

Dynamics of shallow-water assemblages in the Saipan Lagoon

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ABSTRACT: The Saipan Lagoon (Northern Mariana Islands) was first examined for benthic composition and habitat distribution in the late 1940s. Here, we employ a 4-stage approach to evaluate and explain change in the distribution of the 9 habitats previously demarcated. We show that there have been considerable reductions in seagrass, staghorn *Acropora*, and *Acropora palifera* dominated habitats (–3.72, –1.26, and –1.37 km², respectively) that were replaced by 6.16 km² of sand (~20% of the lagoon area). Multiple regressions showed that the spatial extent of *Enhalus* seagrass was positively related with, and best predicted by, the adjacent watershed area and lagoon width. Although the interaction was not as strong, *Enhalus* also increased in accordance with human development. The size of the *Halodule* seagrass and macroalgal habitat was negatively related to water-flow velocities and positively related to human development, while its integrity (i.e. the density of seagrass within a given habitat) decreased with human development. Taken together, the results suggest *Enhalus* and *Halodule* respond differently to proxies of watershed pollution, and contradict contemporary doctrine linking pollution with reduced seagrass density. This study found no relationship between offshore habitats and watershed characteristics, but suggests their expansion and contraction on relatively short time scales is a result of large-scale disturbances such as typhoons. We posit that, while habitat integrity can be altered by human disturbances, habitat identity is only altered under extreme conditions. In summary, this study advances habitat mapping by increasing resolution and accuracy, which, in turn, improves the texture at which reef ecology is used by management.

KEY WORDS: Habitat mapping · Seagrass ecology · Saipan Lagoon · Remote sensing · Watersheds · Coral reefs · Moving window analysis

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INTRODUCTION

For decades researchers have examined ecological systems at large spatial scales and generated maps that reflected major patterns in habitat distributions (Wells 1954, Cloud 1959, Mumby & Harborne 1999, Fourqurean et al. 2003) that have facilitated estimates of harvestable resources (Duenas & Associates, Inc. 1997, Amesbury 1999). Herein, we define habitats as distinct assemblages of co-occurring, benthic-sessile species that are seen consistently throughout a geographic region. More than just a means of quantita-

tively estimating fishery resources, we can examine habitat identity, size, and integrity to address longstanding questions regarding the distribution and dynamics of species assemblages across time. Distilling ecological patterns such as habitat distributions and population dynamics is a means of identifying the mechanisms that drive change, which eventually allows forecasting of future conditions.

A wealth of studies have employed controlled, manipulative experiments that examine 1 or 2 driving variables, such as nutrients and herbivory, when studying mechanisms leading to coral, seagrass, and/or alga

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assemblage change (Smith et al. 2001, Cardoso et al. 2004, Hughes et al. 2004). However, Peters (1991) cautions that the proper design of causal studies can be difficult without first understanding ecological patterns that arise from the abiotic environment. Indeed, quantitative studies relating sets of abiotic variables to ecological measures are desirable, but have been essentially lacking (Hutchinson 1959, Peters 1991, van Woesik et al. 1999).

In the Saipan Lagoon, site-specific transect data show that some benthic assemblages have responded negatively to increased non-point source (uncontrolled) pollution associated with infrastructure and urban development (Houk et al. 2002). The existing doctrine suggests that increases in nutrient loading (Dennison et al. 1993, McGlathery 2001, Lapointe et al. 2004), associated with human disturbances and/or reduced herbivory (Cardoso et al. 2004), shift benthic dominance from seagrass to macroalgae. In some polluted localities of the Saipan Lagoon macroalgal stands have out-competed *Halodule uninervis* beds, leaving a lack of root structures to stabilize sand and little continuous habitat for invertebrates. It remains unclear whether this trend is universal for all species of seagrass. Watershed characteristics serve as proxies of human pollution that may alter seagrass beds and coral populations; however, water-flow velocity and lagoon size are also influential drivers of species assemblages (Daby 2003, Fonseca & Koehl 2006). Studies suggest a negative relationship exists between water-flow velocity and seagrass abundance that is mainly attributed to the removal of small-grain-size sediments (Daby 2003, Fonseca & Koehl 2006).

The Saipan Lagoon was first spatially examined for benthic composition and habitat distribution in the late 1940s (Cloud 1959). Ecological and geographic data were collected throughout the lagoon, and species assemblages were manually inferred during 9 mo of field work, and hand-digitized from aerial photographs. While Cloud's maps were never assessed for accuracy, they are nonetheless a valuable resource to assess change in major habitat types. Using these maps as a base, several subsequent studies have been conducted to estimate fisheries stocks (Duenas & Associates, Inc. 1997, Amesbury 1999), despite the passing of decades of potential ecological change. More recently, habitat maps for the entire Commonwealth of the Northern Mariana Islands (CNMI) have been created using a manual approach (NOAA 2005); field data were assigned to habitats using a hierarchical classification scheme, and maps were digitized by integrating ground data with visual interpretations of IKONOS imagery. These labor-intensive products provide a high spatial coverage not previously available; how-

ever, the broad nature of the habitat classes, due to the high cost associated with ground data acquisition, has limited their ecological utilization. These products have met their desired goals of generating regional statistics, but have limited applicability for several finer scale questions relating abiotic environmental conditions to species assemblages.

While considerable progress has been made in the application of remote sensors to habitat mapping, ground truthing of satellite images has revealed increasing error estimates when increasing the number of habitat classes beyond 6 or 7, due to spectral limitations of 4-band imagery (Andrefouet et al. 2003). A typical, contemporary mapping approach involves: (1) previewing aerial or satellite imagery and defining suspected habitat boundaries, (2) gathering field data from random points stratified within suspected classes (i.e. habitats), (3) subjecting field data to exploratory analyses (e.g. cluster analysis) to define existing classes, (4) using habitat classes as training regions for pixel-based remote-sensing analyses, and (5) assessing the accuracy of the final map product (Mumby & Harborne 1999, Andrefouet et al. 2003). Mumby (2001) pointed out that habitats are not uniform throughout their range, and arbitrary clustering provides assumptions of equality, which, in turn, produce error (i.e. a limited number of habitat classes).

Here, we undertook a 4-stage approach to understand the spatial distribution and dynamics of reef habitats in the Saipan Lagoon. First, we scanned and digitized Cloud's late 1940s map for comparative purposes. Second, we created contemporary habitat maps of the Saipan Lagoon using a novel habitat mapping approach that objectively defined habitat classes, which were subsequently manually digitized. Moving window analysis (MWA) was used as a tool to remove subjectivity from the generation of ecological habitat classes, and guided the manual digitization process. For comparative purposes, habitat maps were also developed using common supervised classifications of IKONOS satellite imagery, representing a process that is realistically available to many coral reef monitoring programs. Third, we compared Cloud's historic habitat map of the Saipan Lagoon with the contemporary habitat distributions. We hypothesize that coral and seagrass habitats have declined in spatial extent in response to human population and development increases over the past 60 yr. Finally, stepwise, multiple regression analyses were employed to quantify relationships between environmental variables and habitat size and integrity. We hypothesize that relations will be strongest in nearshore habitats and will weaken with distance from shore, where natural disturbances may be more influential.

MATERIALS AND METHODS

Study area. This study was conducted in 2004 in the Saipan Lagoon, CNMI. The ~13 km² lagoon is located on the western coast of Saipan (Fig. 1). The majority of the lagoon is 1 to 3 m deep, with 3 channels providing some small 2 to 5 m patch-reef habitats in the outer lagoon.

Moving window analysis. Previously, MWA has been used to understand the spatial influence of point-source discharges (e.g. river discharge) on coral assemblages (West & van Woelik 2001). The same concept was applied here to examine changes in coral, seagrass, and alga assemblages along 8 transect lines extending from the shoreline to the barrier reef, separated by ~2 km (Fig. 1). Initially, video transects were run along each transect line with a camera fastened to a manta-tow board. A global positioning system (GPS) was used to document the exact location and speed of the manta tows. Each analysis window consisted of a 0.5 m × 10 m swath of benthic video, and adjacent windows were separated by ~15 m (Fig. 2). Other window sizes were tested in pilot studies, but the signal to noise ratios were lower for other windows (see West & van Woelik 2001). Ten video frames (0.5 m × 0.5 m, a total of 2.5 m²) were extracted from each window for analysis. In each frame, the benthos under 5 randomly placed data points was recorded as either sand, seagrass (species), macroalgae (genus), carbonate rock (with turf or coralline algae), or coral (genus).

To examine the variance in community structure between consecutive windows, we used the Bray-Curtis dissimilarity index:

$$D_{(y_1, y_2)} = \sum |y_{1j} - y_{2j}| / \sum (y_{1j} + y_{2j}) \quad (1)$$

where \sum represents the summation of all dominant benthos categories and y_{1j} and y_{2j} represent benthos abundance in consecutive windows; the greater the dissimilarity between adjacent windows, the larger D (Fig. 2). Each dissimilarity spike was (visually) examined to determine if inter- or intra-habitat variability was detected during the MWA process. Intra-habitat variability consisted of mono-specific patches of coral (staghorn *Acropora*) or seagrass (*Enhalus*) situated within a mixed-species, homogeneous habitat.

The perceived habitat before and after each variance spike was then quantitatively surveyed for benthic abundance and species composition, using a series of 50 m transects ($n = 3$ to 5; homogeneous substrate permitting)

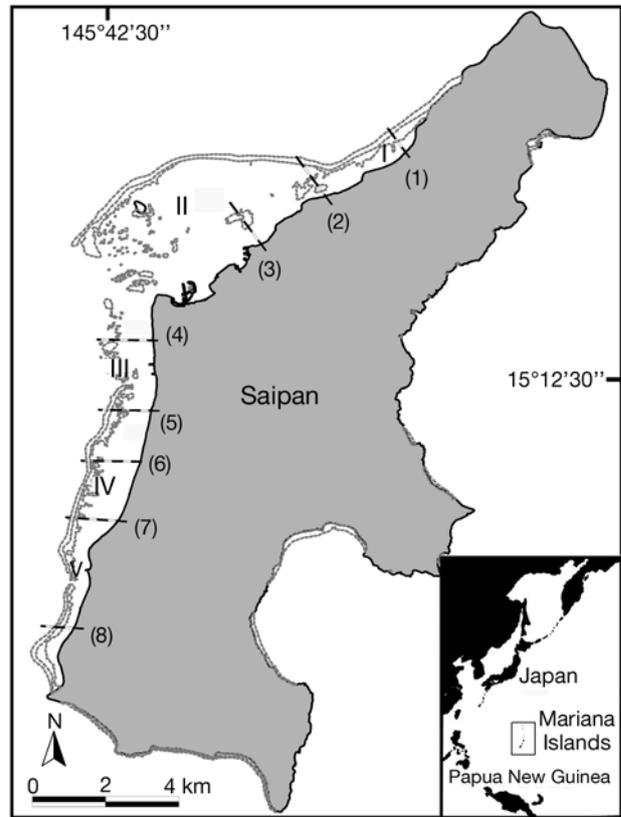


Fig. 1. Map of the Saipan Lagoon with the Mariana Islands inset. Eight moving window analysis transect lines were established throughout the lagoon (1 to 8) to identify habitat classes used for map digitization. IKONOS imagery was spliced into 5 regions to conduct supervised classifications (I to V)

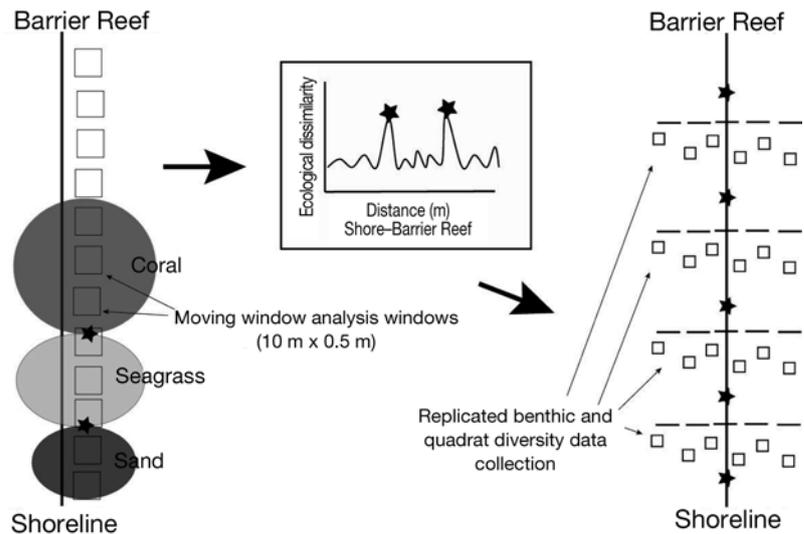


Fig. 2. A flow diagram depicting how moving window analysis (MWA) objectively delineated habitat boundaries. Ecological dissimilarity refers to Bray-Curtis dissimilarity measures between adjacent windows (left and center). Replicated video-transect (5 × 50 m transect lines) and quadrat-diversity data (ten 1 m² replicate quadrats) were used to examine the distinctness of each MWA-derived habitat class (right), where stars indicate transitions

laid parallel to shore in each 'habitat' (Fig. 2). For each 50 m transect, 60 JPEG frames were extracted and the benthos under 5 random data points were recorded ($n = 300 \text{ transect}^{-1}$) following Houk & van Woessik (2006). A Bray-Curtis dissimilarity matrix was generated based upon relative abundance of seagrass (species), corals (genus), macroalgae (genus), turf (<2 cm), and coralline algae, using each 50 m transect as a replicate.

ANOSIM tests (Clarke & Warwick 2001) were used to test the null hypothesis that perceived habitats did not vary in benthic composition. These tests are based upon ranked similarity measures between and within sites, and yield an R-statistic that serves as a measure of site separation. R-values can range between -1 and 1; R-values near zero suggest that the null hypothesis is most likely to be true (i.e. there were no differences between 'habitats'), while high R-values suggest a false null hypothesis. P-values are calculated for each R-statistic using a permuted test of random rearrangement of replicates within differing sites, which then compares the true R-value with the randomly generated distribution.

Species composition data were collected and analyzed similarly. Instead of using replicate transects, 10 replicate 1 m² quadrats were haphazardly placed in each 'habitat'. A species list was generated for each quadrat. Dissimilarity matrices were based on species presence and absence data, using individual quadrats as replicates. ANOSIM tests were used to test the null hypothesis that 'habitats' did not vary in species composition.

Habitat digitization and remote sensing. For comparative purposes a historical habitat classification map developed by Cloud (1959) in the late 1940s was scanned and digitized (0.4 hectare minimum mapping unit, MMU). While the habitat boundaries delineated were less accurate than the contemporary maps (20 to 40 m errors associated with boundary edges), the bulk of the change detected is attributed to the presence/absence of entire habitat polygons between the late 1940s and the present. Because Cloud (1959) did not substantially differentiate among habitats where several species of seagrass and macroalgae co-occurred, these groups were combined for analysis purposes to detect change in the present study.

Contemporary habitat maps were developed by projecting MWA-defined transitions (that were tested for significance using ANOSIM) over an IKONOS image of the lagoon. Statistically similar habitats were hand-digitized from these spatial data by tracing unknown, spectral features between the 2 points. Habitats were digitized using a 0.4 hectare MMU.

In a separate procedure, a supervised classification was developed from IKONOS satellite imagery using all 4 bands: red (0.63 to 0.69 μm), green (0.52 to

0.60 μm), blue (0.45 to 0.52 μm), and near infrared (0.76 to 0.90 μm). Despite their restrictions to very shallow habitats, the red and infrared bands were used to spectrally distinguish between the long blades of *Enhalus acoroides* and the shorter *Halodule uninervis* blades. The satellite image was divided into 5 geographic sections, based upon depth, to reduce the number of habitat classes per classification and improve the overall accuracy (Fig. 1). The regions were: (I) the shallow (1 to 2 m) northern lagoon, (II) the deeper (1 to 8 m) northern lagoon adjacent to the main boat channel, (III) the mid-depth (1 to 4 m) central lagoon adjacent to the most developed watershed, (IV) a shallow (1 to 3 m) section of the southern lagoon, and (V) the very shallow (~1 m) southernmost lagoon separated by a secondary channel. For Regions I, II, III, IV and V, the supervised classifications were conducted using 8, 11, 8, 11, and 9 habitat classes, respectively, for a total of 14 unique classes. Training regions were subjectively selected from each habitat based upon MWA analyses. A maximum-likelihood classifier was used to assign pixels to habitat classes based upon their distances from the class means that were defined by the training regions.

Accuracy assessments were conducted for both the MWA-derived and supervised classification map products. A total of 400 random points, stratified by habitat size, were generated throughout the lagoon. Ground validation surveys were completed for 348 points; cloud cover in the satellite imagery limited the number of validation points to 302 for the supervised classification. Accuracy assessments, including producers and users accuracy, were calculated based upon the agreement between ground validation point classification and the classification of the polygons (Lillesand et al. 2004).

Multiple regressions. The relationship between biological and environmental variables was examined through multiple regression analysis (Zar 1999). Independent, environmental variables were gathered from existing Geographic Information System (GIS) layers that included watershed size (km²), amount of developed land within each watershed (km²), surface water-flow velocity (m s⁻¹), and lagoon width (km) (the GIS layers were produced by, and available from, the CNMI Division of Environmental Quality and P. Houk). Watershed sizes were delineated from digital elevation models using a GIS, while land-use layers were hand digitized. Water-flow data originated from drone studies (P. Houk unpubl. data). All independent variables were standardized (by subtracting the means and dividing by the standard deviations) to allow equal weightings. Dependent variables were *Enhalus* and/or *Halodule* seagrass habitat size (km²) and a measure of integrity for *Halodule* beds (i.e. sea-

grass to macroalgae ratio). Seagrass beds extending 500 m on either side of all major watershed drainage features were measured for surface area and used in subsequent regression analyses. Box-Cox transformations (Box & Cox 1964) were applied to all variables except *Enhalus* to meet the requirement of normality for dependent variables.

RESULTS

Habitat characterization

Extending from the shoreline to the barrier reef the MWA detected 'habitat' boundaries along 8 transect lines. The MWA process did not identify or test the dis-

tinctness of each habitat, but rather focused on boundary detection. High Bray-Curtis dissimilarity measures corresponded with 'habitat' transitions or intra-'habitat' variability (Fig. 3). A typical transect line from the shoreline to the barrier reef passed through: (1) thick *Enhalus* seagrass beds, (2) *Enhalus*, *Halodule*, and *Halimeda macroloba* patches, (3) thick *Halodule* seagrass beds, (4) a sandy mid-lagoon with sparse *Halophila*, (5) a coral and sparse *Halodule* zone, (6) staghorn *Acropora* or branching *A. palifera* (*Iso-pora*), and (7) a coral- or alga-dominated back-reef flat. Despite following a general seagrass-sand-coral sequence, MWA identified unique transitions along several transects, stemming mainly from the non-uniformity of the inner-lagoon and some raised reefs in parts of the northern lagoon.

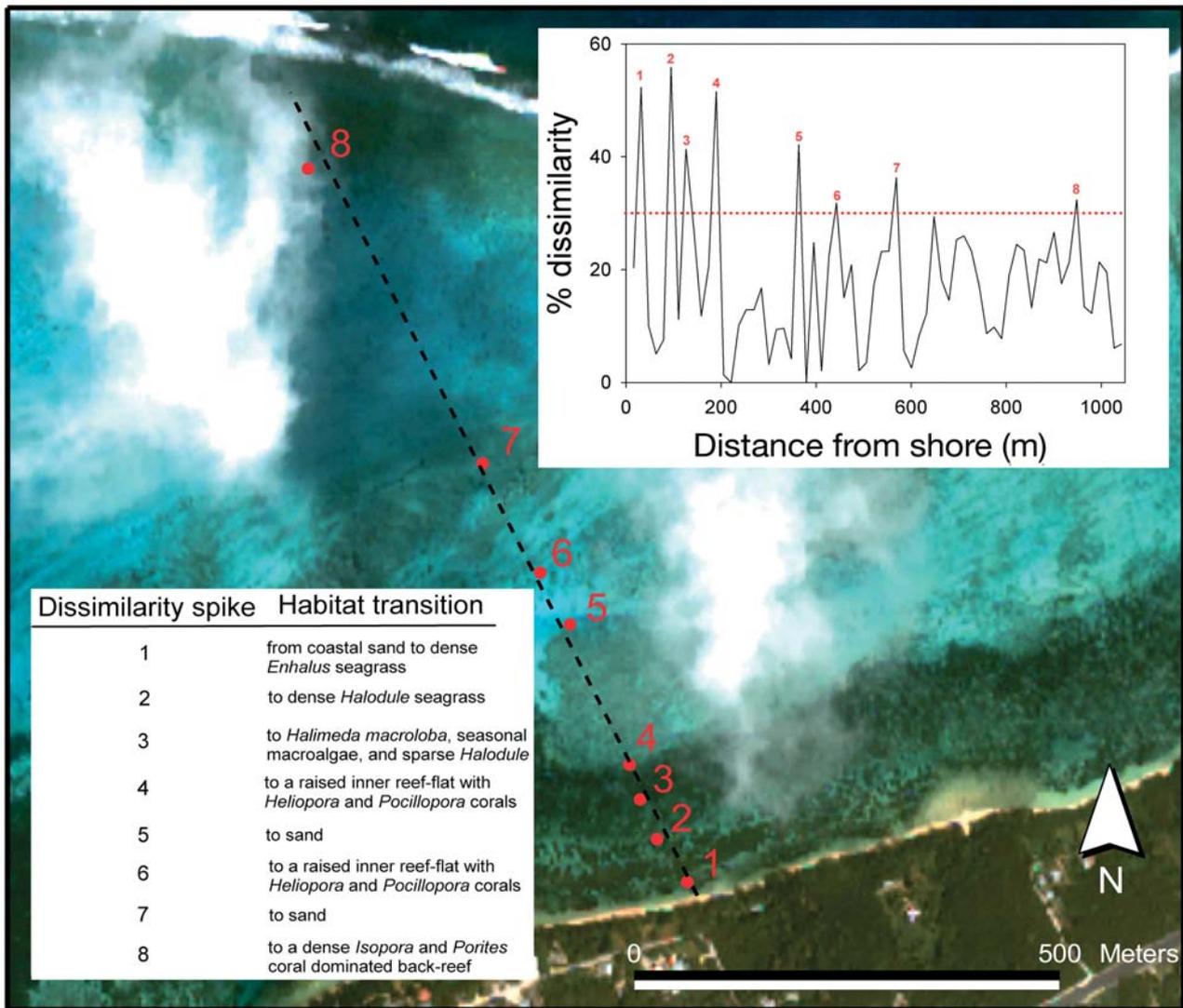


Fig. 3. An example of the moving window analysis results (Transect 2, Fig. 1). Habitat transitions were identified by high dissimilarity (spikes greater than 30%) between adjacent windows; transitions were mapped using a GIS and surveyed for benthic and diversity data (see Fig. 2)

Collectively, benthic and quadrat diversity data showed significant differences among all MWA-defined 'habitats'. Global ANOSIM tests indicated that benthic-video surveys best distinguished between (submerged) vegetation habitats with sand basements, while diversity data derived using quadrats were more accurate at detecting differences among reef habitats with carbonate basements (Table 1). Quadrat diversity data failed to distinguish between the 4 habitats that supported *Halodule* seagrass as the dominant organism (Habitats 13 to 16), while benthic-video data failed to distinguish between habitats with *Acropora* and *Montipora* corals as dominant organisms (Habitats 2, 4, 5, and 6).

Benthic-video data showed clear differences between sand and seagrass habitats, but not among replicated samples within each habitat (R-statistic = 0.79 and 0.31, respectively, $p < 0.01$; Table 1). These results are supported by pairwise comparisons yielding significant differences between the 7 MWA-defined sand and seagrass 'habitats' (R-statistic > 0.5 , $p < 0.01$) (Habitats 11 to 17; Table 2). Notably, *Halodule uninervis* was present in 5 of these habitats, but differences were attributed to: (1) the simultaneous

presence of *Enhalus acoroides* (Habitat 16), (2) a dominance of macroalgae (Habitat 17), (3) the presence of carbonate boulders and coral colonies (Habitat 15), (4) the partial exposure of an underlying Pleistocene basement where macroalgae proliferate in patches

Table 1. Summary of global ANOSIM tests used to determine habitat distinctness. Benthic-video surveys best distinguished between seagrass/sand habitats, while quadrat-based diversity measures best characterized carbonate-structured habitats. (**) symbolizes significant R-values ($p < 0.01$), following Clarke & Warwick (2001)

Data collection	Habitat type	Source of error	Global R
Benthic video	Seagrass/sand basement	Within 'habitat'	0.31
		Between 'habitat'	0.79 (**)
	Carbonate basement	Within 'habitat'	0.62 (**)
		Between 'habitat'	0.55 (**)
Quadrat diversity	Seagrass/sand basement	Within 'habitat'	0.64 (**)
		Between 'habitat'	0.69 (**)
	Carbonate basement	Within 'habitat'	0.33
		Between 'habitat'	0.88 (**)

Table 2. Comparisons between habitat composition and habitat size in the late 1940s (Cloud 1959) and 2004 in the Saipan Lagoon. MWA: moving window analysis; N/A: not applicable

ID	Habitat description	Total area in 2004 MWA delineated (km ²)	Total area in late 1940s (km ²)	Change in area (late 1940s – 2004) (km ²)
1	Outer reef flat, high wave energy	2.18	N/A	N/A
2	Outer reef flat, low wave energy, dominated by live coral growth	0.76	2.84	-0.93
3	Outer reef flat, low wave energy, dominated by macroalgae (mainly <i>Geliedrella acerosa</i>)	1.06		
4	Outer reef flat, low wave energy, dominated by branching coralline algae	0.09		
5	Mid-lagoon raised reefs colonized by <i>Heliopora coerulea</i> and <i>Pocillopora damicornis</i> , coralline, and turf algae	0.59		
6	Staghorn <i>Acropora aspera</i> and <i>A. formosa</i> (live and dead)	1.47	2.73	-1.26
7	Massive <i>Porites</i> and macroalgae (2–3 m depth)	0.38	0.36	0.02
8	Sparse <i>Acropora palifera</i> and massive <i>Porites</i> , sand and loose carbonate framework	0.65	2.74	-1.37
9	Dense <i>Acropora palifera</i> and massive <i>Porites</i> , dominated by live coral	0.72		
10	Coastal sand adjacent to shore	0.42		
11	Sand with sparse seagrass and macroalgae	7.37	1.21	6.16
12	Thick <i>Enhalus acoroides</i> seagrass with little sand	0.76	10.92	-3.72
13	Flat Pleistocene basement overgrown with macroalgae and sparse stands of <i>Halodule uninervis</i>	1.19		
14	Thick <i>Halodule uninervis</i> seagrass with varying amounts of macroalgae	3.88		
15	Outer-lagoon sparse <i>Halodule uninervis</i> mixed with carbonate boulders colonized by limited coral growth	0.33		
16	Sand, <i>Halimeda macroloba</i> , <i>Halodule uninervis</i> , <i>Enhalus acoroides</i> , and macroalgal patches	0.94	4.23	-0.03
17	Macroalgae dominant, limited sand and seagrass	0.10		
18	Deeper (7–9 m) patch reefs associated with a channel	4.20		
19	Deeper (7–9 m) dredged harbor sediments	1.95	2.66	-0.71
20	Cloud cover or wave break — not digitized	2.01	N/A	N/A
	Total (km ²)	31.05	28.79	

(Habitat 13), and (5) the dominance of *H. uninervis*, sand, and macroalgae only (Habitat 14).

In contrast with the benthic-video derived data, the analysis of quadrat diversity data yielded significant differences among reef habitats, but not among replicated samples (R-statistic = 0.88 and 0.33, respectively, $p < 0.01$; Table 1). Pairwise comparisons confirmed the distinctness of 8 reef habitats (R-statistic > 0.5 , $p < 0.01$) (Habitats 2 to 9; Table 2). Three reef-flat habitats were distinguishable based upon the presence of *Acropora*, *Pocillopora*, *Porites*, and other corals (Habitat 2), dominance of fleshy macroalgae (Habitat 3), and the dominance of branching coralline algae (Habitat 4). Four mid-lagoon, reef habitats were distinguishable based upon the frequent occurrence of *Heliopora coerulea*, the blue octocoral (Habitat 5), extensive staghorn *Acropora* beds (Habitat 6), large, massive *Porites* corals (Habitat 7), and sparse (Habitat 8) and dense (Habitat 9) growth of *A. palifera*.

All MWA-defined transitions were incorporated into a GIS layer that was projected over an IKONOS satellite image for digitization (Fig. 4). An accuracy assessment protocol, which used 348 ground validation points, stratified by habitat size, showed an overall accuracy of 77% (Table 3). While their combined area represents ~40% of the lagoon, Habitats 11 (sand) and 13, 14, and 15 (seagrass and macroalgae) showed relatively low producer and user accuracy, respectively.

Supervised classifications

For Regions I, II, III, IV, and V, the supervised classifications accurately distinguished between 8, 11, 8, 11, and 9 habitat classes, respectively, for a total of 14 unique classes. All classifications had high internal accuracies (Kappa = 0.92, 0.95, 0.85, 0.91, and 0.93, respectively). The 302 ground validation points that were stratified by habitat size, but were *not* MWA derived, showed a low overall accuracy of 41% (Table 4). Lowest accuracies were found for habitats where coral, *Halodule*, and seasonal macroalgae co-occurred.

Change since the late 1940s

Cloud (1959) identified and mapped 9 'biotypes' (or major habitat types) in the Saipan Lagoon in the late 1940s. The most notable changes since the late 1940s include considerable reductions in seagrass, staghorn *Acropora*, and *A. (Isopora) palifera* and *Porites* habitats (-3.72, -1.26, and -1.37 km², respectively) (Table 2). These vacancies have been replaced by sand, which increased by 6.16 km² (approximately 20% of the lagoon area). Notably, the loss and emergence of several *Acropora* and seagrass habitats, especially in the outer, northern lagoon contributed to ~65% of this

Table 3. Error matrix for the hand-digitized, moving window analysis derived, habitat map, calculated from 348 ground validation points that were stratified by habitat-area; -: null values

Habitat assigned by MWA-based classification	Ground truth habitat																	Row totals	User's accuracy
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17			
2	8	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	9	88.9	
3	1	16	-	-	-	-	-	-	-	-	-	2	-	1	-	-	20	80.0	
4	1	-	10	-	1	-	-	-	-	-	-	-	-	-	-	-	12	83.3	
5	-	-	2	5	2	-	2	-	-	-	-	-	-	-	-	-	11	45.5	
6	3	-	2	-	17	2	1	-	-	-	-	-	-	-	-	-	25	68.0	
7	-	-	-	-	-	8	-	-	-	3	-	-	2	-	-	-	13	61.5	
8	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	6	100.0	
9	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	8	100.0	
10	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	5	100.0	
11	-	2	-	-	-	-	-	-	-	49	-	-	2	2	-	-	55	89.1	
12	-	-	-	-	-	-	-	-	-	-	26	-	-	-	3	-	29	89.7	
13	-	-	-	-	-	-	-	-	-	1	-	16	6	-	-	-	23	69.6	
14	-	-	-	-	-	-	-	-	-	16	-	5	65	2	2	-	90	72.2	
15	1	1	-	-	-	-	-	-	-	3	-	-	-	10	-	-	15	66.7	
16	-	-	-	-	-	-	-	-	-	-	1	-	2	-	18	2	23	78.3	
17	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	2	4	50.0	
Column totals	14	19	14	5	21	10	9	8	6	73	27	23	77	15	23	4			
Producer's accuracy	57.1	84.2	71.4	100.0	81.0	80.0	66.7	100.0	83.3	67.1	96.3	69.6	84.4	66.7	78.3	50.0		77.3%	

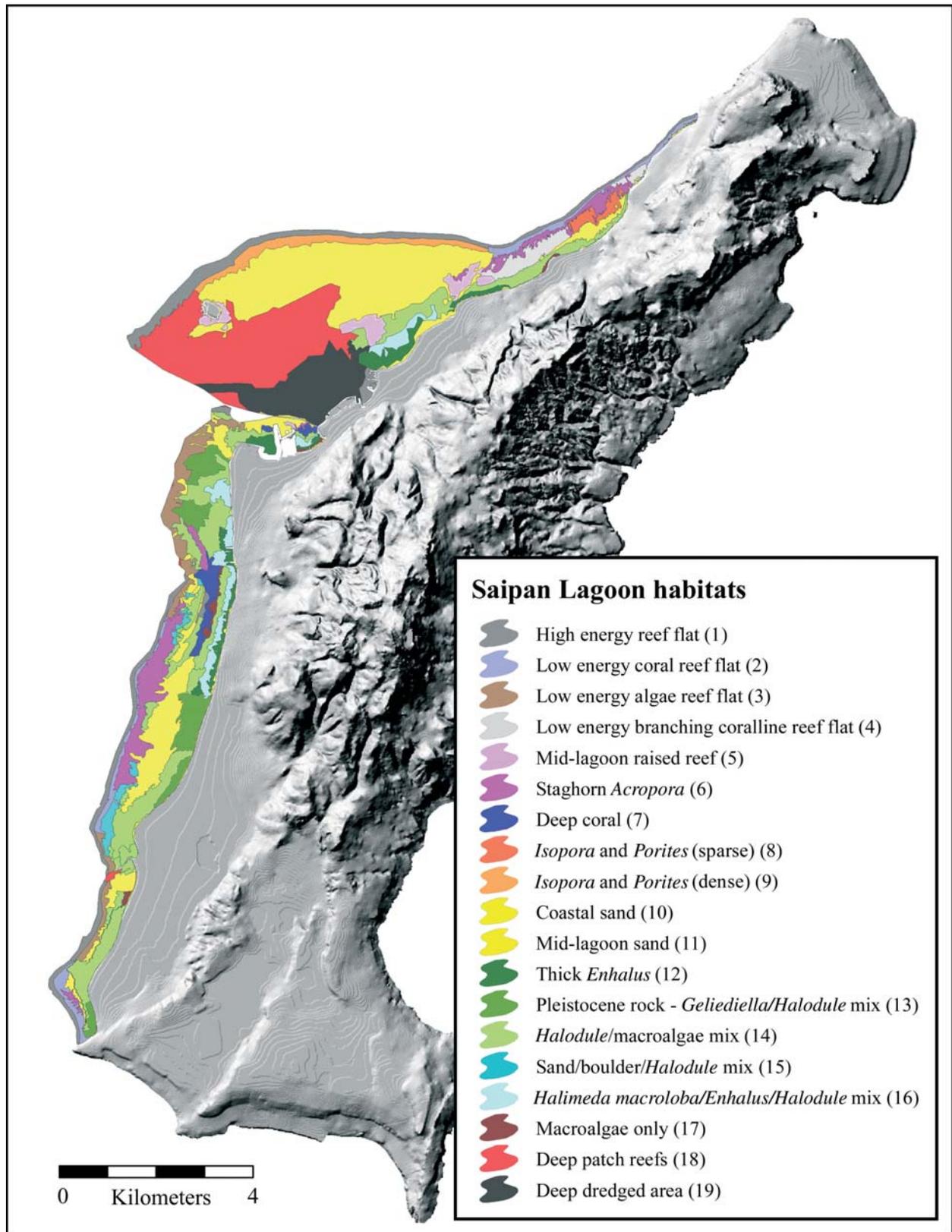


Fig. 4. A hand-digitized habitat map of the Saipan Lagoon based upon moving window analysis defined transitions. The overall accuracy of the map was 77.3% (Table 3). Numbers in parentheses correspond to habitat descriptions in Table 2

trend. Change in the southern lagoon accounted for ~35% of the trend and mainly consisted of large (>0.3 km²) habitat expansions and contractions.

Multiple regressions

Watershed size explained 91% of the variance in the extent of *Enhalus*-seagrass beds (Habitats 12 and 16, $\beta = 0.16$, $R^2 = 0.91$, $p < 0.001$; Table 5). Including additional variables in the stepwise process did not increase the amount of variance explained. Surface water-flow velocity explained the greatest variance in the size of Habitat 14 (*Halodule* and macroalgae) ($\beta = -0.15$, $R^2 = 0.63$, $p < 0.001$); however, including water-

shed development in the stepwise regression provided the best fit ($\beta = 0.06$, $R^2 = 0.74$, $p < 0.001$). A 3-variable model best described the *Halodule*/macroalgae ratio, with clear negative relationships evident between watershed development and water-flow velocity, and a positive relationship with watershed size (Table 5).

DISCUSSION

Overall change since the late 1940s

Nearly 20% of the lagoon changed from supporting *Acropora* corals and *Halodule* and *Enhalus* seagrasses

Table 4. Error matrix for the remotely sensed, supervised classification calculated from 302 ground validation points that were stratified by habitat area. Habitats 10 and 17 were not included in the supervised classification because they were spectrally indistinguishable from Habitats 11 and 14, respectively; -: null values

Habitat assigned by supervised classification	Ground truth habitat															Row totals	User's accuracy
	2	3	4	5	6	7	8	9	11	12	13	14	15	16			
2	6	-	-	-	-	-	-	-	-	-	-	1	-	-	7	85.7	
3	4	5	-	-	-	-	-	-	7	-	4	6	1	1	28	17.9	
4	-	-	1	-	-	-	-	-	-	-	-	1	-	-	2	50.0	
5	-	-	-	1	2	-	-	2	1	-	-	-	-	-	6	16.7	
6	1	2	4	-	12	2	1	1	9	2	3	13	1	5	56	21.4	
7	-	-	-	-	-	1	-	-	2	-	-	1	-	1	5	20.0	
8	-	-	7	-	3	-	4	-	3	-	-	1	-	-	18	22.2	
9	-	-	-	2	-	-	2	4	-	-	-	-	-	-	8	50.0	
11	-	2	2	-	-	5	-	1	23	-	2	-	-	-	35	65.7	
12	-	1	-	-	-	-	-	-	-	14	2	5	-	5	27	51.9	
13	-	2	-	-	1	1	-	-	6	-	9	11	1	1	32	28.1	
14	-	1	-	-	-	1	-	-	6	1	1	28	1	2	41	68.3	
15	1	1	-	-	3	-	-	-	5	-	-	2	8	-	20	40.0	
16	-	-	-	2	-	-	-	-	-	4	-	3	-	8	17	47.1	
Column totals	12	14	14	5	21	10	7	8	62	21	21	72	12	23			
Producer's accuracy	50.0	35.7	7.1	20.0	57.1	10.0	57.1	50.0	37.1	66.7	42.9	38.9	66.7	34.8		41.1%	

Table 5. Results from stepwise, multiple regressions between independent, environmental variables (horizontal axis) and dependent, ecological parameters (vertical axis). Each significant step is presented in bold; asterisk highlights the best fit regression; dash indicates that either the standard error (SE) of β was much greater than the mean, or no substantial improvement to the model (e.g. R^2 value) resulted from the inclusion of additional variables

	Watershed size			Watershed development			Water-flow velocity			Lagoon width		
	Step No.	β (SE)	R^2 (p-value)	Step No.	β (SE)	R^2 (p-value)	Step No.	β (SE)	R^2 (p-value)	Step No.	β (SE)	R^2 (p-value)
<i>Enhalus</i> (n = 7)	1*	0.16 (0.03)	0.91 (<0.001)	-	-	-	-	-	-	2	0.05 (0.03)	0.96 (0.001)
<i>Halodule</i> (n = 14)	-	-	-	2*	0.06 (0.03)	0.74 (<0.001)	1	-0.15 (0.03)	0.63 (<0.001)	-	-	-
Seagrass combined (n = 14)	-	-	-	2*	0.15 (0.03)	0.82 (<0.001)	1	-0.19 (0.05)	0.51 (0.004)	-	-	-
<i>Halodule</i> /macroalgae ratio (n = 10)	3*	0.35 (0.23)	0.8 (0.16)	1	-0.36 (0.16)	0.43 (0.039)	2	-0.38 (0.19)	0.69 (0.017)	-	-	-

to merely supporting sand over the past 45 yr. These habitats are integral for resource management because *Acropora* stands provide framework for many reef organisms, while healthy seagrass assemblages provide nursery grounds for juvenile fishes and invertebrates (Mumby 2006). Differing watershed characteristics were identified as plausible drivers of change in the nearshore seagrass habitats; however, spatially inconsistent declines in the offshore seagrass and coral dominated habitats may be a consequence of natural disturbances.

Change in nearshore habitats

The wealth of literature relating seagrass abundance and diversity to environmental variables relates primarily to studies conducted within much larger seagrass beds than the Saipan Lagoon (Terrados et al. 1998, Duarte 1999, Lapointe et al. 2004, Schaffelke et al. 2005). Terrados et al. (1998) found that seagrass diversity decreased as the amount of silt and clay sediments increased (e.g. toward land), with *Enhalus acoroides* being the most tolerant species. Our findings suggest *Enhalus* is most dependent upon watershed size, although a positive relationship with human development was also evident. In regions where watershed sizes are adequate for *Enhalus* to exist, the extent of growth increases in direct proportion to human development and size of the associated watershed. Indeed, a review of historical aerial photographs from 1976, 1999, and the present show an increase in the spatial extent of *Enhalus* (we note that there is no complete set of aerial photos available to calculate percentage change accurately). In support of our perspective, Erftemeijer & Herman (1994) suggested that seasonal increase in *Enhalus* biomass, in southern Sulawesi, Indonesia, was driven by nearby river discharge. In the present study, *Halodule uninervis* seagrass habitats exhibited substantial variability in coverage (minimum and maximum of 11 to 85%), apparently resulting from differential macroalgal growth (Habitats 14, 15, and 16; Fig. 4). This study shows that *Halodule* habitats (14, 15, and 16) are reduced by increased surface water-flow velocity, but increased because of watershed development. However, this increase in size does not equate to more seagrasses, because the integrity of this habitat (measured by the *Halodule*/macroalgae ratio) decreased with watershed development. In other words, the morphological and/or physical characteristics of *Enhalus* may prevent the invasion and overgrowth by macroalgae, while *Halodule* is susceptible to overgrowth in heavily developed watersheds. In

summary, the regression analyses depict that macroalgae proliferated in response to adjacent development and threatens the integrity of nearshore *Halodule* stands.

These data provide evidence for differential seagrass response to human disturbance, which is positive for *Enhalus* and negative for *Halodule*. This contradicts the reported doctrine of negative relationships between seagrass 'health' and watershed pollution, including nutrients (Dennison et al. 1993, McGlathery 2001, Lapointe et al. 2004), when seagrasses are lumped within one functional group. Our results agree with those of Schaffelke et al. (2005), who suggested that increased watershed pollution affects seagrass species differently and is dependent on seagrass morphology and thallus size.

Change in offshore habitats

Aerial photo compilations show that several offshore habitats (seagrass beds, sandy regions, and staghorn *Acropora* stands) are dynamic, with a capacity to expand and contract on relatively short-time scales (authors' pers. obs.), potentially coinciding with disturbances such as typhoons (averaging 4 yr⁻¹ in the CNMI; Eldredge 1983), *Acanthaster planci* outbreaks (~10 yr cycles since at least 1969; Houk et al. 2007), climate-induced bleaching (observed in 2000), and extreme low tides (observed in 1972; Randall 1991). It is well documented that coral species, and thus species assemblages within habitats, respond differently to these disturbances (Colgan 1987, Randall 1991, Loya et al. 2001). The present study found no relationships between offshore habitat integrity and watershed characteristics; however, we posit that habitat identity may be altered by the above noted disturbances. Indeed, during a thermal stress event in 2000, climate-induced bleaching killed ~40% of the staghorn *Acropora* corals, and the once live coral habitat was transformed into a branching-coralline-algae-dominated back-reef (Habitat 6 transformed to Habitat 4; Fig. 4). The proliferation of articulated-coralline algae (*Amphiroa*) may be transitional, and dependent upon the dead coral framework for persistence, since much of the present-day, sand-dominated habitat that was previously staghorn *Acropora* in the late 1940s supports only remnant coral fragments, with sparse branching-coralline algal growth. Currently, the conditions throughout the sand-dominated lagoon appear favorable for staghorn recovery (e.g. extremely low levels of macroalgae), but the time frame of recovery may depend on the maintenance of trophic interactions.

Management considerations

Identifying broad habitat classes has been beneficial to our regional understanding of where certain reef types exist, but greater process-level insight best matches the scale of resource management. The broad nature and lower overall accuracy of supervised classifications suggest their limited application for local resource management; however, continued advancement in automated mapping is facilitating species-based mapping (Hochberg & Atkinson 2000, Andrefouet et al. 2004) and affording assessments of population dynamics at large spatial scales.

Here, watershed size and human development were quantitatively related to the extent of seagrasses and integrity, suggesting that seagrass species may be effectively used as indicators of watershed pollution. Current efforts are underway to limit further impacts to the nearshore environment by stipulating 'acceptable' limits of ecological change into local policy. At a larger scale, watershed management goals are being re-focused to enhance existing *Halodule* habitat integrity and reduce the extent of *Enhalus* seagrass in appropriate localities. For habitats that are influenced by natural disturbances, and community composition is cyclical by nature, metapopulation theory can assist with planning. Unoccupied, suitable patches are fundamental aspects of a species' regional population and may contribute to persistence across time (Hanski 1999). Maintaining unoccupied patches in an appropriate state for recolonization should be an added management goal for the continued persistence of the biologically productive and economically desirable coral habitats. Disregarding the significance of unoccupied habitat patches could mirror the negative effects associated with forest fragmentation (Verheyen et al. 2004). One means of achieving these goals would be through the implementation of a network of marine protected areas that are habitat inclusive, to ensure long-term protection of valuable marine resources and to best defend against another 20% loss of valuable resources in the coming decades.

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