Land use is a better predictor of tropical seagrass condition than marine protection

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Land use is a better predictor of tropical seagrass condition than marine protection

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ABSTRACT

Effective coastal conservation requires a better understanding of how human activities on land may directly and indirectly affect adjacent marine communities. However, the relationship between terrestrial and marine systems has rarely been considered in terrestrial and marine reserve design. Seagrasses are affected by land-based activities due to their proximity to terrestrial systems and sensitivity to fluxes of terrestrially-derived organic and inorganic material. Our study examines how land use patterns adjacent to seagrass meadows influence the ecological integrity of seagrass using a suite of seagrass condition metrics on a landscape level across the Philippine archipelago. Using canonical correlation analysis, we measured the association between environmental variables (land use and seagrass abiotic conditions) with biotic variables (seagrass species richness and abundance). Terrestrial protection adjacent to seagrass meadows, defined as the absence of various anthropogenic land use perturbations, had significant positive effects on seagrass condition. The watershed area, and area of farmland and human development, had the most negative effect on seagrass condition. Using analysis of covariance and regression, we examined how marine protected area (MPA) establishment, size, and age, affected seagrass biotic conditions while holding environmental conditions constant. The relationship between biological and environmental canonical factors did not vary as a function of an MPA. This study provides evidence that land use is more important than marine protection for tropical seagrass condition. Our results demonstrate the complementary connection between land and sea, justifying the 'ridge-to-reef' approach in coastal conservation. Proper management of seagrasses should account for stewardship of the adjacent watersheds.

1. Introduction

The accelerating loss of marine and terrestrial biodiversity and the ecosystem services it provides to people has been a growing concern globally (Turner et al., 2007; Waycott et al., 2009; Cardinale et al., 2012; Tittensor et al., 2014; McCauley et al., 2015). Habitat loss is the second most important driver of past extinctions and the current leading driver which endangers species on land (Tershy et al., 2015), and human impact has had the greatest effect on coastal biodiversity (Lotze et al., 2006). Globally, >US$21 billion is spent annually to prevent and mitigate this loss (Waldron et al., 2013). The creation of protected areas is a well-established tool to reduce this trend via reducing habitat loss and mortality from harvesting (Pimm et al., 2001). There are > 200,000 protected areas worldwide (Chape et al., 2005; Jenkins and Joppa, 2009; Juffe-Bignoli et al., 2014), and ~4400 of those are marine protected areas (MPAs) (Wood et al., 2008), totaling 3.4% of marine area (Juffe-Bignoli et al., 2014). However, up to 421.9 million people worldwide live near the borders of protected areas, resulting in over 83% of MPAs and 95% of terrestrial protected areas (TPAs) being highly impacted by humans (Mora and Sale, 2011).

Many coastal MPAs are at least potentially impacted by human activities on land such as human development and growing human populations (Mora and Sale, 2011), and these MPAs are not necessarily mitigated by marine protection (Valiela et al., 2001; Freeman et al., 2008; Packett et al., 2009). The coastal ecotone is an interconnected set of habitats made up of coastal, estuarine, wetland and freshwater systems that is high in organismal diversity and density (Sheaves, 2009), and important for ecosystem function and services (Beck et al., 2001). This ecotone is important in the transfer of organic and inorganic material between terrestrial and marine ecosystems (Cloern, 2007). However, it is also where 60% of the world's growing human population is located, resulting in direct habitat conversion for housing, transportation, energy, and agriculture, and in indirect conversion due to increased physical disturbance, eutrophication and sedimentation (Musters et al.,

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2000; Sala et al., 2000; Hughes et al., 2009). In developing countries, the daily subsistence of coastal inhabitants is largely derived from these transitional zones (Nordlund et al., 2010; De la Torre Castro et al., 2014; Cullen-Unsworth et al., 2014).

Seagrasses are shallow-water coastal marine plants that provide important ecosystem services such as carbon sequestration (Fourqurean et al., 2012), wave attenuation (Bradley & Houser 2009), and habitat and nursery area to a variety of commercially important fish and invertebrates (Hughes et al., 2009). Seagrasses are often used to assess the health of the nearshore marine environment (Martinez-Crego et al., 2008) with studies showing that siltation from suspended inorganic solids (Bach et al., 1998) and upstream watersheds (Freeman et al., 2008), sediment burial (Duarte et al., 1997), water pollution and sediment deposition (Van Katwijk et al., 2011) all impact seagrass condition. Seagrass species population declines are due both directly or indirectly to anthropogenic impacts (Waycott et al., 2009; Short et al., 2011), and there is a call to reduce watershed nutrient and sediment inputs to seagrasses to stem seagrass loss (Orth et al., 2006).

Consequently, there is growing interest in integrating terrestrial and marine conservation in the coastal zone (Cicin-Sain and Belfiore, 2005; Stoms et al., 2005; Richmond et al., 2007; Tallis et al., 2008; Beger et al., 2010; Klein et al., 2010; Alvarez-Romero et al., 2011). However, the establishment of marine and terrestrial protected areas has largely proceeded independently, without examination of the costs or benefits of co-locating marine and terrestrial protected areas (Stoms et al., 2005). While others have modeled different land-use scenarios on coral reef and seagrass response (Tulloch et al., 2016), this has not been empirically measured.

This study measures the relative importance of marine protection vs. land use to the integrity of tropical seagrass communities on a landscape level at 54 sites across 35 islands throughout the Philippine archipelago. Here, we examine the impact of all MPAs regardless of management practices and levels of compliance compared to the impacts of land use. Specifically, we examined the independent and synergistic effects of marine protection vs. land use, the environmental conditions of the seagrass ecosystem, and the resulting effects on an array of abiotic and biotic indices of seagrass condition.

2. Methods

Our goal was to determine whether seagrass condition varied as a function of environmental attributes, marine protection, and land use. To address this goal, we sampled 54 seagrass meadows adjacent to 35 islands ranging in area from small islands of <1 km^2 (Agutaya) to large islands of over 100,000 km^2 (Luzon) (Fig. 1). We surveyed approximately 50% of the latitudinal range of the Philippine archipelago from the northernmost site in the Pangasinan province to the southernmost in the Negros Oriental province.

We selected sites based on geographic representation of marine protected areas and a variety of land uses across the archipelago, and accessibility for conducting fieldwork. Each island exhibited a combination of different land uses ranging from minimal human impact (de facto protected or TPAs) to highly impacted islands (multiple combinations of land uses), while the marine areas were categorized as protected (MPAs) or unprotected.

2.1. Definition of marine protection

Forty-two percent of the sites were located inside MPAs, and included both formal (n = 16) and de-facto (n = 7) MPAs. Formal MPAs were established as fisheries management tools through either the National Integrated Protected Areas System Act of the Philippines (NIPAS) or the Local Government Code of 1991 and the Fisheries Code of 1998, which gave local governments the authority to manage their nearshore marine waters in cooperation with the national government (Russ and Alcala, 1999). De facto MPAs were those managed by private island owners who prevented fishing around their islands. MPAs ranged from complete to incomplete protection; some included no-take zones (n = 15), while others had some level of fishing controls (n = 9). We collected data on the size of each MPA and the year each was established [Appendix 1]. Other studies have found that MPA age and size are among key features that optimize marine biodiversity protection (Claudet et al., 2008; Vandeperre et al., 2011; Edgar et al., 2014). In the Philippines, MPAs in practice have a spectrum of management schemes and compliance to those schemes. Here, we did not attempt to examine the impact of different management schemes, we did not rate the efficacy of MPAs, or assess levels of compliance, but rather we attempted to understand the impacts of MPAs of all types compared to the impacts of TPAs.

While positive effects of an MPA have been demonstrated within 5 years of establishment, previous studies used age >10 years as a threshold for an old MPA and <5 years as a new MPA (Claudet et al., 2008; Molloy et al., 2009; Babcock et al., 2010; Vandeperre et al., 2011; Edgar et al., 2014). Edgar et al. (2014) considered an area >100 km^2 as a large MPA, and an area <1 km^2 as a small MPA. Based on these criteria, we categorized an MPA of <5 years as new and older than 5 years as old, and an MPA <1 km^2 as small, and an MPA larger than 1 km^2 a large MPA. Globally, almost half of all MPAs are small 1 km^2 and are new (Wood et al., 2008). In our suite of samples, 65% were old/large, 17% were old/small, 9% were new/large, and 9% were new/small.

2.2. Definition of terrestrial protection

Since there is a lack of officially designated coastal terrestrial protected areas in the Philippines, we developed a proxy for terrestrial protection based upon level of human land use in two zones: (1) the watershed, or catchment that drained into the seagrass meadow, and (2) a 50-m wide coastal strip on the island adjacent to each seagrass meadow. Using ArcMap, we obtained Basemap satellite imagery (World Imagery) of the islands from ArcGIS online (ESRI, 2011). Using ArcCatalog, we created a geodatabase for each island. Using ArcMap, we created a new layer and shapefile for each island outline. With the polygon tool, we heads-down digitized islands by manually tracing each island outline. We digitized whole islands if they were smaller than 5 km^2, while for the 3 larger islands (Luzon, Negros, Mindoro), we only digitized the affected watershed.

To delineate the watershed that affected each seagrass bed, we overlayed ArcGIS Online's Topographic and World Shaded Relief layers with low resolution (15 m imagery). We adjusted the transparency of the layers using the effects toolbar (50% transparency) and toggled between the two layers. Using ArcCatalog, we created a shapefile for each watershed, and using the draw, trace function and point drawing tools in ArcGIS, we manually traced the watershed that drained into each of the seagrass meadows based on the changes in elevation (ESRI, 2011). To calculate the area of each island and the total area of each watershed, we opened the attribute table for each shape file, added a field for area, then calculated the geometry in square kilometers.

We classified land use in the following categories: human development (houses, commercial development, roads), vegetation (forests, scattered trees), bare ground (exposed soil, fallow farmland), farmland, and aquaculture. We considered areas containing native vegetation as protected (Klein et al., 2010). Unlike marine protection, which was a binary code, terrestrial protection ran along a gradient of different forms of land uses and vegetation in each watershed or coastal trip.

We created a feature class for each land use category, visually assessed the type of land use, and used the polygon and the edit vertices tool to trace out land use types for each island or watershed. We kept each land use category in separate feature classes. Our layers had resolutions that varied from low resolution (15 m imagery, Landsat 5; https://landsat.usgs.gov/) to high resolution (60 cm imagery,

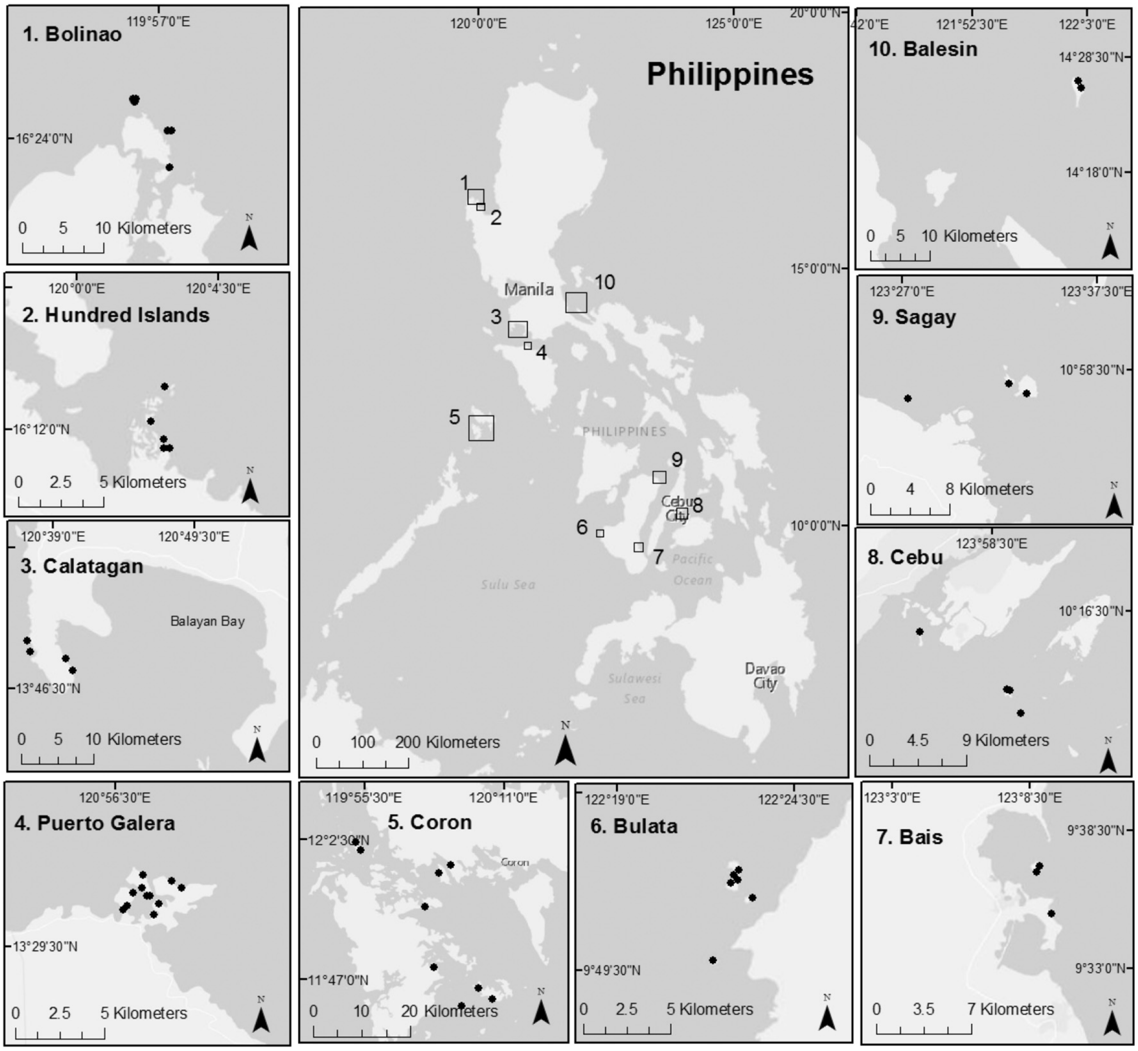

Fig. 1. 54 seagrass beds in 10 regions in the Philippines were selected for the final model; 24 seagrass beds (44% of sites) were inside MPAs: 1) Bolinao – 5 seagrass beds, 2) Hundred islands – 7 seagrass beds, 3) Calatagan – 4 seagrass beds, 4) Puerto Galera – 11 seagrass beds, 5) Coron – 9 seagrass beds, 6) Bulata – 6 seagrass beds, 7) Bais – 3 seagrass beds, 8) Cebu – 4 seagrass beds, 9) Sagay – 3 seagrass beds, 10) Balesin – 2 seagrass beds.

Worldview 3 satellites; https://www.digitalglobe.com/resources/satellite-information), so we compared ArcMap's Basemap imagery to Google Earth by finding the island with the associated GPS coordinates and cross-referenced houses and other recognizable features.

After digitizing all feature classes, we opened the attribute table of each feature class and created a new field for area, and calculated the geometry of each feature class in square kilometers. We summed the areas of each feature class to obtain the total area covered by each land use, and we did this for each island and for all the watersheds that corresponded to each meadow.

2.3. Seagrass ecological survey

We surveyed 54 seagrass meadows around 34 islands and/or peninsulas in the Philippines between June and August in 2011 and 2012. Due to logistical constraints, we visited each seagrass meadow only once during the rainy season. Around some islands, we surveyed multiple seagrass sites; each meadow was within 0.25 km from the shore.

We measured multiple indices for all seagrass species across sites, and focused additional sampling on *Enhalus acoroides*. As a canopy forming, climax species in this tropical seagrass assemblage, *Enhalus acoroides* dominates the dry weight biomass of a meadow, and is relatively insensitive to siltation and lower light levels, and may indicate reduced environmental state (Terrados et al., 1998). At each site, we established two 50-m transects parallel to shore in the middle of each seagrass bed: one on the shallow, shoreward side of the bed, and the second 50 m seaward from the first. At the 0 m, 25 m, and 50 m points along each line we measured salinity (refractometer), water temperature (Suunto D4), and depth (meter tape), and measured underwater horizontal visibility using a secchi disk.

We placed 0.25 m^2 quadrats at 10 or 12 randomly assigned points along each 50 m transect. Within each quadrat we measured seagrass species richness, percent cover, shoot density, above-ground biomass, and canopy height using standardized SeagrasssNet methods (http://www.SeagrassNet.org).

2.3.1. Sediment sample collection

We obtained three replicate sediment cores from 10 cm depth in the middle of each seagrass bed using a 0.03 m^2 core. The contents of the first two cores were sun dried and stored in plastic bags for subsequent quantitative grain size analysis and sediment component identification. The third core was divided into three 50 g subsamples that were frozen in HDPE plastic bottles upon returning to the mainland, and used for sediment percent organics.

2.3.2. Quantitative grain size analysis

We used the dry sieving method to determine grain size of the sediment collected from each site. Fifty grams of the sediment collected from the cores were oven-dried for 24 h at 50 °C, and sieved to grain sizes ranging from gravel to very fine sand. Samples were subsequently binned into three grain size classes: (1) coarse size class sediment, which included gravel (2–4 mm), very coarse (1–2 mm), and coarse sand (0.50–1 mm), (2) medium size class sediment, which included medium (0.25–0.50 mm) and fine sand (125–250 μm), and (3) fine size class sediment, which included very fine sand (62.5–125 μm) and silt (3.90625–62.5 μm).

2.3.3. Sediment classification

After sieving, we sorted known calcareous material from unknown material using a dissecting scope, then placed the remaining sediment in a test tube and acidified them with a 10% HCl solution to remove unknown carbonate material. After all the unknown calcareous components disappeared (anywhere between 2 and 4 days), we dried out the remaining material and classified it as terrestrial material, and the proportion of terrestrial material was calculated out of the total weight of the subsample.

2.3.4. Sediment organic matter

The relative organic carbon content of the sediment from each site was measured using Loss on Ignition (LOI) methods. Sediment collected from each seagrass bed was frozen for transportation and then dried at 50 °C for 24 h. We homogenized each sample using a mortar and pestle and weighed 2–3 g in a crucible. Three samples per site were divided into three replicates for a total of 9 crucibles per station used for organic carbon analysis, for a total of 9 crucibles per site; we used the mean of those crucibles to estimate percent organic matter of the sediment at each site. The sediment, including the crucible, was weighed using a balance to get the initial weight. The sediment and the crucibles were placed in an oven at 550 °C for 16 h, then removed and left to cool before weighing for LOI (Craft et al., 1991).

2.4. Statistical analyses

To assess the effect of terrestrial and marine protection on the state of seagrass communities, we employed a three-part analysis that included: canonical correlation analysis (CCA), analysis of covariance (ANCOVA), and regression.

CCA was used to examine the relationship between environmental variables and fish diet in marine protected areas (Loury et al., 2015), the effect of environmental variables such as tidal exposure and water motion on biological variables such as seagrass biomass, growth rates, C:N and N:P of seagrass tissue (Erftemeijer and Herman, 1994), as well as the effects of temperature, dissolved inorganic nitrogen, rainfall, daylight exposure and wind speed on seagrass density, growth rate, root: shoot ratio and percent cover (Lin and Shao, 1998).

To test whether land use had an effect on the state of seagrass communities in each of the sites, we employed a CCA to find sets of predictor variables that most strongly associated with sets of response variables (Quinn and Keough, 2002). We considered biological variables the response variables, and environmental variables the predictor variables. We considered the mean biological and environmental variables for each site as independent replicates (i.e. a single value per variable per site). Environmental variables included both physical variables (salinity, depth, visibility, sediment characteristics), and land use variables that characterized terrestrial protection included area of human development, area of aquaculture, area of farmland and area of vegetation in the greater watershed, and area of human development, aquaculture, farmland, and vegetation within a 50-meter coastal strip that ran parallel to the seagrass meadow (Table 1). CCA extracts paired sets of variables along with their coefficients such that CC1 is the most explanatory pair, followed by CC2 and so on. The null hypothesis is that there is no correlation between any of the pairs of canonical factors, using Bartlett's χ^2 tests (Quinn and Keough, 2002).

Using Eigen analysis, CCA computes coefficients and loadings for each set, and we interpreted the canonical correlations between the canonical factors using the signs associated with the variables within each set. Canonical coefficients are unbound and show the direction of the relationship, while canonical loadings measure the strength of the linear relationship between the original variables and the derived canonical variate (Quinn and Keough, 2002). Previous studies considered variables with canonical loadings >0.5 to show a good fit between the x and y variables with larger values of canonical coefficients showing

Table 1
Summary of canonical correlation analysis (CCA) performed on seagrass biological and environmental/land-use variables. Canonical coefficients showed the direction of the relationship between biological and environmental/land use variables; we interpreted coefficients >0.3 as meaningful. Canonical loadings are for the two significant roots (CC1 & CC2). Canonical loadings highlighted in bold best explained the CCA model.

	CC1 (canonical correlation) = 0.814, p = 0.000 R_c-squared = 0.846		CC2 (canonical correlation) = 0.790, p = 0.001 R_c-squared = 0.830	
	Canonical coefficients of CC1	Canonical loadings of CC1	Canonical coefficients of CC2	Canonical loadings of CC2
Environmental variables				
Watershed area bare ground (km^2)	0.136	0.521	0.016	−0.062
Watershed area human development (km^2)	−0.790	−0.001	−0.236	0.241
Watershed area aquaculture (km^2)	0.019	0.347	0.327	0.139
Watershed area farmland (km^2)	0.309	**0.376**	−0.334	0.073
50 m coastal strip area bare ground (km^2)	0.229	0.503	0.261	−0.106
50 m coastal strip area farmland (km^2)	0.324	0.191	0.249	**0.401**
50 m coastal strip area human development (km^2)	0.578	0.038	0.817	**0.481**
50 m coastal strip area aquaculture (km^2)	−0.354	**0.356**	0.089	0.163
Watershed area	0.542	**0.589**	−0.422	−0.204
Salinity (ppt)	−0.025	−0.252	0.282	0.253
Depth (m)	0.656	−0.243	−0.015	−0.190
Horizontal visibility (m)	−0.337	**−0.258**	0.268	0.217
Sediment Loss on Ignition (LOI)	0.249	**0.395**	0.024	−0.040
Proportion terrestrial material (Phi 0)	0.126	0.156	0.264	0.195
Medium size class sediment per kg	−0.291	−0.180	−0.569	**−0.506**
Fine size class sediment per kg	−0.171	0.060	0.018	−0.004
Biological variables				
Seagrass species richness	0.676	**0.893**	0.660	0.108
Total seagrass biomass (g)	0.160	0.042	−0.097	−0.495
Canopy height *Enhalus acoroides* (m)	−0.477	**−0.715**	−0.369	−0.113
Canopy height all other species	−0.023	−0.025	−0.311	**−0.352**
Total seagrass % cover (m^2)	0.090	0.755	−1.195	**−0.609**
Total seagrass density (m^2)	−0.028	0.736	0.060	0.038

greater effect (Erftemeijer and Herman, 1994). We included variables with at least 0.4 for canonical loadings and 0.3 for canonical coefficients in our interpretation. Significant canonical factors show strong associations between biological & environmental variables. To graphically represent those associations, we divided each graph into four quadrats and placed the biological canonical factors on the y axis and the environmental canonical factors on the x axis, and used the coefficients and loadings from each set to interpret the CC graphs.

To ask if there was an effect of marine protection on the biological canonical factors after controlling for environmental canonical factors, we employed one-way ANCOVAs. We plotted the biological canonical factors on the y-axis and the environmental canonical factors on the x-axis. We performed three separate one-way ANCOVAs to test for the difference in slopes between the sites that had 1) an MPA (present or absent), 2) large MPAs (defined as >1 km^2), small MPAs (defined as <1 km^2), and sites without MPAs, and 3) old MPAs (defined as >5 years old), new MPAs (defined as <5 years), and sites without MPAs.

If the interaction term in the ANCOVA (e.g. CC1 environmental $\times$ MPA age) was not significant, we concluded that the slopes of the relationship for each level (e.g. MPA age = young, old) of the categorical variable were equivalent and we ran a reduced model, concluding that the covariate did not affect the relationship between MPAs and biological variables. A significant interaction in the ANCOVA model indicated that the two slopes differed, meaning that the covariate (CC1 or CC2 environmental canonical factors) had an effect on the relationship between MPAs and biological canonical factors.

The final step was to determine the nature of the difference in slopes. We performed separate linear regressions, one for each level of the categorical variable in the model (i.e. presence or absence of MPA, old versus new versus no MPA, and small versus large versus no MPA) to test if each of the slopes differed from zero, and by how much.

3. Results

Land use associated with terrestrial protection had significant effects on seagrass richness and abundance, while marine protection did not have an effect. Our CCA found a strong relationship between environmental and biological variables, and the first two canonical variate pairs were significant ($p < 0.001$ for both) (Table 1). The first CCA showed low areas of farmland were associated with high seagrass species richness and the second CCA found low areas of human development and farmland were associated with high seagrass abundance. Farmland and urbanization were the primary land-use variables that determined seagrass condition, with greater levels of farmland and urbanization leading to worsening condition, as evident by the results of the CCA.

3.1. Relationship between biological and environmental variables

3.1.1. Effect of land use

For the first canonical root or CC1, there was a significant negative relationship between biological and environmental canonical factors ($r = 0.814$, $p < 0.000$). Sites in the upper left hand side corner had seagrass meadows with high seagrass species richness and low *Enhalus acoroides* canopy height, associated with high visibility and low sediment organic matter, and small watersheds, small areas of farmland in the watershed, but high areas of aquaculture on the coast. Sites in the lower right hand corner were characterized by abundant *Enhalus acoroides*, low visibility, low areas of aquaculture at the coast, and high sediment organic matter, large watersheds with large areas of farmland (Table 1, Fig. 2). In CC1, lower values along the y-axis corresponded to high *Enhalus acoroides* canopy height and low seagrass species richness, while the greater values corresponded to high seagrass species richness and low *Enhalus acoroides* canopy height. Lower values along the x-axis corresponded with high visibility and high areas of coastal aquaculture, small watersheds and low sediment organic matter, and a set of environmental characteristics, or land uses that related to terrestrial protection (i.e. low areas of farmland in the watershed). Higher values along the x-axis corresponded with low visibility, low areas of coastal aquaculture, large watersheds, high sediment organic matter, and a set of environmental characteristics related to the land use without terrestrial protection, (i.e. high areas of farmland in the watershed) (Fig. 2).

For the most part, we choose to characterize sites on the meadow level. However, we separated canopy height of mixed species seagrass beds into two groups. The first corresponded to the canopy height of *Enhalus acoroides*, a climax species that is less sensitive to siltation (Terrados et al., 1998), and the second group to canopy height of all the other species in the bed. This distinction is evident in CC1, where

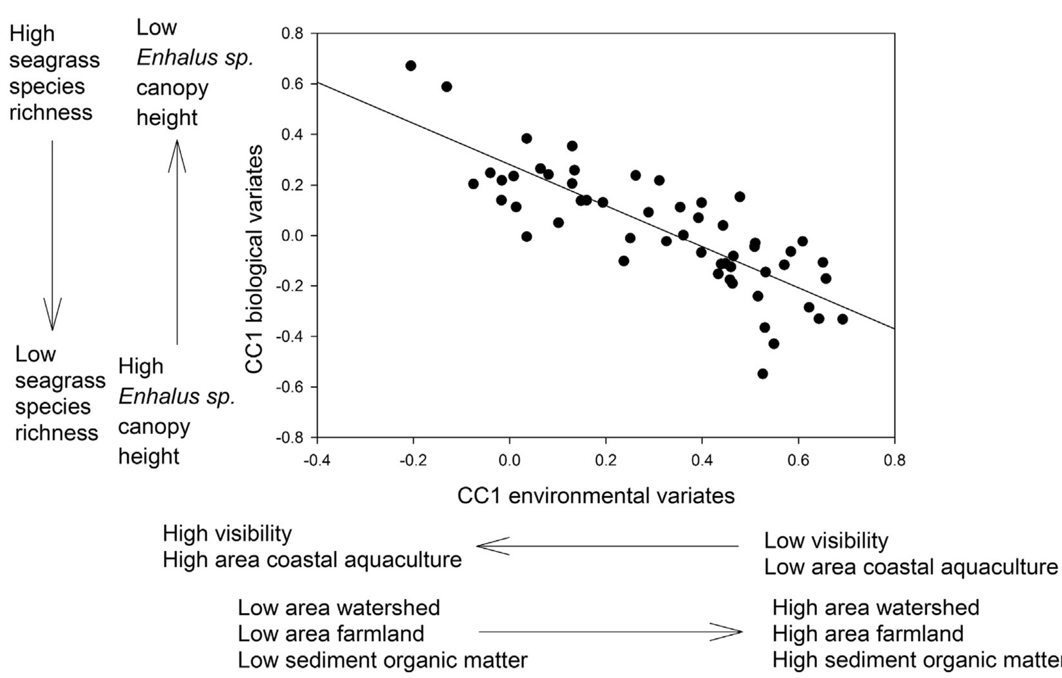

Fig. 2. CC1 environmental versus CC1 biological variables.

seagrass species richness was in the opposite direction of *Enhalus acoroides* abundance. The CC1 y-axis shows that *Enhalus acoroides* canopy height was negatively associated with seagrass species richness. Moreover, the CC1 x-axis shows that *Enhalus acoroides* canopy height was positively associated with large watersheds containing greater areas of farmland.

For the second canonical root, or CC2, there was a significant positive relationship between biological and environmental canonical factors ($r = 0.790$, $p = 0.001$). Sites in the lower left hand corner were meadows with high seagrass abundance associated with more medium grained sediment, low areas of coastal human development and low areas of coastal farmland, while sites in the upper right hand corner were seagrass meadows with low abundance, associated with high areas of coastal human development and high areas of coastal farmland (Table 1, Fig. 3). In CC2, the lower values on the y-axis corresponded to high seagrass canopy height and percent cover, while the higher values corresponded to low seagrass canopy height and percent cover. Lower values along the x-axis corresponded to environmental characteristics such as more medium grained sediment and a set of environmental characteristics such as low areas of coastal farmland and coastal human development. Higher values along the x-axis correspond with less medium grained sediment and environmental characteristics related to land uses, such as increased area of coastal farmland and human development adjacent to the seagrass bed (Fig. 3).

In sum, our CCA found greater seagrass condition (greater seagrass species richness and abundance) was associated with smaller watersheds with reduced area farmland in the watershed, and reduced human development and farmland along the coast.

3.1.2. Effect of marine protection

We found no significant effect of marine protection on seagrass condition. Our ANCOVA tested for a difference in slopes of the relationship between the biological and environmental factors, as a function of the covariates (Figs. 2, 3). The relationship between the CC1 biological canonical factors and CC1 environmental canonical factors did not vary as a function of the presence or absence of an MPA, MPA size (small, large, no MPA), nor MPA age (new, old, no MPA). The relationship between CC2 biological canonical factors and CC2 environmental canonical factors did not vary as a function of the presence or absence of an MPA, MPA size (small, large, no MPA), nor MPA age (new, old, no MPA).

4. Discussion

4.1. Overall results

We examined the relative importance of land use versus marine protection as indirect drivers of seagrass condition and found that terrestrial influences had the most important effect on seagrass abundance and richness, and the proximate drivers for these conditions were related to sediment characteristics. In contrast, marine protection had little impact on seagrass condition. These results support a conservation strategy we propose that *land use is more important than marine protection for maintaining tropical seagrass abundance and species richness.*

4.2. Land use

Land-use practices such as conversion of forest to agricultural lands increased the risk of fine sediments carried by surface runoff, with resulting changes in benthic community composition (Dadhich and Nadaoka, 2012). Similarly, in a subset of sites from this present study, we measured the relative contribution of sediment runoff to seagrass beds, and found less abundance and diversity of seagrass species in sites with greater amounts of sediment captured in sediment traps (Quiros, 2016). In this study, sediment characteristics and visibility were the only in situ abiotic variables that had an influence in our model. We found greater seagrass species richness in meadows with greater visibility and lower sediment organic matter (Fig. 2), and greater seagrass abundance in meadows with medium-grained sediment (Fig. 3). Folmer et al. (2012) modeled the effects of sediment characteristics on seagrass beds and found that seagrass density increases with decreasing grain size and increasing sediment organic matter up to a certain point, after which fine grain sized sediment has a negative impact on seagrass shoot density due to decreased pore water exchange, leading to hypoxic sediment conditions. Increasing siltation and the resulting changes to sediment conditions leads to diminished growing

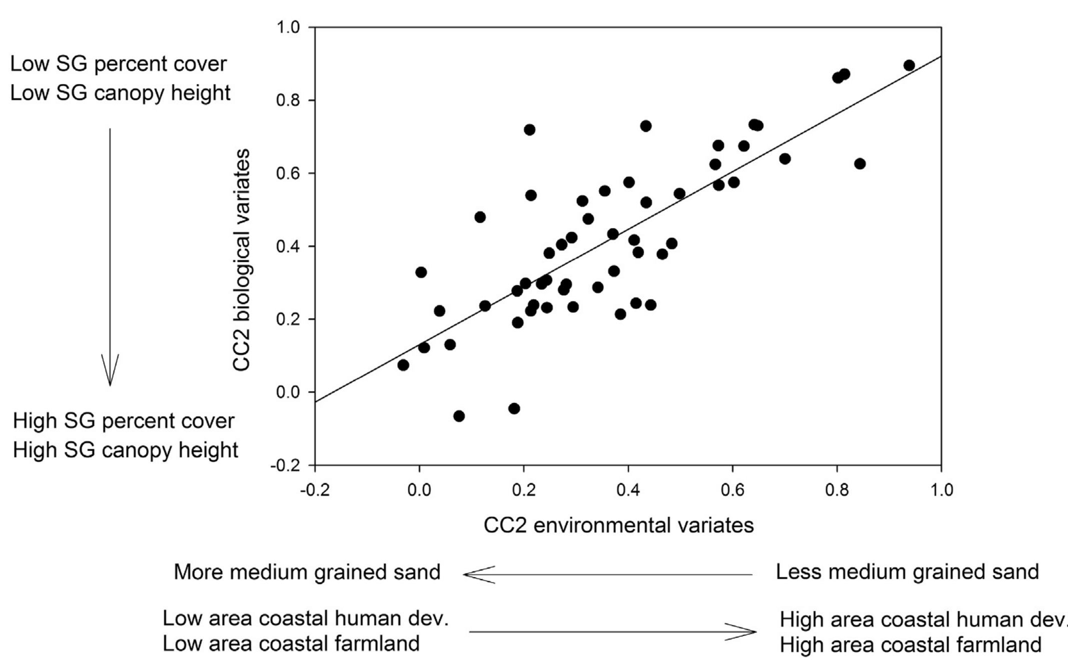

Fig. 3. CC2 environmental versus CC2 biological variables.

conditions for tropical seagrasses (Bach et al., 1998), and experimental burial of nearshore marine sediments with terrestrial sediments resulted in anaerobic sediment conditions (Norkko et al., 2002), while increased organic matter in sediments resulted in lower seagrass growth rates (Mascaró et al., 2009).

As ecosystem engineers, seagrasses provide a physical structure that enhances diversity (macro- and microalgae, sponges, corals, bivalves, and other sessile invertebrates), provides shelter from predators, and provide important ecosystem functions (primary and secondary production, nutrient cycling, fish and invertebrate settlement and protection) (Orth and Heck, 1980). However, due to their proximity to shore, seagrass communities are vulnerable to changes to both land and sea use (Orth et al., 2006; Cullen-Unsworth et al., 2014). Human causes of seagrass loss can result from direct marine-based activities (e.g. dredging, coastal and marine development, fishing disturbance, mooring, anchoring, and aquaculture) as well as indirect land-based activities (e.g. nutrient and sediment loading from terrestrial urbanization, agriculture development, deforestation) (Short and Wyllie-Echeverria, 1996).

With expanding human populations in the coastal zone, it is important to evaluate the efficacy of potential protection strategies in mitigating anthropogenic threats (Mora and Sale, 2011). In nearshore coastal ecosystems, land-sea interactions are linked via watershed drainages and land use practices; land clearing for urban development, agriculture, and forestry have altered the composition and concentration of sediment, nutrients, organic carbon, contaminant, and disease fluxes from land to sea (Thrush et al., 2004; Tomasko et al., 2005; Crain et al., 2009). The effects of these alterations vary and may include decreasing light availability for photosynthesis (Bach et al., 1998), burial of benthic communities (Thrush et al., 2004), and changes in nutrient loading leading to increased eutrophication (Tewfik et al., 2007), leading to changes in seagrass community composition, productivity, and function (Orth et al., 2006). As a result, it important to consider both marine and land-based strategies for mitigating declines in seagrass condition.

4.3. Marine protected areas

While MPAs can protect seagrass communities against overfishing and habitat damage from destructive fishing practices (Short and Wyllie-Echeverria, 1996), we found that indirect impacts of land-based human activities, not controlled by marine protection, were most important in determining seagrass condition. Urbanization, coded as human development (defined as the presence of houses, commercial development and roads) and land conversion to farmland were the most important land uses that determined seagrass condition. Short et al. (2006) similarly found that land-based human activities (tourist development, mangrove clearing, shoreline hardening) that altered sediment and nutrient fluxes to adjacent nearshore areas led to decreased seagrass percent cover in Placencia, Belize, and Freeman et al. (2008) found that seagrass loss both inside and outside of MPAs was due to decreased subsurface light intensity from a sediment plume caused by deforestation in the adjacent watershed.

The only significant human activity potentially mitigated via the establishment of MPAs in our model was aquaculture inside the MPA, but that would not stop aquaculture from occurring adjacent to MPAs and having their effects spill over into the MPA. Delgado et al. (1999) found that aquaculture in proximity to seagrasses resulted in excess organic matter and over a long time periods, reduced seagrass growth and abundance, and this persisted after the cessation of aquaculture operations. In CC1, however, large areas of aquaculture at the coastal strip were associated with seagrass beds in good condition, defined by high seagrass species richness. One explanation is that only 10 of our sites had ongoing aquaculture present (19% of all sites), and aquaculture comprised an average of 14% area of the watershed. The aquaculture observed were artisanal bamboo fish pens, with only one site having industrial aquaculture activities. The artisanal bamboo fish pens may have had minimal impact on the seagrass meadows adjacent to the pens. Furthermore, large areas of aquaculture were associated with small watersheds and small areas of farmland. The effect of the land-based input could have been stronger than the effect of the adjacent artisanal aquaculture.

4.4. Coastal watersheds

In a broader sense, the size and nature of the adjacent terrestrial watershed is an important determinant of seagrass condition. We found low seagrass richness and increased *Enhalus acoroides* cover (a seagrass species known to be robust to disturbance) associated with large watersheds and greater areas of farmland. This may result from larger and steeper watersheds being more likely to both have overall greater run-off and thus sediment flows than smaller watersheds, compounded by the increased fluxes of sediment from land conversion to human development and agriculture (Thrush et al., 2004; Cabili and Cuevas, 2011). One limitation of this study was that it did not incorporate the steepness of the slopes into the model. The steepness of the watershed or island could be related to the size of the watershed or island, and the type of land use in the watershed.

Another limitation of this study was the confounding variables in the suite of environmental variables. One such variable was watershed size. Small watersheds were associated with small areas of farmland, low sediment organic matter, and high areas of coastal aquaculture. These small watersheds were associated with meadows of high visibility, high seagrass species richness and low *Enhalus acoroides* canopy height. Furthermore, large watersheds were associated with larger areas of farmland but with small areas of aquaculture. The combination of large watersheds with farmland could also increase the land to sea impact of sediments and nutrients to the nearshore marine area.

It is interesting to note that we found more cases of large watersheds with large areas of development; and the few cases of small watersheds with high coastal farmland and high human development had high seagrass abundance. Seagrass abundance and species diversity were decoupled; watershed size was associated with seagrass species richness but not with seagrass abundance. Given our model, if we were interested in seagrass species richness, we would advocate for protecting larger watersheds because the size of the catchment draining to the seagrass meadow apparently has a greater effect on seagrass species richness. If we were interested in seagrass abundance, we would advocate for small areas of human development and farmland, regardless of watershed size.

Larger watersheds, steep watersheds and land conversion from forest to agriculture or land clearing likely have increased sediments entering the nearshore marine (Thrush et al., 2004). *Enhalus acoroides*, as a seagrass species more tolerant to siltation, can thrive in diminished physical conditions. A more fine-grained review across seagrass species may reveal further interspecific differences in tolerance.

4.5. Conservation implications

Biodiversity in seagrasses is important for ecosystem functioning, fishery production, trophic interactions and species diversity (Duffy, 2006). However, seagrass meadows, and the ecosystem services they provide, are decreasing all over the world (Waycott et al., 2009). In the coral triangle, seagrass ecosystems are given marginal importance in conservation and management (Unsworth et al., 2010). One reason for the lack of management of seagrass resources is the perception by local users that seagrass meadows are less vulnerable to threats by human activities and perceived as less important compared to coral reefs and mangroves (De La Torre-Castro and Rönnbäck, 2004). However, in one fishing community in the Philippines, seagrass habitat yielded greater daily biomass caught per fisher than coral reef habitat, while in another community, there was no difference in daily biomass caught per fisher; and both communities had greater participation in seagrass fishing than coral reef fishing (Quiros, 2016).

Here, we demonstrate that a major impact to seagrass abundance and richness is human activities occurring on land, particularly human development and farmland. These patterns were evident across a large spatial scale (>800 km), and over many seagrass meadow – island pairs (n = 54). Models on the effects of land use on coral reef systems have suggested the importance of the adjacent watershed to coral reef integrity (Beger et al., 2010; Klein et al., 2010), leading to the suggestion that at times, terrestrial conservation may be a better investment than marine conservation (Klein et al., 2010). Our research provides actual data from a landscape level comparative study demonstrating that, for Philippine seagrass systems, land use is more important than marine protection and that the primary causal factor may be siltation. This mechanism is supported by Quiros (2016) who found that in a subset of seagrass meadows from this present study, seagrass meadows adjacent to human development and farmland had the most sediment collected in sediment traps, lower visibility, a greater proportion of fine sediments, and the lowest seagrass species richness, percent cover, shoot density, and length. Furthermore, there were no differences in the daily sediment catch rate, light attenuation, and proportion fine and silty sediment between seagrass meadows without human development and farmland.

These results suggest that mitigating human activities on land adjacent to seagrass communities will yield significant conservation benefit, and may be a better use of limited conservation funding than marine protection. Future conservation efforts could model the cost and feasibility of actions on land that affect the ocean, incorporating trade-offs between management objectives, and finding priority areas that maximize both terrestrial biodiversity and coastal-marine water quality (Álvarez-Romero et al., 2015). Coastal land use, fisheries and marine protected areas are generally managed by different sectors of society (Crowder et al., 2006). Our results further demonstrate the complementary connection between land and sea, justifying the 'ridge-to-reef' approach in coastal conservation (Richmond et al., 2007; Rude et al., 2015; Teneva et al., 2016). Hence, implementing terrestrial protection as a tool for seagrass conservation will take increased cooperation and collaboration between terrestrial and marine conservation agencies and practitioners.

Seagrasses in the Philippines provide important ecosystem services and functions including artisanal fisheries, storm protection, and mitigation of sedimentation for adjacent coral reef systems (Duarte, 2000; Fortes, 2013). Seagrass conservation however, is in its infancy, especially for threats emerging from land. National plans for marine and terrestrial protection are emerging, for the most part independent of one another. Our research indicates we can have significant gains in seagrass condition by coordinating these processes.

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Appendix 1

Appendix Table 1
Canonical correlation analysis data table with sites, island name, region, GPS, covariates (MPA, MPA size, MPA age), means for 6 biological and 16 environmental variables are included in the data table.

Site	Island	Island area (km^2)	Region	Lat	Long	Protection	MPA	Large MPA	Old MPA
Agutaya	Agutaya	0.08	Bulata	9°51′44.01″N	122°23′12.61″E	TPA	0	0	0
St_Tropez	Balesin	4.24	Balesin	14°25′44.64″N	122° 2′29.82″E	MPA	1	1	0
Mykonos	Balesin	4.24	Balesin	14°26′24.51″N	122° 2′14.12″E	MPA	1	1	0
BOQ_St1	Boquete	0.86	Puerto Galera	13°31′5.85″N	120°57′3.65″E	TPA	0	0	0
CAL_KAM	Luzon	109,964	Calatagan	13°50′3.77″N	120°37′0.66″E	None	0	0	0
CAL_PIER	Luzon	109,964	Calatagan	13°49′16.18″N	120°37′13.94″E	None	0	0	0
CAL_PAG	Luzon	109,964	Calatagan	13°47′49.45″N	120°40′25.21″E	TPA	0	0	0
CAL_PAG	Luzon	109,964	Calatagan	13°48′44.50″N	120°39′56.95″E	None	0	0	0
CAM_St1	Camantilis	0.12	Pangasinan	16°11′24.49″N	120° 2′46.69″E	TPA	0	0	0
CAM_St2	Camantilis	0.12	Pangasinan	16°11′25.10″N	120° 2′57.44″E	TPA	0	0	0
Cebu_St1	Gapas gapas		Cebu	10°15′30.17″N	123°54′53.21″E	MPA	1	0	0
Hilutungan	Hilutungan	0.14	Cebu	10°12′37.15″N	123°59′16.51″E	TPA/MPA	1	0	1
Nalusuan	Nalusuan		Cebu	10°11′25.40″N	123°59′59.93″E	MPA	1	0	1
HilutunganVil	Hilutungan	0.14	Cebu	10°12′34.34″N	123°59′24.68″E	None	0	0	0
Sangat	Sangat	5.30	Coron	11°58′42.10″N	120° 3′43.60″E	TPA	0	0	0
Decalve	Busuanga		Coron	11°59′38.71″N	120° 5′5.71″E	MPA	1	0	1
MalcatopE	Malcatop East	0.21	Coron	12° 1′11.28″N	119°55′3.43″E	None	0	0	0
MalcatopW	Malcatop West	0.84	Coron	12° 2′5.68″N	119°54′34.74″E	TPA/MPA	1	0	1
BugurMPA	Bugur	0.14	Coron	11°54′56.02″N	120° 2′15.04″E	TPA/MPA	1	1	1
Ditaytayan	Ditaytayan	0.92	Coron	11°43′57.65″N	120° 6′17.28″E	TPA/MPA	1	0	0
Tanglaw	Bulalacao		Coron	11°45′59.69″N	120° 8′11.51″E	MPA	1	0	0
Bulalacao	Bulalacao		Coron	11°44′43.44″N	120° 9′42.66″E	None	0	0	0

(continued on next page)

Appendix Table 1 (*continued*)

Site	Island	Island area (km^2)	Region	Lat	Long	Protection	MPA	Large MPA	Old MPA
MonteMar	Culion		Coron	11°48′18.11″N	120° 3′11.12″E	TPA	0	0	0
BambooBr	Danjugan		Bulata	9°52′35.04″N	122°22′48.18″E	TPA/MPA	1	1	1
ThirdLagoon	Danjugan		Bulata	9°52′17.13″N	122°22′45.89″E	TPA/MPA	1	1	1
TurtleBeach	Danjugan		Bulata	9°52′26.45″N	122°22′37.59″E	TPA/MPA	1	1	1
TabonBeach	Danjugan		Bulata	9°52′11.84″N	122°22′31.98″E	TPA/MPA	1	1	1
DEW St1	Dewey	0.15	Pangasinan	16°24′29.68″N	119°57′35.58″E	None	0	0	0
DEW St2	Dewey	0.15	Pangasinan	16°24′30.08″N	119°57′50.36″E	None	0	0	0
Governor	Governor	0.08	Pangasinan	16°12′15.93″N	120° 2′22.31″E	MPA	1	1	1
MDA	M Daku		Sagay	10°57′14.29″N	123°33′44.54″E	MPA	1	1	1
MDI	M Diuytay	0.24	Sagay	10°57′43.48″N	123°32′45.90″E	MPA	1	1	1
Medio	Medio	0.94	Puerto Galera	13°31′14.68″N	120°57′18.52″E	TPA/MPA	1	1	1
OLY_St1	Olympia		Bais	9°37′2.93″N	123° 8′54.32″E	None	0	0	0
OLY_St2	Olympia		Bais	9°36′49.94″N	123° 8′46.84″E	None	0	0	0
PD	Pulong Daku		Bais	9°35′10.12″N	123° 9′22.89″E	MPA	1	0	0
Boquete	Boquete	0.86	Puerto Galera	13°30′43.90″N	120°56′52.75″E	TPA	0	0	0
NMedio	Medio	0.94	Puerto Galera	13°31′39.22″N	120°57′21.02″E	TPA	0	0	0
WBoquete	Boquete	0.86	Puerto Galera	13°30′35.75″N	120°56′44.16″E	None	0	0	0
PiratesCove	Mindoro	10,572	Puerto Galera	13°30′26.39″N	120°57′40.79″E	MPA	1	1	1
SMedio	Medio	0.94	Puerto Galera	13°31′1.31″N	120°57′28.04″E	MPA	1	1	1
SchoolMedio	Medio	0.94	Puerto Galera	13°31′1.99″N	120°57′33.55″E	None	0	0	0
LittleLaLaguna	Mindoro	10,572	Puerto Galera	13°31′28.50″N	120°58′12.88″E	MPA	1	1	1
Guilid	Mindoro	10,572	Puerto Galera	13°30′46.63″N	120°57′49.68″E	TPA/MPA	1	1	1
Quezon	Quezon	0.01	Pangasinan	16°13′21.39″N	120° 2′48.12″E	MPA	1	1	1
Sabang	Mindoro	10,572	Puerto Galera	13°31′15.22″N	120°58′31.36″E	None	0	0	0
Shell	Shell	0.01	Pangasinan	16°11′41.24″N	120° 2′47.08″E	TPA	0	0	0
SIA_St1	Siapar	2.60	Pangasinan	16°22′4.12″N	119°57′42.98″E	None	0	0	0
SIL_GC	Silaqui	0.10	Pangasinan	16°26′37.99″N	119°55′18.42″E	None	0	0	0
SIL_St1	Silaqui	0.10	Pangasinan	16°26′25.19″N	119°55′25.42″E	TPA	0	0	0
SIL_St2	Silaqui	0.10	Pangasinan	16°26′26.64″N	119°55′19.55″E	TPA	0	0	0
SIL_St3	Silaqui	0.10	Pangasinan	16°26′35.23″N	119°55′30.25″E	TPA	0	0	0
Suyac	Suyac	0.02	Sagay	10°56′56.28″N	123°27′17.74″E	None	0	0	0
Turtle	Turtle	1.36	Bulata	9°49′46.89″N	122°21′58.68″E	TPA	0	0	0

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