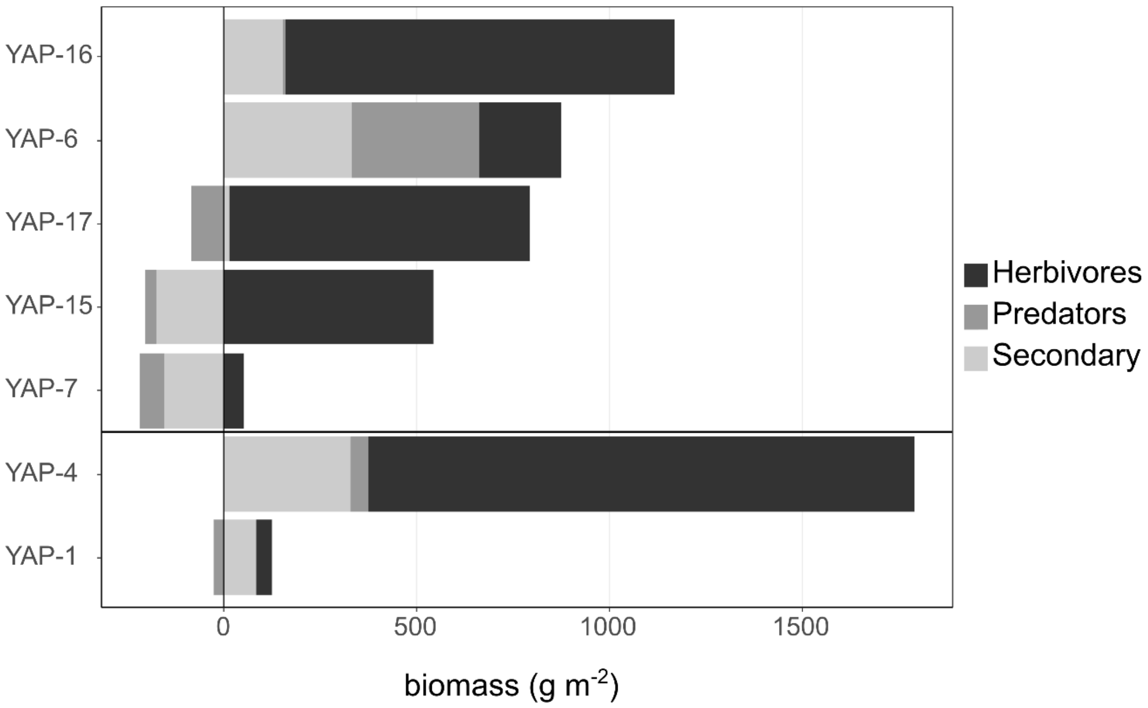


*Figure 9: Changes in trophic level biomass from 2011-2016 for MPA sites. Sites above the solid black line belong to cluster 1, below the line belong to cluster 2.*

The ecological results were added to the MCA plot as a *post hoc* MPA outcome (i.e., fish assemblage condition comparisons between MPA and reference sites, signed positive or negative; Figure 5). MPA outcomes correlated with both dimensions (Dim 1: $R^2 = 0.28$, $p = 0.03$; Dim 2: $R^2 = 0.26$, $p = 0.04$). Positive MPA outcomes correlated with strong MPA leadership, enforcement, community input in decision-making, and MPA infrastructure. Negative MPA outcomes correlated with a lack of enforcement, low levels of input or consultation with community members, an absence of strong MPA leadership, and a perception that MPAs are not working. While ecological outcomes were generally similar within clusters, there were two notable instances where a mismatch between social clusters and ecological outcomes existed (4 and 7, individuals 12-14 and 15-17, respectively, (Figure 10). Site 4 had positive MPA outcomes, yet lacked the social-political infrastructure of other positive MPAs. Conversely, site 7 had negative MPA outcomes but governance structure that mirrored MPAs with positive outcomes.

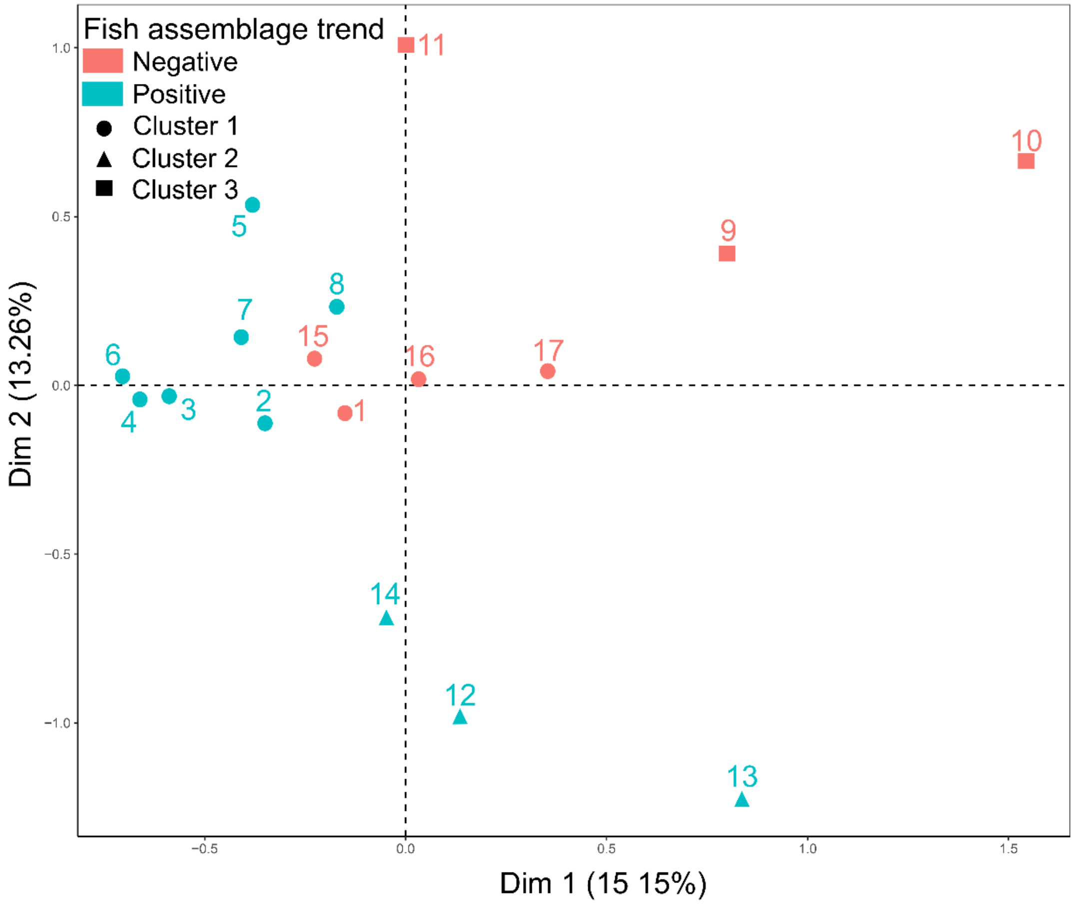


*Figure 10: Biplot of relationship between MPA clusters and fish assemblage outcomes. Colors indicate trend in fish assemblage metrics. Shapes indicate MPA social cluster. Cluster 1 and cluster 3 contained sites with negative MPA outcomes.*

### *Social perception of fisheries trends outside of MPAs*

Social surveys highlighted a general perception that fishery resources were improving for non-MPA reefs (Figure 11). Yet, temporal analysis shows that the majority of non-MPA sites have not improved throughout time (Figure 12).

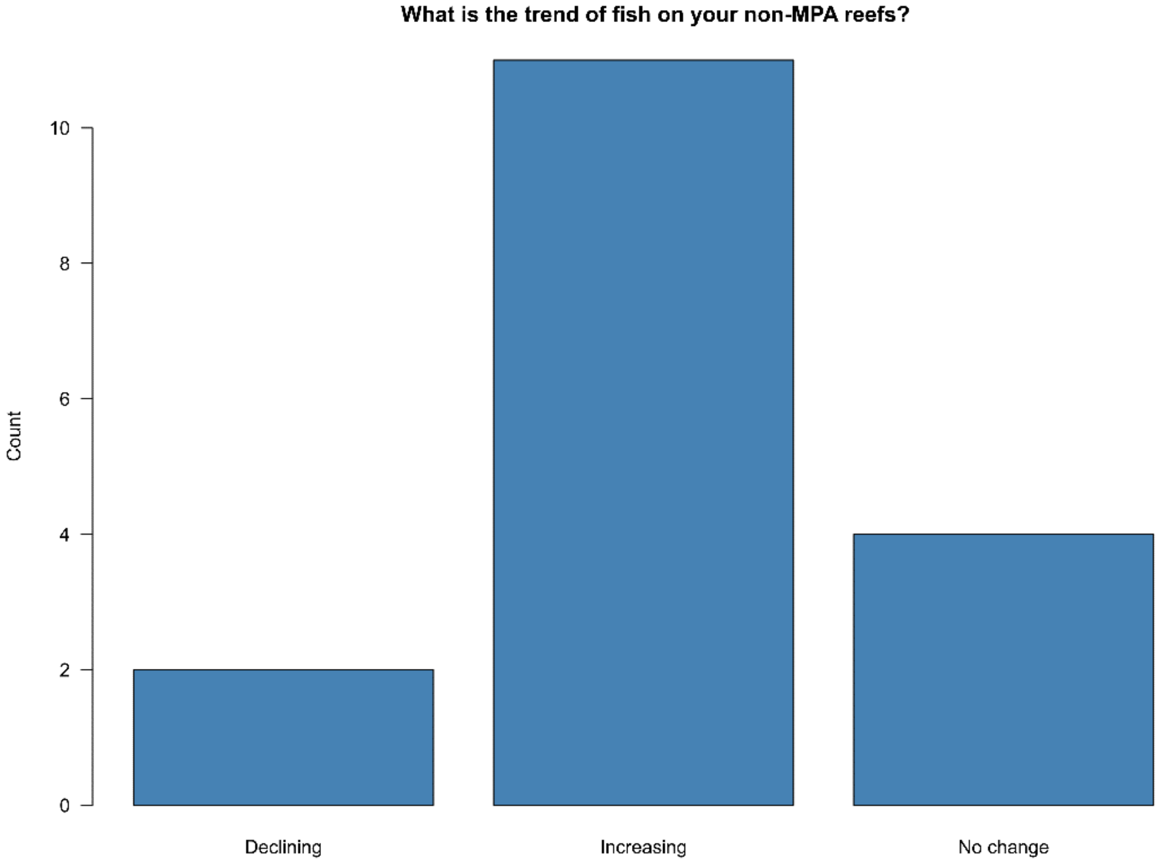


*Figure 11: Histogram of responses to the question pertaining to the perception of fishery resources on Yap.*

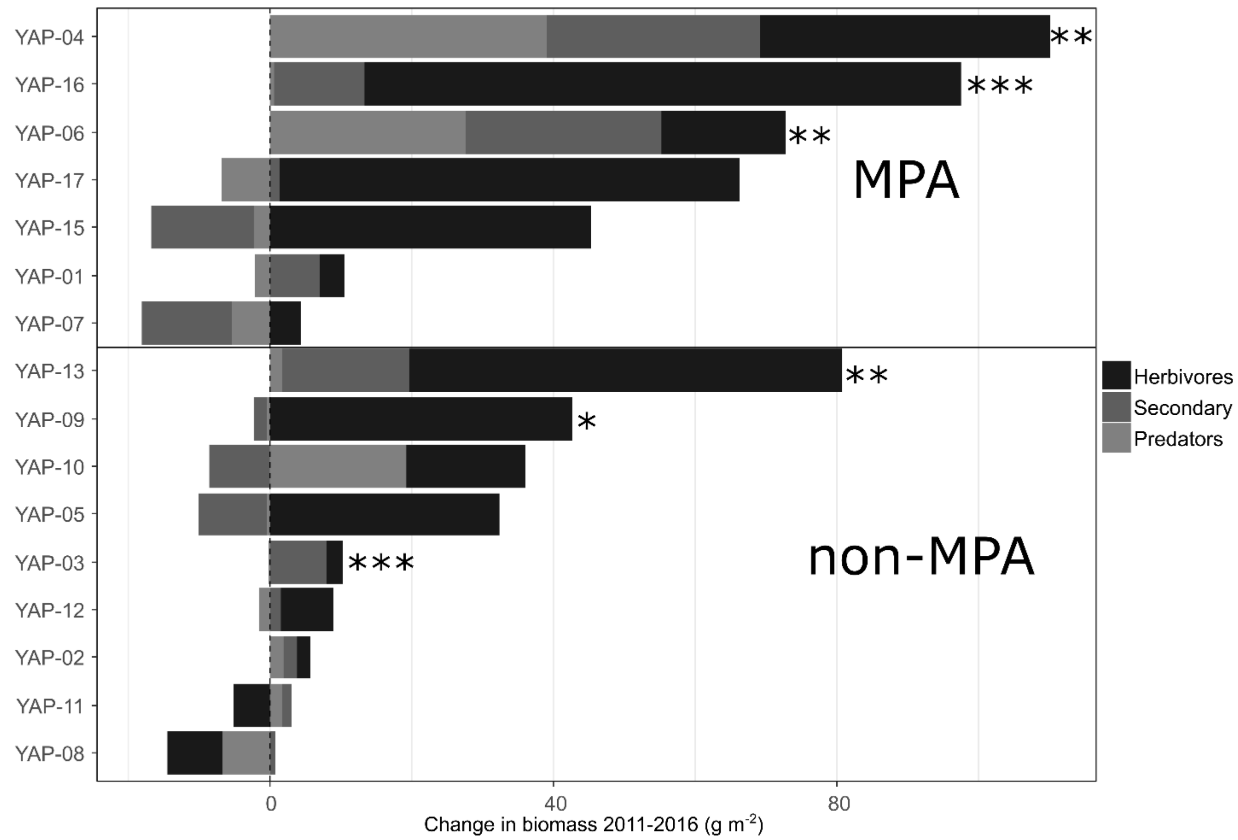
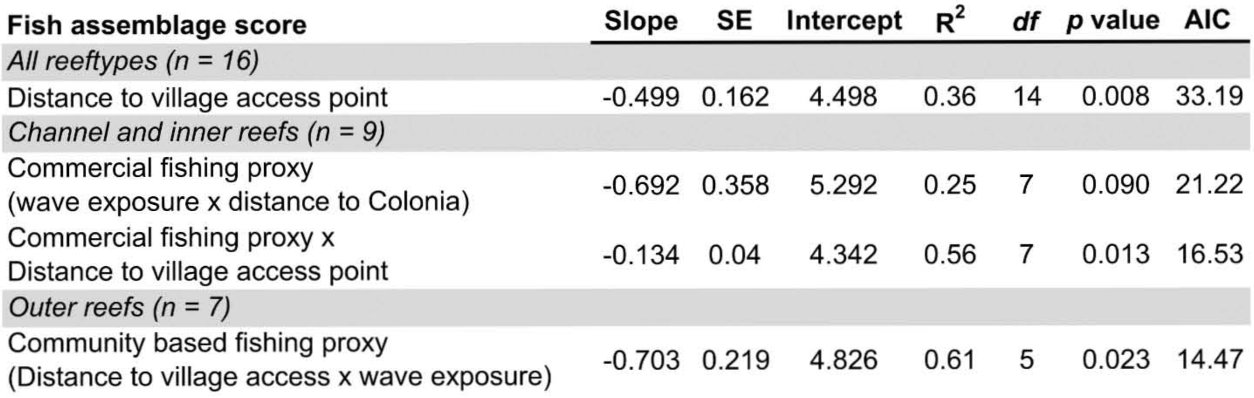


*Figure 12: Changes in fish biomass by trophic level.* *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Further, stepwise-forward regressions suggested that a human footprint existed and predicted a gradient of fish assemblage conditions across Yap (Table 6). Proximity to local fishing access was most influential in predicting fish assemblage condition (Figure 13). Reefs closest to community access points had low fish assemblage scores ($R^2 = 0.36$, $p = 0.008$). Channel and inner reefs were best described by an interaction of distance to village access point and a proxy for commercial fishing (distance to main port x wave energy; $R^2 = 0.56$, $p = 0.013$, $df = 7$; Figure 14).

*Table 6: Results of stepwise-forward regression models describing fish assemblage score.*



| **Fish assemblage score** | **Slope** | **SE** | **Intercept** | **$R^2$** | ***df*** | ***p* value** | **AIC** |
|---|---|---|---|---|---|---|---|
| *All reeftypes (n = 16)* | | | | | | | |
| Distance to village access point | -0.499 | 0.162 | 4.498 | 0.36 | 14 | 0.008 | 33.19 |
| *Channel and inner reefs (n = 9)* | | | | | | | |
| Commercial fishing proxy<br>(wave exposure x distance to Colonia) | -0.692 | 0.358 | 5.292 | 0.25 | 7 | 0.090 | 21.22 |
| Commercial fishing proxy x<br>Distance to village access point | -0.134 | 0.04 | 4.342 | 0.56 | 7 | 0.013 | 16.53 |
| *Outer reefs (n = 7)* | | | | | | | |
| Community based fishing proxy<br>(Distance to village access x wave exposure) | -0.703 | 0.219 | 4.826 | 0.61 | 5 | 0.023 | 14.47 |

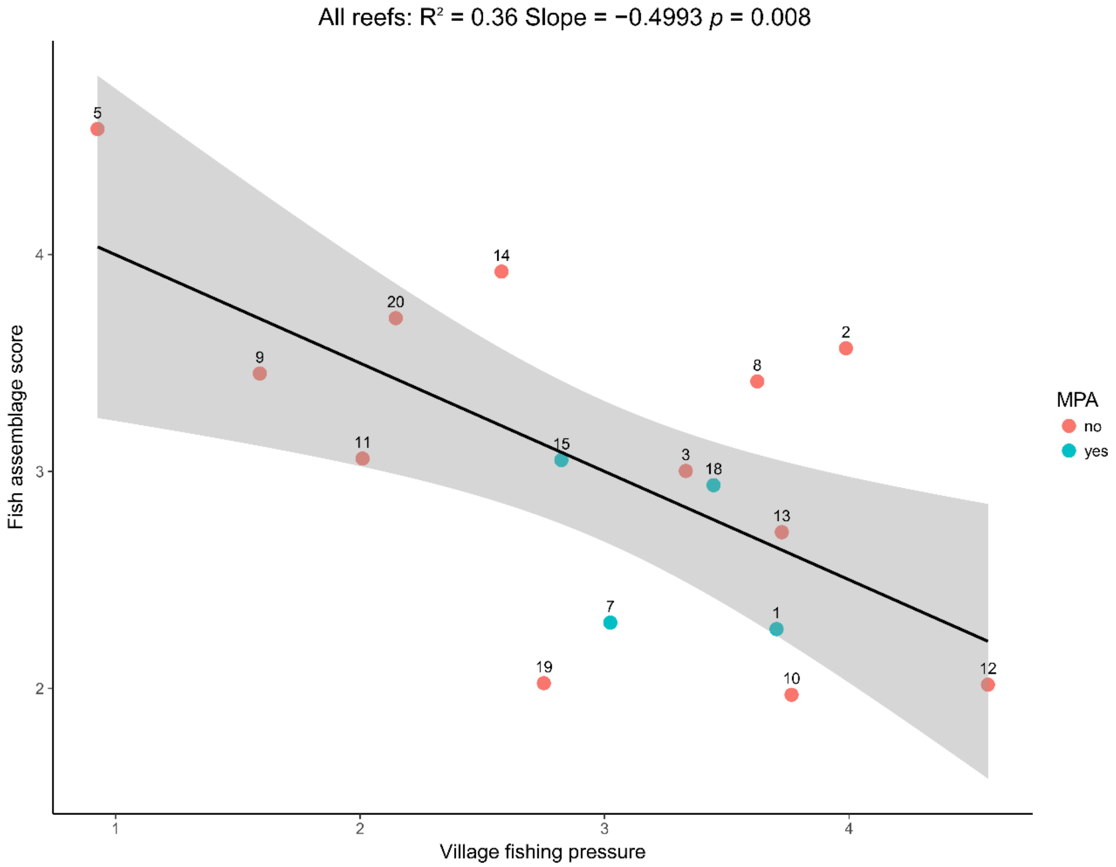


*Figure 13: Best-fit model describing fish assemblage score for all reef types. Fish assemblage score decreases with increased village fishing pressure (proximity to local access points). Shaded area represents 95% CI.*

Correlation testing revealed that local fishing access and commercial fishing were not associated ($R^2$ = -0.24, $p > 0.05$) suggesting that the two types of fishing may have unique impacts. Outer reef fish condition scores were best predicted by community-based fishing proxy (close distance to local access point X low wave energy; $R^2$ = 0.61, $p = 0.023$, $df = 5$; Figure 15). This model suggests that villages will utilize the habitats that are most accessible with the most favorable conditions. Proxies for pollution were not linked to fish assemblage trends for either inner or outer reefs.

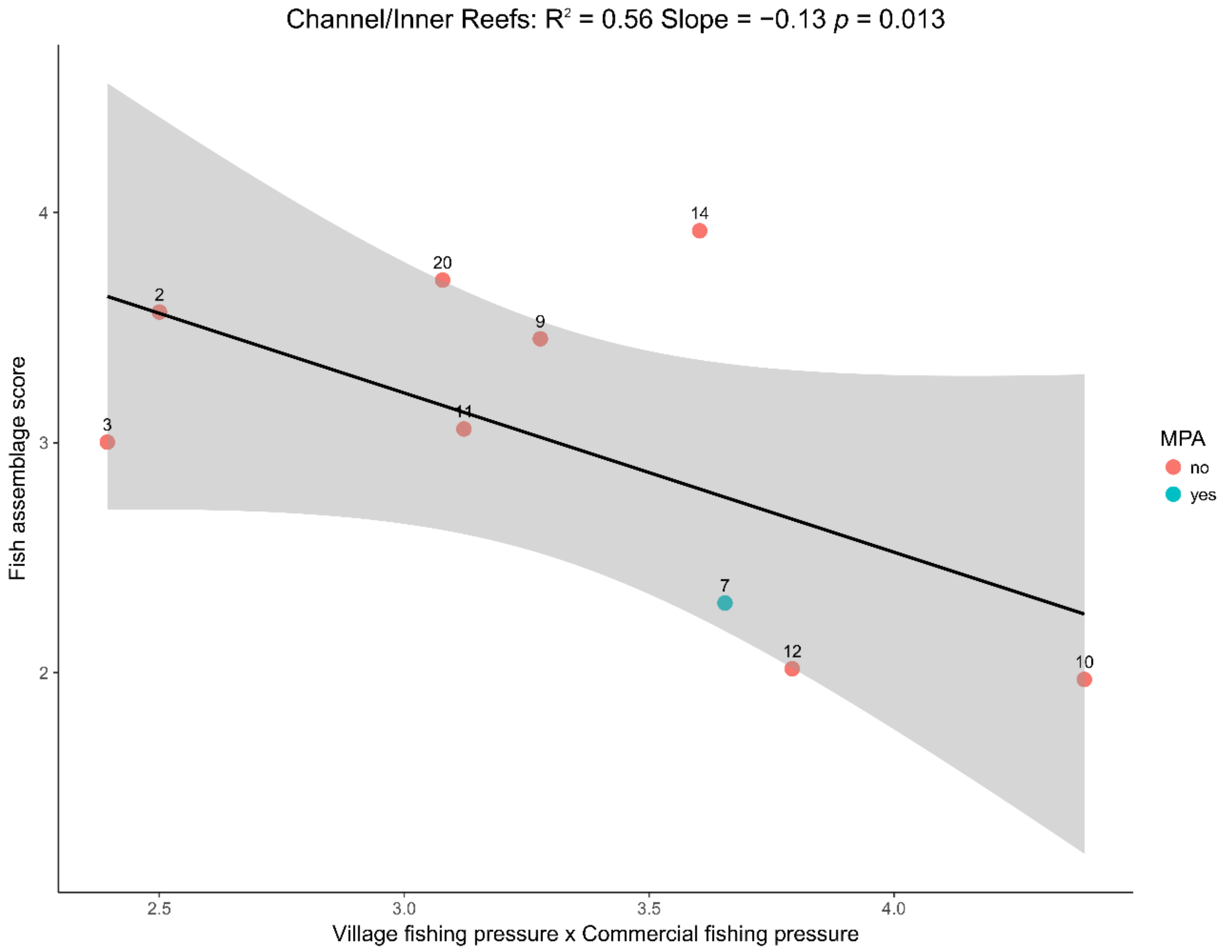


*Figure 14: Best-fit model describing fish assemblage score for channel & inner reef sites. Fish assemblage score is a function of the interaction between village fishing pressure (proximity to local access points) and commercial fishing pressure (proximity to Colonia x wave energy). Shaded area represents 95% CI.*

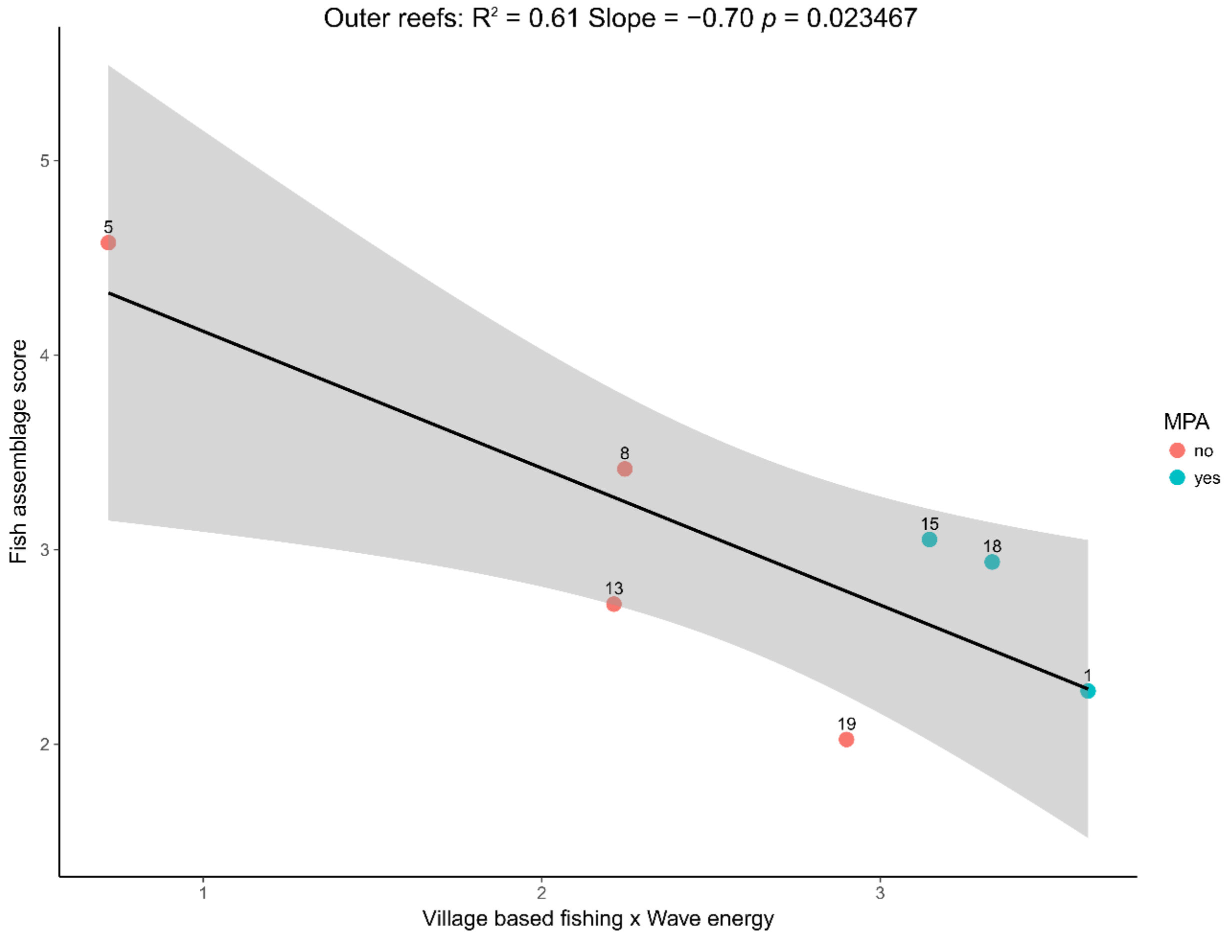


*Figure 15: Best-fit model describing fish assemblage scores for outer reef sites. Fish assemblage score decreases with increased village fishing pressure (proximity to local access points) and wave energy. Shaded area represents 95% CI.*

## Discussion

Successful ecological outcomes in Yap were linked to an underlying social structure characterized by positive attributes for governance and social cohesion. Local management groups, key individuals, and high levels of enforcement were the most important aspects of governance. In turn, these positive governance features were associated with beneficial MPA infrastructure, such as public signboards and boundary markers (Di Franco et al. 2016). While strong governance has previously been linked with successful management and conservation (Christie and White 2007), the present results suggested that social cohesion could play an equal or even greater role. The greatest ecological outcome was associated with a village that lacked key leaders and management groups, but instead relied upon communal fishing and perceived social benefits of MPAs, which foster social cohesion. In contrast, MPAs with poor ecological outcomes lacked key governance features, perceived a decline in the state of the fishery, and had low levels of community cohesion. As a result, fish assemblages on these reefs, as well as non-MPA reefs, were structured by access and proximity to people, similarly reported 5 years ago (Houk et al. 2012a). Therefore, beyond governance, a link between social cohesion and reef health existed that may reveal solutions for ecological shortcomings in coral reef social-ecological systems.

### *Social structure linked to positive ecological outcomes*

Research into the underlying social conditions for conservation success has grown substantially (Bodin et al. 2014, Epstein et al. 2015, Damiens et al. 2017). Resource ownership and customary tenure have consistently been identified as key attributes of conservation and management success (Aswani 2005, Aswani et al. 2007, Cinner 2007). Intuitively, resource owners place a greater dependency on management success for their livelihoods, and by fitting the scales of governance and resource use, an adaptive form of management can flourish. Here, customary marine tenure helps us understand why Yap MPAs are among the best in Micronesia (Houk et al. 2015), yet fish assemblage condition differed substantially across the island. Therefore, ownership and tenure that matches social and ecological scales may be a key prerequisite and ideal first step to bolster management success. In support, Sievanen et al. (2013) found that successful management in Fiji was inseparable from resource-user participation. In order for a nationwide ecosystem-based management initiative to take root and succeed, coordination with individual villages, where resource management and use actually occur, was required. The proposed fix to this governance mismatch was moving conservation planning down to the scale of individual villages. Elsewhere, transferring decision-making from the central government to individual villages allowed Kenyan coastal communities to implement adaptive management actions (Cinner and McClanahan 2015). In turn, contextually appropriate management actions originating from local needs led to a positive change in the fishery status. This social structure may have ultimately led to greater social-ecological outcomes and provided a buffer against inappropriate management decisions. Clearly, decentralized decision-making can lead to management success, but variability still exists within systems that have decentralized resource management. Unraveling this variation may reveal specific aspects of governance and social cohesion that constitute primary drivers of positive ecological change.

Beyond ownership and tenure that existed across Yap, this study supported the growing consensus that MPAs with strong dedicated management groups and individuals, management plans, and enforcement capabilities resulted in positive ecological outcomes (Gutiérrez et al. 2011). In turn, widely accepted indicators of conservation success (i.e., MPA signboards, boundary markers, etc.) were physical features associated with a strong underlying governance structure. Di Franco et al.

(2016) also highlight that social-ecological returns to small-scale fisheries can arise from MPAs with five key features centered on governance processes and physical management features. However, the link between social characteristics that lead to governance and physical management features is poorly understood. Our results highlight that social cohesion was a key attribute leading to strong governance and physical MPA features. Social groups that were inclusive and built around networks of communication exhibited greater ecological outcomes. Prell et al. (2010) showed that communication networks help to spread trust among resource users. Similarly, Gutiérrez et al. (2011) highlighted that trust and communication led to an increased sense of social cohesion, which ultimately led to tangible fisheries outcomes. These compelling aspects of social cohesion are important to consider because they ultimately promote social-ecological resilience. Seminal work by Ostrom (1990) emphasized the role that social cohesion plays in buffering against both social and ecological change. Communities with shared goals can navigate ever changing social and political regimes, while maintaining a sustainable relationship with the ecosystem. The combined results and doctrine suggested that management targeted at communal forms of fishing may translate to increased levels of social cohesion, a novel concept in fisheries management and conservation. Innovative approaches might include providing greater resource access for social forms of fishing to build the trust and communication that were linked with cultural and community buy-in to management.

Leadership was a second key social attribute leading to conservation success. Social network theory suggests that centralization of decision-making is important, but how well connected leadership is to the community is critical to the long-term viability of conservation (Prell et al. 2009). Communities with strong leaders, potentially akin to those in cluster 1 here, may only see positive ecological outcomes while dedicated individuals are in place. Alternatively, if a bottom-up approach to leadership exists, less emphasis may be placed on any individual chief or leader to drive positive ecological outcomes, and replacement of leaders will have less effect on the resources. In support, recent findings in adaptive planning frameworks show that bottom-up decision making in small rural communities is critical to inform higher levels of leadership (Chapin et al. 2016). It was suggested that this approach can spread and integrate contextually appropriate conservation strategies. Given that cultural identity is a pillar of Yapese society, it is likely that the ingredients for social cohesion are present, but exist along a gradient throughout the island.

While social cohesion and strong leadership were primary attributes of positive ecological outcomes, physical management infrastructure may provide a reminder, or perpetual reinforcement of conservation success. Correlation coefficients for physical features indicated their strongest link with governance (correlations with governance latent variable and MPA boundary marker: $R^2$ 0.59, $p = 0.002$; MPA signboard: $R^2$ 0.55, $p = 0.004$). While MPA features and elements of governance have also been observed elsewhere in the Philippines (Pollnac et al. 2001), their role may best be to reinforce the social norms associated with long-term success of those MPAs (Christie et al. 2009). Indeed, MPAs in the Philippines with these features were the most resilient to natural disturbances. Therefore, physical MPA features might provide a buffering effect during periods of management transition that ultimately promotes linked social-ecological resilience.

### *Perception of fishery status*

Attempts to utilize perception as an indicator of ecological status have had varying success (see Bennett 2016 for review). Yasué et al. (2010) found that community members perceived greater fish abundances in and around MPAs in the Philippines. However, this perceived increase did not align with the biological data. This study revealed a similar result, with most non-MPAs showing no significant increase in fish biomass. While using perception may not be the panacea to social-ecological monitoring, it does provide a foundation to build successful conservation. Positive perceptions, whether accurate or not, are important for garnering support for conservation (Biggs et al. 2011, Bennett and Dearden 2014). The perception that fishery resources are generally increasing can be used to highlight programs and initiatives that provided positive social-ecological outcomes on Yap to spread success.

### *Potential drivers of ecological gradients in non-managed areas?*

Non-managed fisheries on Yap existed along a gradient predicted by proximity to resources. Micronesia, like much of the world, has become increasingly dependent on and engaged in the global cash-based economy. Commercial fisheries in the region have been expanding over the last several decades, with several fisheries nearing overexploitation (Houk et al. 2012b, Rhodes et al. 2014). While Yap has some of the least developed fisheries, commercial pressures still exist. Respondents from one of the villages near the population center (site 7) indicated that some community members sell fish to the local markets and felt the MPA limited access to fishery resources. At the same time, this village had clearly defined and dedicated leadership. This unraveling of the social cohesion despite strong leadership resulted in poor fish assemblage metrics. However, by identifying the social triggers that compromised fisheries, an improved management framework can grow (Ayers and Kittinger, 2014). Here, the social trigger may have been lack of access to alternative forms of income. The production and sales of betelnut now represents an important economic contribution to Yap, valued at US$5.6 million in 2016 (Yap Bureau of Statistics & Planning 2016). While most of the villages near the population center indicated their participation in the betelnut industry, site 7 indicated they did not, and thus, a greater reliance was placed upon their fisheries resources. This was similarly reported elsewhere in Tajona, Madagascar, where increased fishing effort after the economic collapse of a valuable cash crop existed (Cinner et al. 2009). Communities lacking alternative economic avenues may be more inclined to overexploit their resources. Thus, the growing diversity of alternative source of income on Yap are promising (e.g.,export of betel nut, SCUBA diver access fees, cultural shows, etc.).

### *Improving MPAs and management on Yap*

Further integration of the MPAs on Yap into a true “network” could also be beneficial. The leading definition of an MPA network is vague and open to interpretation, requiring MPAs to operate “co-operatively and synergistically, at various spatial scales and with a range of protection levels that are designed to meet objectives that a single reserve cannot achieve" (IUCN-WCPA 2008). Grorud-Colvert (et al. 2014) categorized MPA networks into five types: *ad hoc*/regional, conservation, management, social, and connectivity. The local MPA network on Yap is *ad hoc* in nature, with designation of new MPAs occurring opportunistically. Over time, this network has evolved and incorporated elements of a social network, providing members with opportunities for knowledge exchange. However, in order to obtain broader ecological goals, formal coordination between villages is necessary. Green et al. (2014) suggest that marine reserves that address fisheries management, biodiversity conservation, and climate change adaptation require six factors: habitat representation; risk spreading; protecting critical, special and unique areas; reserve size, spacing, location, and duration; protecting climate resilient areas; and minimizing and avoiding threats. Common amongst these factors is the need for different MPAs to play different roles. Some villages on Yap have customary tenure over large reef areas of the lagoon, allowing them to protect unique areas or create large reserves. Combing spatial coverage targets such as these with important design principles may provide the people of Yap with improved fisheries and resilient ecosystems.

### *Conclusions*

Interdisciplinary studies that combine social and ecological analytical tools are critical to the longevity of social-ecological systems, as they reveal why conservation actions have variable returns. Overall, this study highlights the role that social cohesion plays in management success and recommends adapting policies that can bolster information sharing and trust among resource users. Community-based management that does not solely rely on leaders and champions could potentially yield sustained ecological outcomes. Community driven decision-making may also be more resilient to social and ecological changes, and more adaptable to changing environmental conditions. Given the relatively short time that MPAs on Yap have been implemented (3 – 8 years), the positive departures from reference sites were encouraging. Perceptions of improving resources were likely a result of success within MPAs. Yet, MPAs cover 24% of reefs on Yap, and despite perceived improvements in fishery resources, most reefs are not improving. Addressing management in areas where leadership or social cohesion was lacking may be an important next step in advancing conservation. Ultimately, supporting policies that account for these key social structure features will lead to improved fisheries management and greater social-ecological resilience.

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