Landsc Ecol (2026) 41:47
https://doi.org/10.1007/s10980-026-02310-5

RESEARCH ARTICLE

Applying a seascape ecology approach enables biophysical and eco-cultural evaluation of marine protected areas

Alan M. Friedlander · Lisa M. Wedding · Denise Antolini · Eric K. Brown · Callie Stephenson · Courtney E. Stuart · Jenny L. Yagodich · Noelani Puniwai

Received: 5 August 2025 / Accepted: 1 February 2026

Abstract

Context To properly determine the efficacy of marine protected areas (MPAs), a seascape perspective that integrates ecosystem elements at scales commensurate with the resources and their users is needed.

Objectives In 1983, the State of Hawaiʻi established the Pūpūkea Marine Life Conservation District (MLCD) on the North Shore of Oʻahu to conserve unique ecological resources and provide recreational opportunities. In 2002, the total marine area under protection was expanded by 0.7 km^2 (545%), and restrictions on harvest were added through a community-driven process. We aimed to evaluate the biophysical and eco-cultural effects of this rezoning process using a seascape ecology approach.

Methods We applied a seascape ecology approach using landscape ecology theory to evaluate the new marine protected area design. The approach incorporated traditional ecological knowledge with in situ surveys and remote sensing, allowing us to examine unique biophysical conditions, specific ecological resources, and the eco-cultural and historical context of the Pūpūkea MLCD.

Results Examination of the cultural seascape of Pūpūkea illuminated numerous important species, heiau (places of worship), and wahi pana (storied places) that detailed the ways the local community was historically tied to ocean resources and the subsequent loss of those connections. The expansion and rezoning of the Pūpūkea MLCD resulted in an increase in habitat diversity, depth range, and structural complexity across the protected area seascape. Between 2003 and 2016, overall fish biomass increased by 60%, driven primarily by herbivorous species. Conversely, fish biomass outside the protected area remained low and relatively constant over this period.

Conclusions We found that multiple moʻolelo (stories) speak to a historical coastal community highly interconnected with a sense of place, ocean rhythms, and fishing resources. The application of a seascape ecology approach and remote sensing technology allowed us to understand the eco-cultural context, quantify the biophysical context, evaluate broad-scale

---

A. M. Friedlander (✉) · C. Stephenson
Hawaiʻi Institute of Marine Biology, University of Hawaiʻi at Mānoa, Kāneʻohe, Hawaiʻi 96744, USA
e-mail: alan.friedlander@hawaii.edu

L. M. Wedding · C. E. Stuart
School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK

D. Antolini · C. Stephenson · J. L. Yagodich
Mālama Pūpūkea-Waimea, Haleʻiwa, Hawaiʻi 96712, USA

E. K. Brown
US National Park Service, National Park of American Samoa, Pago Pago, America Samoa 96799, USA

N. Puniwai
Kamakakūokalani Center for Hawaiian Studies, University of Hawaiʻi at Mānoa, Honolulu, Hawaiʻi 96822, USA

changes, and characterize the ability of this MLCD to protect and restore the area's ecosystems. These results demonstrated that an adaptive, community-driven rezoning process produced an effective ecosystem-based protected area design that led to improvements in a number of fish assemblage metrics over time, which may allow for this community to reconnect with the cultural seascape and sense of place that once guided the stewardship of these marine resources.

Keywords Adaptive management · Community-driven zoning · Geographic information system (GIS) · Hawaiʻi · Fish biomass · Marine protected areas · Seascape ecology · Ecosystem recovery

Introduction

Coral reef ecosystems face overexploitation and severe depletion on a global scale (Hughes et al. 2017; Anthony et al. 2020), and the failure of conventional management measures to stem this decline has led many to argue for an ecosystem-based approach to ensure the sustainability of fisheries and maintain the non-fisheries benefits of the ecosystem for society (Harvey et al. 2018; Obura et al. 2019). Marine protected areas (MPAs) have been increasingly recommended as a tool for an ecosystem-based approach to management, which have been shown to be a highly effective means of conserving biodiversity and managing fisheries, while also restoring and preserving overall ecosystem function (Gaines et al. 2010; Lubchenco and Grorud-Colvert 2015). MPAs also contribute to the long-term livelihoods of island people through the strong cultural and economic connections between islanders and the sea, as well as supporting their interdependence on a healthy marine environment for survival and prosperity (Christie et al. 2017).

MPAs often encompass heterogeneous habitats; therefore, effective design and conservation of individual MPAs or MPA networks require careful consideration of seascape structure, function, and ecological connectivity (Young et al. 2018; Berkström et al. 2020; Gardner et al. 2024). Landscape ecology examines spatial patterns and ecological processes at multiple spatial and temporal scales, including scales larger than those of typical ecological science approaches (Turner 1989). Large-scale views, in particular, provide a strong theoretical basis and set of tools for the appropriate design of protected areas (Turner et al. 2001; Wiens 2009).

The concept that landscape patterns influence ecological processes is widely accepted (McGarigal and Marks 1995), and consequently, many terrestrial conservation efforts employ a landscape ecology approach in protected area design (Wiens 2009). Landscape ecology approaches have been successfully applied to inform terrestrial reserve design (Hoctor et al. 2000). More recently, these approaches have been adapted to marine environments, enabling scientists and managers to view these systems through a seascape lens and inform MPA design (Wedding et al. 2011a; Olds et al. 2016). Furthermore, MPA evaluations can be aided by landscape ecology approaches when assessing the wider-scale impact of management strategies outside of MPAs themselves (Young et al. 2018). Seascape ecology also encompasses the land–sea continuum, recognizing that terrestrial processes such as sedimentation, nutrient runoff, and coastal development influence nearshore habitat structure, connectivity, and ecological function across marine landscapes (Delevaux et al. 2018).

MPAs are spatially discrete management units, making it possible to compile georeferenced and remotely sensed data in a Geographic Information System (GIS). These data can be used to characterize and quantify seascape patterns and evaluate whether existing MPA designs include appropriate depth ranges, topographic complexities, and ecologically relevant, interconnected habitat mosaics (Wedding et al. 2011b; Claudet et al. 2011; Friedlander et al. 2011). Metrics for quantifying landscape patterns are predominantly calculated from the analysis of remotely sensed imagery or their derived products (e.g., categorical maps) and integrated within a GIS framework(Lepczyk et al. 2021). Seascape metrics offer valuable, spatially explicit insights to inform optimal MPA design (Pittman et al. 2007; Wedding et al. 2008).

Beyond the biophysical context, a seascape ecology approach enables the inclusion of cultural relationships and connections with marine environments (Wedding et al. 2024; Wedding 2025). Often elicited through analyzing perceptions, observations, and traditional ecological knowledge (TEK), the inclusion of cultural values is not yet mainstream in seascape ecology studies, management, or public discourse (Pungetti 2012). Yet, incorporating multiple ways of understanding the seascape, such as interweaving contemporary technological methods with TEK, can fill knowledge gaps to yield a more holistic perspective of the seascape's socio-cultural and biophysical aspects (Johannes 2002; Aswani and Ruddle 2013; Stori et al. 2019). In cultural seascape ecology, the concept of seascapes encompasses the regionally important interconnections with the ocean, which can extend inland through estuaries and a complex social-ecological network of processes. This culturally grounded framing positions seascape ecology within a broader family of integrative approaches—such as ecosystem-based management, social–ecological systems, and spatial conservation planning—while offering a distinct, process-based lens for understanding how spatial patterns shape ecological and cultural dynamics across scales.

Ecosystem-based management (EBM) provides an integrative framework for sustaining ecosystem health while balancing human uses (McLeod and Leslie 2009), whereas social–ecological systems (SES) research emphasizes feedbacks between human and ecological components that shape resilience and adaptive capacity (Berkes et al. 2004). Similarly, spatial conservation planning (SCP) identifies and prioritizes areas that efficiently meet biodiversity or cultural targets (Margules and Pressey 2000; Moilanen et al. 2009). In comparison, cultural seascape ecology (SE) is a process-based, multi-scalar framework that examines how the spatial configuration, heterogeneity, and connectivity of marine environments influence both ecological functioning and the cultural relationships people maintain with the ocean (Boström et al. 2011; Pittman 2018; Wedding et al. 2025). Integrating SE with EBM, SES, and SCP provides a mechanistic and place-based understanding of how spatial patterns mediate ecological processes and eco-cultural values, thereby strengthening the design, evaluation, and adaptive management of MPAs (Olds et al. 2016; Wedding et al. 2025).

Together, this conceptual framing underscores how a cultural seascape ecology approach can advance both the scientific understanding and practical evaluation of MPAs by linking spatial patterns, ecological processes, and cultural connections. These principles are particularly relevant in Indigenous and place-based management systems, where ecological processes and cultural practices are deeply intertwined across the seascape. For example, the Hawaiian biocultural resource management system, practiced in the pre-contact era, divided large islands into social-ecological regions (moku) and further into interrelated social-ecological communities (ahupuaʻa), within which a nested network of scaled kinship-derived sections (ʻili, moʻo, etc.) exists (Winter et al. 2018). In coastal communities, where people are closely connected to the ocean, understanding the ecological dynamics and cultural implications of seascapes is vital for safeguarding human and ecosystem health, and for selecting appropriate conservation targets, methods, and recovery metrics (Opdam 2020). Recognizing and incorporating these enduring cultural linkages and traditional ecological knowledge (TEK) within contemporary management supports the sustainability of both customary practices and biophysical systems (Mulrennan and Scott 2000).

In Hawaiʻi, declining fisheries resources (Nadon 2017; Friedlander et al. 2018) has led to calls for the expanded use of MPAs as a tool for effective management. Hawaiʻi established its first MPAs over 50 years ago and has since established numerous protected areas of varying sizes, habitat types, and protection levels. These MPAs permit a wide range of activities within their boundaries (Friedlander et al. 2019). Designation of many of these areas was not based on comprehensive ecological selection criteria but rather was reactive and opportunistic, responding to user conflicts, safeguarding protected species, or reflecting the initiatives of local communities. Consequently, MPAs in Hawaiʻi have not been as effective in restoring coastal fisheries as originally envisioned (Friedlander et al. 2007b).

On the North Shore of Oʻahu, Hawaiʻi, the neighborhood board was approached in the 1970s by divers and other users who expressed concerns about the declining health of the nearshore marine ecosystem. In 1974, based on mailed questionnaires and interviews, shoreline users ranked the Pūpūkea Beach Park on the North Shore as one of the top sites for a new marine conservation district on Oʻahu (Kimmerer and Durbin 1975). In 1978, the Hawaiʻi Department of Land and Natural Resources (DLNR) initiated public meetings to discuss the creation of a Marine Life Conservation District (MLCD) in the area. MLCDs are specifically designed to conserve and replenish marine resources around the state and are nominated through public recommendations, legislative mandate, biological surveys, and other means (Hawai‘i Division of Aquatic Resources 1992). At the time of establishment in 1983, the North Shore of O‘ahu had a small population with a rural agricultural lifestyle. The designation of the MLCD officially restructured the community’s relationship with this popular area for diving and fishing, replacing resource use with more conservation-oriented regulations. Due to concerns expressed by fishermen when the Pūpūkea MLCD was established, several extractive activities were permitted, including line fishing from shore, spear fishing on snorkel, and netting in Sharks Cove (Fig. 1).

By the 1990s, residents recognized that existing rules were ineffective and difficult to enforce and brought their concerns to the North Shore Neighborhood Board, which relayed them to elected officials. In response, the state senator requested that DLNR convene a stakeholder task force, which met extensively for two years. The task force included representatives of ten different interest groups within the community, including commercial, recreational, and subsistence fishers, resulting in the inclusion of Waimea Bay within the MLCD. After extensive public hearings, the area of the MLCD was expanded in 2002, with minor rule revisions in 2003 and 2021. The MLCD now covers 0.71 km^2 (expanded from 0.11 km^2), and fishing is generally prohibited. Limited exceptions are allowed: hand-harvesting of up to one kg day^{-1} of two seaweed species (*Asparagopsis taxiformis* and *Enteromorpha prolifera*) is permitted throughout the MLCD, and shore fishing is allowed in Waimea Bay only (Fig. 1), with a maximum of two rods per person. In addition, seasonal commercial net fishing is permitted in Waimea Bay for two coastal pelagic species (*Decapterus* spp. – August and September; *Selar crumenophthalmus* – November and December).

To evaluate the effectiveness of the expansion of the Pūpūkea MLCD, we applied a seascape ecology approach to quantify ecosystem patterns at scales relevant to the marine resources and assess the eco-cultural context of management. We hypothesized that the increased size of the Pūpūkea MLCD would result in greater habitat diversity, depth variability, and structural complexity, prompting increases in the diversity, abundance, and biomass of fishes within the protected area over time compared to unprotected, adjacent areas.

Materials and methods

Study area

Pūpūkea is a prominent headland consisting of an erosional rock platform cut into coral limestone of Late Pleistocene age, which is surrounded by a flat sandy sea floor (Noormets et al. 2002). The area is exposed to large winter swells with wave periods of 14-20 s and breaking face heights of 2-15 m (Fletcher et al. 2008). As a result, Holocene reef accretion is a thin veneer of living corals resting on antecedent Pleistocene limestone foundations, creating a rugged karst morphology (Grigg 1998).

Cultural seascape ecology.

Seascape ecology theory was applied to integrate TEK with scientific insights in evaluating the unique biophysical conditions, specific ecological resources, and the eco-cultural and historical context of Pūpūkea. We first assembled marine-related stories and cultural practices local to the Pūpūkea and Waimea Bay study sites along O‘ahu’s North Shore. We conducted informal interviews with local community members, who shared oral histories and directed us to foundational texts grounded in Native Hawaiian epistemology. We reviewed historical and cultural sources, including mo‘olelo (stories) and archival compilations, focusing on marine-related practices and land tenure records specific to ocean resource use within the Pūpūkea MLCD and its adjacent coastal areas. To contextualize recent management history, we compiled legal documents and administrative records obtained from the DLNR and the Pūpūkea Task Force detailing the establishment and expansion of the MLCD.

We conducted a qualitative content analysis of mo‘olelo, oral histories, and archival sources to identify recurring ecological and cultural themes related to marine resource use, species importance, and place-based management. Key cultural sites (heiau, wahi pana) and resource species were georeferenced and compared spatially with current MLCD boundaries and habitat types using ArcGIS Desktop (ESRI

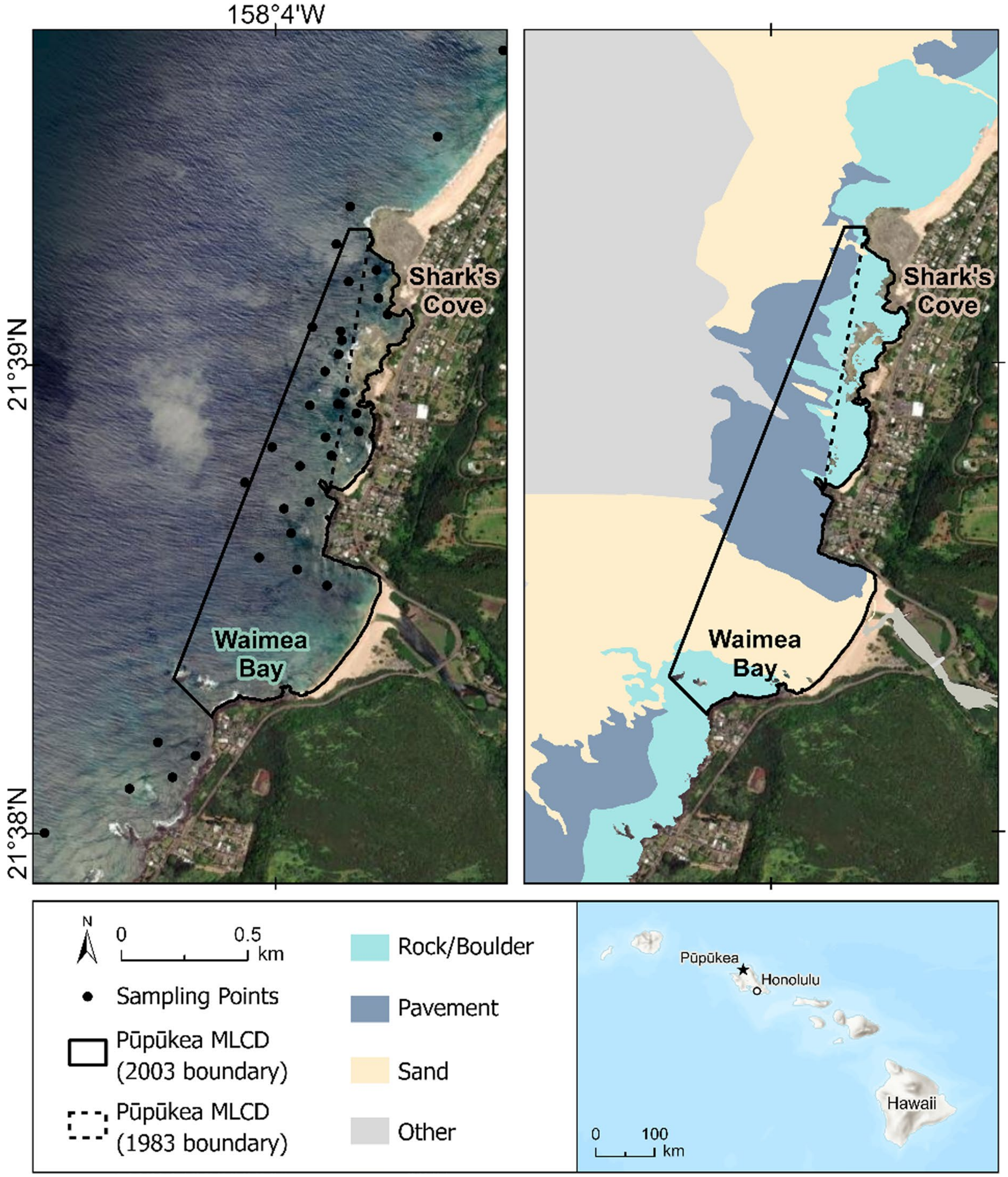

Fig. 1 Boundaries of Pūpūkea Marine Life Conservation District (MLCD) pre and post boundary expansion. Black dots represent the locations of surveys conducted in the present study. The entire geographic extent of the control area is not shown to highlight the details within the MLCD. Insert—Location of Pūpūkea on the island of Oʻahu in the main Hawaiian Islands

2011). This allowed us to examine how rezoning aligned with historically significant fishing and ceremonial areas, and to assess the extent to which current management protects culturally important resources.

Sample design

This study used a multi-pronged approach to characterize the habitats and associated fish assemblages before and after MPA expansion. Remotely sensed data were used to generate information on depth, topographical complexity, and benthic habitats. These were combined with in situ surveys to collect fish assemblage metrics for each habitat type.

In situ survey sites were assigned to hardbottom habitat types using a stratified random sampling approach implemented in ArcGIS (ESRI 2011, Fig. 1). Within each major habitat type, sampling was further stratified by management regime (MLCD and open access). Within the MLCD, a total of nine survey sites per year were conducted within colonized hardbottom habitat (≥ 10% live coral cover) and fifteen surveys sites within uncolonized hardbottom habitats based on a previous sample size optimization analysis (Friedlander et al. 2007a). A total of 27 sites were surveyed in the open access areas, all of which were in uncolonized hardbottom habitat. In the field, divers navigated to these sampling points and surveyed a single 25 × 5 m transect to quantify fishes and benthic cover. The same location points within each habitat type were revisited once each survey year beginning in 2003, and within the same season (June–August) to monitor changes in the fish assemblages. These months are the calmest season for surf and the time period when fish assemblage structure tended to be more temporally stable (Friedlander and Parrish 1998).

Bathymetric LiDAR

Light detection and ranging (LiDAR) data were obtained from the U.S. Army Corps of Engineers Scanning Hydrographic Operational Airborne Lidar Survey (SHOALS) system (Irish and Lillycrop 1999). Topographic and bathymetric measurements were made using infrared (1064 nm) and blue-green (532 nm) scanning laser pulses, with data collected in Hawai‘i between 1999 and 2000. The vertical and horizontal accuracies are ± 20 cm and ± 1.5 m, respectively. Depth detection by SHOALS ranges from a minimum of 0–1.5 m to a maximum of approximately 40 m. The spatial resolution of the SHOALS LiDAR data is 4 m.

Seascape ecology approach

Perimeter (km) and area (km^2) of the 1983 and 2003 MLCDs and associated benthic habitat types (e.g., geomorphic structure, biological cover) were measured using ‘Hawth’s Analysis Tools’ Version 3.27 (Beyer 2004) (see Battista et al. 2007 for details on Hawai‘i benthic habitat maps and methodology). Patch Analyst was applied to characterize several seascape metrics (e.g., Shannon’s diversity and evenness indices and mean patch fractal dimension) within the two reserve boundaries. NOAA Biogeography Branch benthic habitat maps were used to derive two-dimensional (2D) seascape metrics around each sampling point, applying a 100 m radius buffer based on prior studies that demonstrated strong relationships between coral reef fish assemblages and 2D metrics at this spatial scale (Pittman et al. 2007; Kendall and Miller 2008). Within the 100 m buffer, the habitat richness and area (m^2) of: (1) coral, (2) coralline algae, (3) macroalgae, (4) turf, and (5) sand/mud were calculated in MATLAB software (The MathWorks, Inc. 2011).

LiDAR data were interpolated using Inverse Distance Weighting via the ArcGIS Spatial Analyst extension (ESRI 2011) (see Wedding et al. 2008; Wedding and Friedlander 2008 for details on Hawai‘i LiDAR data). Bathymetric grids with a cell size of 4 m were created, where various geomorphic metrics (e.g., slope, aspect, bathymetric variance, slope of slope) were derived. Aspect, representing the compass direction of the slope, was calculated using the aspect function of the ArcGIS Spatial Analyst extension (ESRI 2011). Bathymetric variance, representing the roughness of the seafloor topography, was calculated using MATLAB moving window analysis (The MathWorks, Inc. 2011). Slope of slope, representing the maximum rate of maximum slope change between neighboring cells, was derived using the slope tool of the ArcGIS Spatial Analyst extension (ESRI 2011). These rasters were used to summarize the mean, standard deviation, and range of three-dimensional (3D) metrics using ‘Zonal Statistics’ in Hawth’s Analysis Tools (Beyer 2004).

In situ benthic assessments

In 2003, 2006, 2007, and 2024, in situ benthic surveys were conducted inside the MLCD along the same 25 × 5 m transects upon completion of the visual fish survey (see below). For 2003, 2006, and 2007, benthic habitats were surveyed using an in situ planar point intercept quadrat method (Jokiel et al. 2015). Each transect was stratified into 5 × 5 m segments with quadrat placement randomly allocated within each segment ($n = 5$ quadrats). Benthic cover was estimated using a 1 m^2 quadrat divided into 100 (10 × 10 cm) smaller squares. A subset of 25 randomly selected intersections were marked and used for substrate identification based on previous acceptable error and optimal sampling time (Friedlander et al. 2007b). Each intersection was identified using the substrate categories of scleractinian coral, crustose coralline algae (CCA), turf algae, macroalgae, other invertebrates, and unconsolidated substrate. Percent cover for each substrate category was derived by dividing the number of points by the total number of intersections ($n = 25$) within each quadrat.

Owing to improvements in camera technology and the time-consuming nature of in situ benthic surveys, photographic transects were conducted in 2024 along the same 25 m transects. A camera was positioned ca. 0.65 m off the bottom and photos were taken at each meter for a total of 25 photos. Photos were then imported into CoralNet image annotation software (Beijbom et al. 2015). Twenty-five random points were overlaid on five photographs, which were randomly selected in a similar manner to the quadrats described above and the benthic component under each point was identified using the same substrate categories.

Fish sampling methodology

Fish surveys were conducted in 2003, 2006–2008, 2011, 2016, 2020–22, and 2024 and at the same time as the benthic surveys. Fish assemblages at each location were quantified using standard underwater visual belt transect survey methods (Brock 1982). A diver swam a 25 × 5 m transect at a constant speed and identified to the lowest possible taxon all fishes visible within 2.5 m to either side of the centerline (125-m^2 transect area). Swimming duration varied from 10–15 min, depending on habitat complexity and fish abundance. Nomenclature followed Randall (2007). Total length (TL) of fishes was estimated to the nearest cm and converted to weight using the following length–weight relationship: $W = a\mathrm{TL}^b$, where the parameters a and b are constants for the allometric growth equation, TL is standard length in cm, and W is weight in g. Length–weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawai‘i (Hawai‘i Cooperative Fishery Research Unit, unpublished data) and were supplemented with information from other published and web-based sources. When length–weight information did not exist for a given species, the parameters from similar bodied congeners were used. Fish species diversity was calculated from the Shannon–Weaver diversity index: $H' = -\sum_{i=1}^{S}(pi \text{ X } [lnpi])$, where p_i is the proportion of all individuals counted that were of taxa i (Ludwig and Reynolds 1988). The evenness component of diversity was expressed as: $J = H'/\ln(S)$, where S is the total number of species present (Pielou 1977).

Fish taxa were categorized into four trophic guilds (herbivores, secondary consumers, planktivores, and piscivores) according to various published sources (Friedlander and DeMartini 2002; DeMartini et al. 2005). Resource species targeted by commercial, recreational, and subsistence fishers in Hawai‘i were identified following Williams et al. (2008).

Statistical analyses

Variation in benthic assemblage structure among years for the major benthic functional groups was investigated using permutation-based multivariate analysis of variance (PERMANOVA). A Bray–Curtis similarity matrix was created from percent cover of major benthic functional groups. Prior to analysis, benthic functional group cover data were arcsine square root transformed to meet the assumptions of normality. Interpretation of PERMANOVA results was aided using individual analysis of similarities (ANOSIM). The ANOSIM R statistic represents pairs of years that are either well separated ($R > 0.75$), overlapping but clearly different ($R > 0.5$), or barely separable at all ($R < 0.25$). Differences in scleractinian coral and CCA among years were compared using a one-way analysis of variance (ANOVA) with unplanned comparisons between pairs examined using the Tukey–Kramer hsd (honestly significant difference) test for ANOVA ($\alpha = 0.05$). Percent cover data were arcsine square root transformed prior to analysis to meet the assumptions of normality.

A Principal Components Analysis (PCA) was used to create composite variables of the 2D and 3D seascape metrics described above. All variables were centered and standardized prior to analysis. The PCA axes were then used to compare fish assemblage characteristics (e.g., species richness, numerical abundance, biomass, diversity, and evenness) using Generalized Regression Models. A normal response distribution, identity link function, and Maximum Likelihood estimation method were used for fish species richness, numerical abundance, diversity, and evenness. An exponential response distribution, log link function, and Maximum Likelihood estimation method was used for fish biomass to account for the high variation among sites.

Comparison of fish assemblage metrics between the Pūpūkea MLCD and adjacent areas open to fishing were conducted using Linear Mixed Models (LMMs). Transects and years were treated as random effects to account for repeated measurements and all response variables (i.e., fish assemblage metrics) were transformed based on rank. Drivers of fish assemblage structures between the MLCD and open areas were investigated using PERMANOVA with a Bray–Curtis similarity matrix created from biomass of fish taxa. Prior to analysis, fish assemblage structure was $\ln(x+1)$ transformed. Similarity of percentages analysis (SIMPER) was used to determine the fish taxa most responsible for the percentage dissimilarities between the MLCD and open areas using Bray–Curtis similarity analysis of hierarchical agglomerative group average clustering.

Detrended Correspondence Analysis (DCA) with detrending by segments was used to examine fish assemblage structure within the MLCD among years. Taxa biomass (g m^{-2}) was log-transformed and rare species were downweighted. The top 10 species with the largest weights based on response weight scores were plotted for visualization purposes.

Results

Cultural seascape ecology

The ʻāina (landscape) surrounding the Pūpūkea MLCD is rich in cultural history with numerous sacred sites, heiau (places of worship), and wahi pana (storied places) (Fig. 2). The valley may have been settled as early as 400 A.D., but little is known prior to the eleventh century. The cultural history and understanding of this seascape are rooted in the place names Waimea, which means ‘sacred water’, and Pūpūkea, which refers to a white shell used in fishing heʻe (octopus). Stories from before written history speak to the community’s interconnectedness with their ocean resources. Multiple pōhaku (stones) within the region are named in reference to fishers, such as Nā ʻUkali o Pele, which represent a family of fishers turned to stone by the akua (goddess) Pele in honor of their reverence to her, and Piliaʻama, a konohiki (headman of land division) within Waimea and storied fisherman. Another region, known commonly today as Three Tables, is named Kalua o Maua in reference to a fisherman’s wife, Maua, who was immortalized as a floating stone that signaled pūnāwai (submarine groundwater springs).

According to Hawaiian stories, the high chief Kama Puaʻa was given a gift from the high priest — Kahuna Nui Kahikiʻula — the gift was all lands beginning with ‘wai’, including Waimea (Kamakau 1961). After this, the ahupuaʻa (watershed from mountain to sea) of Waimea and Pūpūkea were given to the Papa Kahuna. King Kamehameha took the island of Oʻahu in 1795, and gave Waimea Valley to his Kahuna Nui, whose name was Hewahewa. He was the last Kahuna to preside over the heiau (place of worship) in the valley. Hewahewa died in 1837 and is buried in Waimea Valley. Known as the “valley of the priests,” Waimea Valley was originally part of the larger moku (district) of Koʻolauloa but was added to the district of Waialua in the 1800s.

The valley is surrounded by three major heiau. Located on the Kāpaeloa side of the outer entrance to the valley, Kūpopolo Heiau was built under the direction of Kahahana, the Chief of Oʿahu, by Kahuna Nui Kaopulupulu who lived in the valley in the 1700s. When the placement of the heiau was deemed inadequate for their needs, Pu’u o Mahuka was built on the puʻu (bluff) called Keanaloa. Another sacred site, located on the water’s edge at the southwestern side of Waimea Bay, is called Ke Ahu Hapu ʻu. This temple is dedicated to the shark god Kaneaukai (Puniwai 2020). Puʻu o Mahuka and Kūpopolo are human sacrificial temples, and Kaneaukai is a fishing shrine or temple.

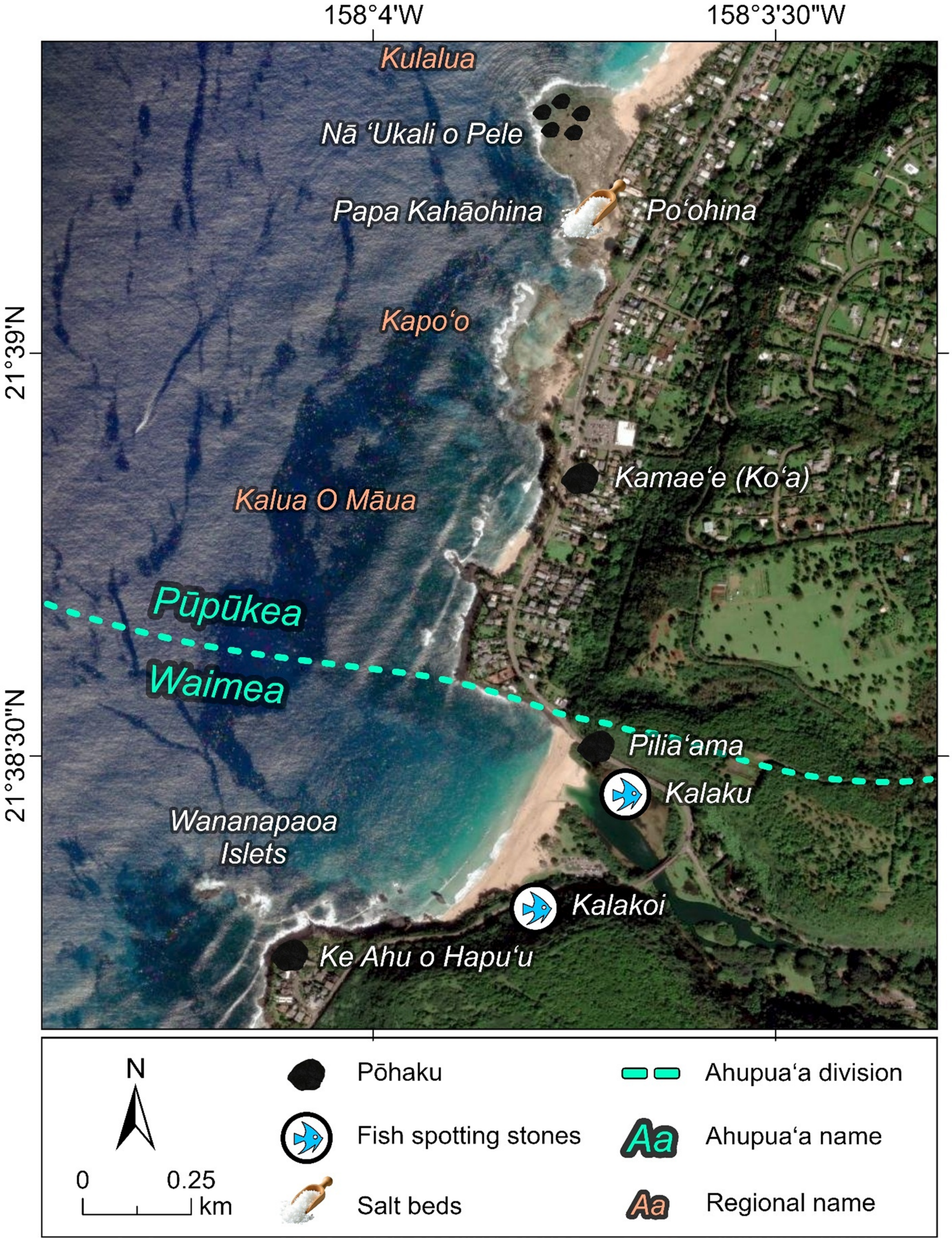

Fig. 2 Hawaiian place names associated with the Pūpūkea Waimea area on the north shore of Oʻahu

Over the past few centuries, Waimea was a large Hawaiian settlement, with a healthy water source, abundant fish stocks, and traditional crops. Moʻolelo speak to abundant resources of kala (*Naso unicornis*, Bluespine Unicornfish), moi (*Polydactylus sexfilis*, Sixfinger Threadfin), ʻoʻio (*Albula glossodonta,* Shortjaw Bonefish), āholehole (*Kuhlia* spp., Hawaiian Flagtail), uhu (Scaridae, parrotfishes), opule (*Anampses* spp, Pearl Wrasse), ʻoʻopū hinana (juvenile Hawaiian stream goby, multiple species), manini (*Acanthurus triostegus*, Convict Tang), and pāpaʻi (crabs, multiple species). Some of the first records of fisheries in the region come from the early 1800s, during the Māhele ʻĀina, when multiple claims were made to privatize areas within the MLCD used for fishing of ocean and stream species, as well as salt-making ponds. Around this time, Waimea Bay became the sandalwood capital of Hawai ʻi and huge cargo ships would anchor offshore to load sandalwood; however, by the 1830s, sandalwood was beginning to disappear, and the trade soon ended. Ocean resources were also strained, leading to kapu (fishing prohibitions) being placed in 1850 on uhu, and on kala and moi in 1857. In 1898, a huge flood, exacerbated by deforestation, drove the inhabitants from Waimea Valley, most of whom moved to the beach area but eventually moved away.

Seascape structure

The total area within the MLCD increased from 0.11km^2 to 0.71km^2 (+545%) after the 2002 boundary expansion, while habitat diversity and evenness increased by 59% and 25%, respectively (Table 1). The mean patch fractal dimension increased by 33% following boundary expansion. In contrast, the total perimeter-to-area ratio of the MLCD decreased by 74% (Table 1, Fig. 1). Average depth increased from 3.6 m (±2.6 SD) to 8.1 m (±4.2 SD) following boundary expansion and the maximum depth within the MLCD increased from 12 to 17 m (Table 1, Fig. 3).

Biological cover prior to boundary expansion was dominated by macroalgae (63%), followed by uncolonized hard bottom (24%), with virtually no coral (Table 2). Following the MLCD expansion, biological cover consisted of a mixture of uncolonized hard bottom (33%), macroalgae (26%), turf algae (25%), and coral (12%).

The first four PCA axes explained 86.9% of the variability in seascape metrics. The major loadings for PC1 (46.1% of total variance) were slope, rugosity, fractal dimension, variance in depth, and slope^2 (Table 3). Fractal dimension, rugosity, slope, slope^2, and variance in depth were highly correlated and orthogonal to depth and turf algae cover in ordination space (Fig. 4). The major loadings for PC2 (17.8%) were depth, turf algae cover, and sand. Macroalgae and turf were major loadings for PC3 (13.8%), while coral cover and sand were the major loadings for PC4 (9.3%).

Comparisons of benthic communities within the MLCD over time

Following MLCD expansion, turf algae comprised 56.1% of the substrate within the MLCD on average, followed by CCA (14.4%), uncolonized substrate (12.8%), scleractinian coral (11.3%), macroalgae (4.5%), and other invertebrates (0.8%) (Table 4). Scleractinian coral showed a large drop in cover from 17.8% in 2006 to 5.8% in 2024 and was

Table 1 Summary of benthic habitat geomorphic structure and biological cover from NOAA Biogeography Branch Hawaiʻi benthic habitat maps (Battista et al. 2007) within the 1983 and 2003 Pūpūkea MLCD boundaries

Seascape metrics	1983 boundary	2003 boundary	Percent change
Reserve area (km^2)	0.11	0.71	545.46
Reserve perimeter (km)	2.97	5.21	75.42
Perimeter to area ratio	27.88	7.34	-73.67
Depth (m)			
Average (±SD)	3.59 (±2.61)	8.09 (±4.23)	125.35
Depth range	0—12.07	0—16.97	40.60
Shannon's diversity index	0.91	1.45	59.34
Shannon's evenness index	0.65	0.81	24.62
Mean patch fractal dimension	1.35	1.79	32.59

Fig. 3 **a** Depth, **b** slope of slope (i.e., rate of change of slope, which is a measure of habitat complexity), and **c** aspect inside the Pūpūkea MLCD.

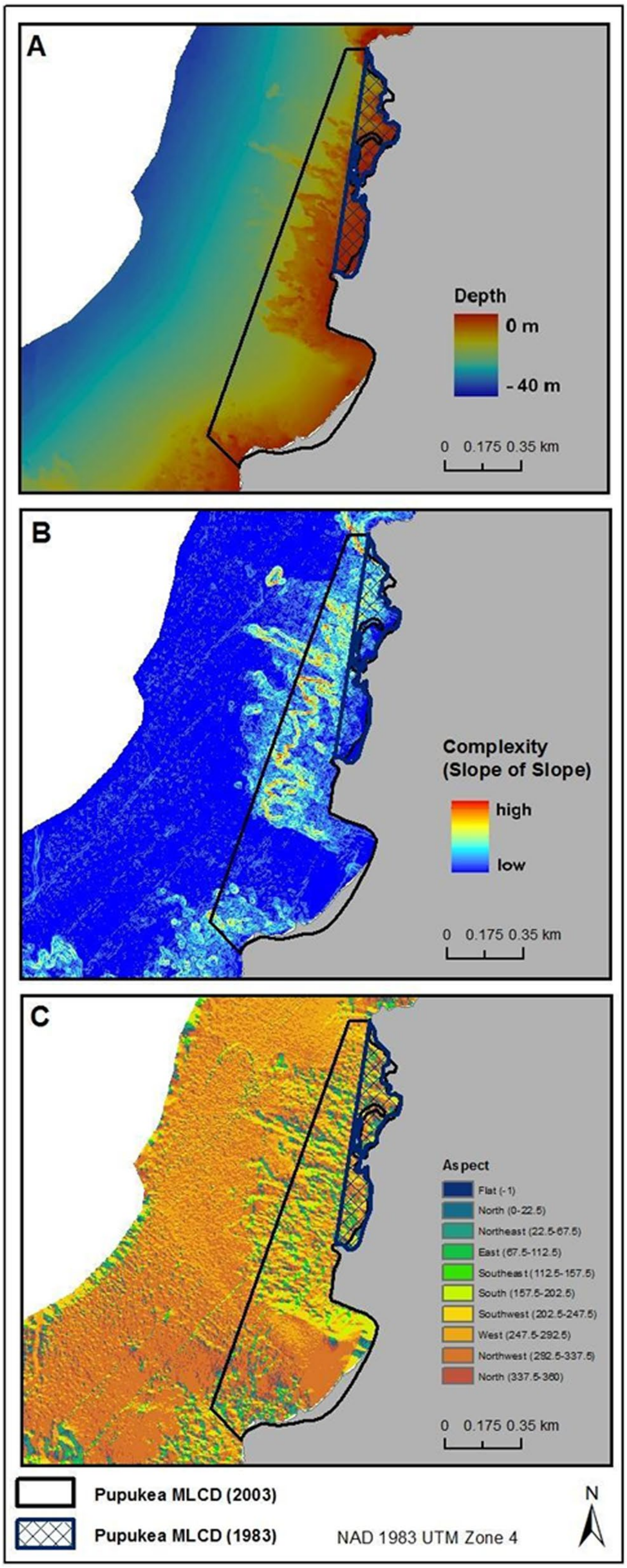

Table 2 Summary of seascape structure and biological cover within the Pūpūkea MLCD before and after expansion derived from NOAA benthic habitat maps, boundary analysis from GIS, and LiDAR bathymetric grids

	1983 boundary		2003 boundary	
Geomorphic structure	km^2	% of total	km^2	% of total
Land	0.025	23.78	0.025	3.53
Pavement	–	–	0.262	36.90
Rock/boulder	0.079	73.7	0.182	25.68
Sand	0.001	0.07	0.236	33.27
Scattered coral/rock	0.003	2.45	0.003	0.38
Unclassified	–	–	0.002	0.24
Biological cover	km^2	% of total	km^2	% of total
Coral 10%- < 50%	–	–	0.086	12.07
Macroalgae 10%- < 50%	0.067	62.81	0.181	25.53
Turf 10%- < 50%	0.003	2.45	0.003	0.38
Turf 50%- < 90%	0.012	10.88	0.177	24.97
Uncolonized 90%-100%	0.001	0.08	0.237	33.28
Unclassified	0.025	23.78	0.027	3.77

significantly different among years ($F_{3,95} = 12.23$, $p < 0.001$), with 2024 significantly different from 2006 and 2007 and 2006 significantly different from 2003 (all $p < 0.05$). CCA, which is settlement habitat for coral larvae, showed no significant difference among years ($F_{3,95} = 1.79$, $p < 0.155$) but increased slightly over time. There was a significant difference in benthic functional group structure among years (pseudo-$F_{3,95} = 6.85$, $p = 0.001$); however, pairwise comparisons between years were barely separable (all Rs < 0.25), except for 2003–2006, which was different but still overlapping (R < 0.5).

Comparisons of fish assemblage characteristics between the MLCD and open areas

Species richness, numerical abundance (num. m^{-2}), biomass (g m^{-2}), and diversity of the fish assemblage were all significantly higher in the Pūpūkea MLCD when compared to open areas across all years and ranged from 11.0% higher for diversity to a nearly fourfold difference for biomass (Table 5). Evenness was significantly higher in the open area compared to the MLCD by 7.7%. Within the MLCD, herbivores accounted for 70.2% of total biomass, followed by invertivores (20.5%), planktivores (5.0%), and top predators (4.3%). Biomass outside the MLCD was also dominated by herbivores (51.0%), followed by invertivores (42.4%), planktivores (3.9%), and top predators (2.7%). There was a significant difference in fish assemblage structure between the MLCD and open areas based on biomass (PERMANOVA pseudo-$F_{1,19} = 16.24$, $p < 0.001$). The species most responsible for the dissimilarity between these areas were *Acanthurus leucopareius* (21.6% of total dissimilarity), *Scarus rubroviolaceus* (12.8%), *Acanthurus olivaceus* (7.6%), *Kyphosus* species (6.8%), and *Naso lituratus* (4.9%) (Table 6).

Seascape metrics and fish assemblage characteristics

Composite seascape metrics explained much of the variation in fish assemblage characteristics within the MLCD, ranging from 50.3% for numerical

Table 3 Principal Components Analysis loading matrix of 2D and 3D seascape variables. Values in bold denote higher loading values. Values in parentheses in the table header denote the amount of variance explained by each principal component axis

Seascape variables	PC1 (46.1%)	PC2 (17.8%)	PC3 (13.8%)	PC4 (9.3%)
2D coral (m^2)	**0.451**	**0.485**	−0.142	**0.708**
2D macroalgae (m^2)	0.371	−0.242	**−0.848**	−0.159
2D turf algae (m^2)	0.095	**−0.694**	**0.598**	0.255
2D sand (m^2)	**−0.630**	**0.512**	0.331	**−0.441**
3D depth	−0.130	**0.930**	0.114	0.103
3D depth var	**0.847**	−0.013	0.302	−0.222
3D slope	**0.963**	0.086	0.067	−0.122
3D slope^2	**0.838**	0.014	0.135	0.241
3D rugosity	**0.927**	0.105	0.213	−0.173
3D fractal	**0.911**	0.154	0.107	−0.231
3D aspect	**−0.514**	−0.114	0.356	0.146

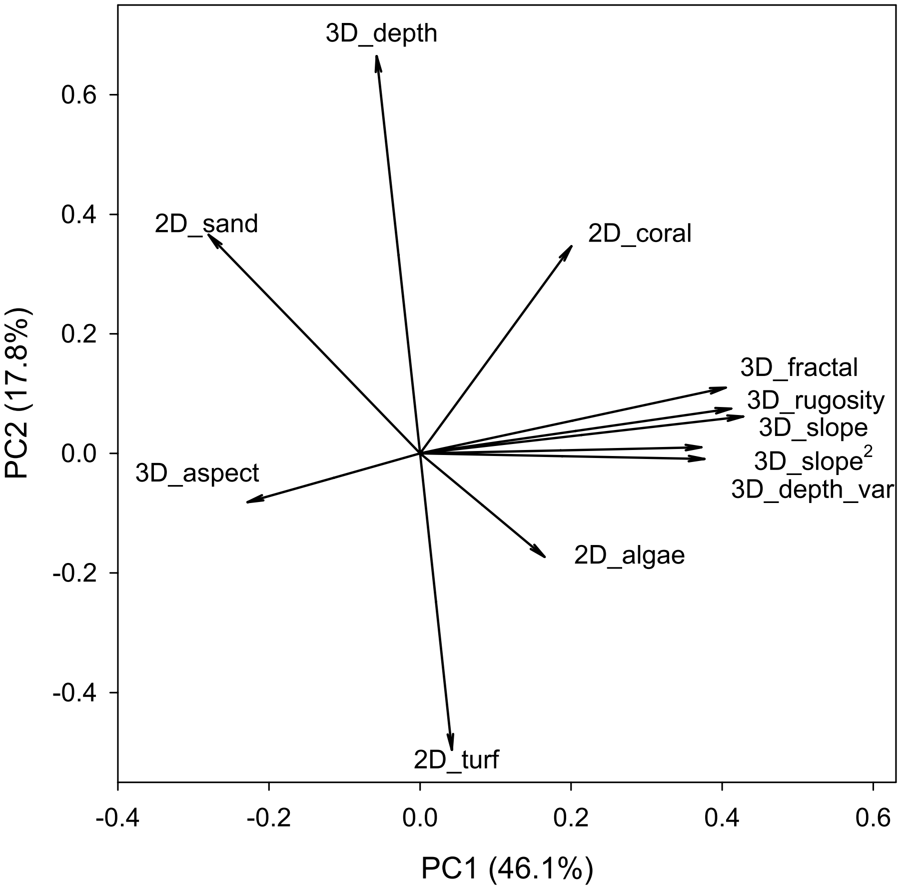

Fig. 4 Principal component analysis of seascape metrics. Values were centered and standardized prior to analysis

Table 4 Benthic functional group percent cover among years within the Pūpūkea MLCD. Values are means with standard deviations in parentheses. CCA crustose coralline algae

Year	CCA	Scleractinian coral	Other invertebrates	Macroalgae	Uncolonized substrate	Turf algae
2003	15.07 (9.6)	9.10 (7.64)	0.07 (0.22)	2.27 (1.71)	8.97 (6.28)	64.53 (9.77)
2006	15.40 (11.27)	17.76 (8.13)	1.37 (1.27)	3.63 (4.58)	17.59 (8.38)	44.26 (12.66)
2007	10.00 (7.01)	12.66 (6.52)	1.13 (1.39)	6.22 (5.32)	11.65 (8.51)	58.34 (9.27)
2024	17.27 (13.09)	5.83 (4.49)	0.47 (0.86)	6.03 (7.86)	13.13 (12.94)	57.27 (16.94)
Average	14.43 (10.82)	11.34 (8.15)	0.76 (1.16)	4.54 (5.59)	12.83 (9.85)	56.10 (14.54)

abundance to 86.8% for diversity (Table 7). PC1, which was highly correlated with measures of structural complexity, was positively and significantly correlated with all fish assemblage characteristics, most notably with species richness. PC2, which correlated with depth, turf algae cover, and sand, was negatively and significantly associated with all fish assemblage characteristics, with the strongest relationship being fish biomass. PC3 correlated with macroalgae and turf algae and was negatively but more weakly associated with all fish assemblage characteristics. Coral cover and sand were the major loadings for PC4, which was positively but weakly correlated with all fish assemblage metrics.

Table 5 Comparison of fish assemblage metrics between the Pūpūkea MLCD and adjacent areas open to fishing. Values are means with standard deviations in parentheses. Statistical results of Linear Mixed Models (LMMs). Transects and years were treated as random effects to account of repeated measurements and all fish assemblage metrics were transformed based on rank

Assemblage metric	MLCD	Open	F	p
Species	20.00 (5.19)	13.07 (5.79)	71.67	<0.001
Number m^{-2}	0.97 (0.55)	0.56 (0.41)	30.76	<0.001
Biomass ($g\ m^{-2}$)	92.78 (82.66)	23.43 (30.94)	127.27	<0.001
Diversity	2.12 (0.41)	1.91 (0.41)	11.67	0.001
Evenness	0.72 (0.14)	0.78 (0.11)	10.24	0.002

Table 6 Similarity of percentages (SIMPER) for the fish species most responsible for the percentage dissimilarities between the MLCD and open areas across all years using Bray–Curtis similarity analysis of hierarchical agglomerative group average clustering. Values are means with standard deviations in parentheses. *Diss.* dissimilarity. % contrib. is the percentage of each species contribution to overall dissimilarity

Species (Avg. Diss. = 61.12)	MLCD	Open	Diss	% contrib
Acanthurus leucopareius	20.29 (9.17)	2.72 (1.72)	14.73 (2.32)	21.63
Scarus rubroviolaceus	10.64 (4.58)	0.65 (0.78)	8.74 (2.12)	12.84
Acanthurus olivaceus	8.47 (3.84)	2.26 (1.24)	5.21 (1.96)	7.65
Kyphosus species	5.38 (3.25)	0.15 (0.43)	4.62 (1.56)	6.78
Naso lituratus	4.12 (1.57)	0.32 (0.38)	3.32 (2.42)	4.87
Acanthurus nigrofuscus	5.53 (1.64)	1.94 (0.72)	3.07 (2.17)	4.50
Acanthurus triostegus	4.07 (3.09)	2.06 (2.36)	2.65 (1.18)	3.89
Caranx melampygus	3.49 (3.18)	0.59 (0.42)	2.54 (1.14)	3.73
Ctenochaetus strigosus	2.09 (1.07)	0.10 (0.09)	1.74 (1.94)	2.55
Monotaxis grandoculis	1.80 (4.11)	0.51 (1.06)	1.73 (0.53)	2.54

Table 7 Results of Generalized Regression Models of fish assemblage characteristics and Principal Component Axes. Values for PC1-4 are partial pseudo-R^2s. *** = $p<0.001$, ** = $p<0.01$, * = $P<0.05$. Sign (±) denotes direction of interaction

Assemblage characteristic	Log likelihood	Generalized R^2	PC1	PC2	PC3	PC4
Species	91.273***	0.863	+0.356***	−0.227***	−0.115***	+0.165***
Number m^{-2}	17.818***	0.503	+0.302***	−0.182**	+0.001	+0.017
Biomass ($g\ m^{-2}$)	147.755***	0.664	+0.233***	−0.328***	−0.033*	+0.070**
Diversity	12.963***	0.868	+0.250***	−0.272***	−0.134***	+0.211***
Evenness	13.775***	0.712	+0.188***	−0.224***	−0.112**	+0.187***

Temporal trends in fish assemblages

Overall fish biomass in the expanded Pūpūkea MLCD increased by 59.7% between 2003 and 2016 (Fig. 5), which was driven mainly by increases in herbivore biomass, predominately large schools of surgeonfishes (e.g., *A. leucopareius* and *A. olivaceus*) and large parrotfishes (e.g., *S. rubroviolaceus*). Biomass declined by 25.6% between 2016 and 2022 but increased slightly (3.3%) by 2024. Biomass outside the MLCD has remained low and relatively constant since 2003.

Fish assemblage structure within the MLCD based on biomass varied over time, with the first two axes of the DCA explaining 35.2% of total variation (Fig. 6). Large changes in assemblage structure occurred between 2006 and 2007–2008, which was correlated with increases in biomass of the ember parrotfish

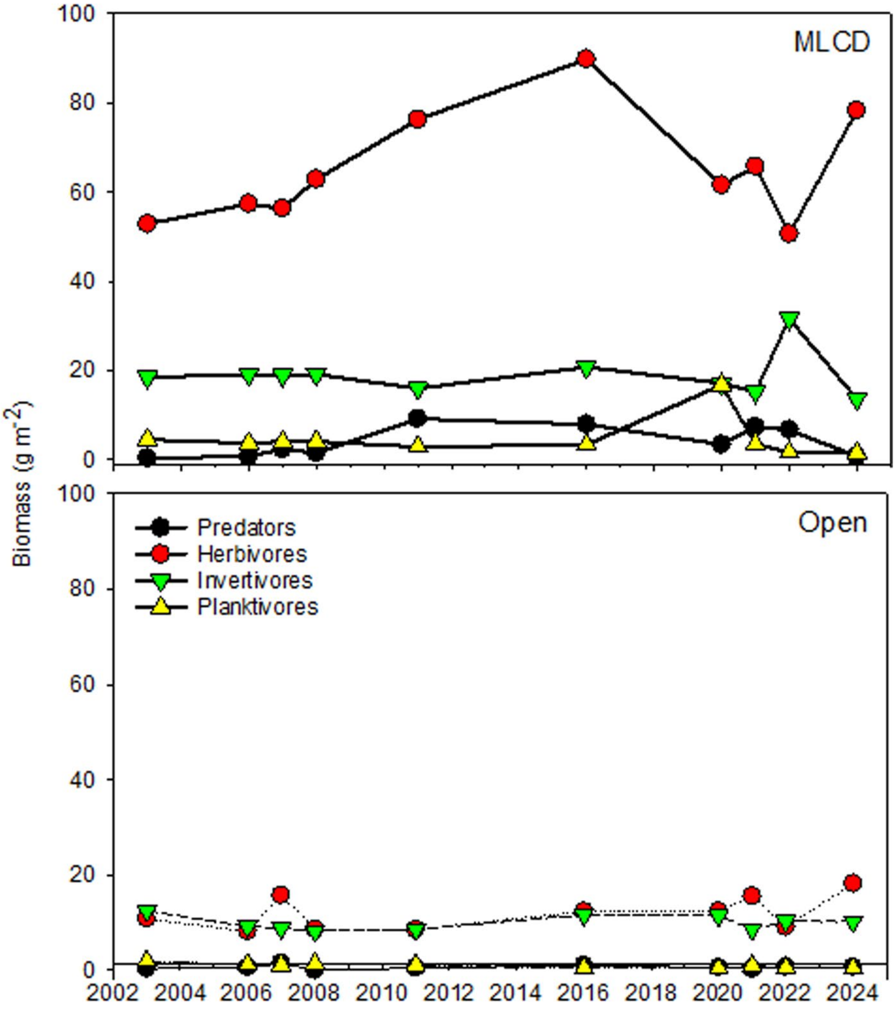

Fig. 5 Total fish biomass (g m^{-2}) by trophic group in the (A.) Pūpūkea MLCD and (B.) adjacent areas open to fishing

(*S. rubroviolaceus*). More recent years (2020–2024) were correlated with schooling surgeonfishes, including *A. leucopareius*, *A. olivaceus*, *A. nigrofuscus*, and *A. triostegus*.

Discussion

Concerns by the local community were the impetus for an adaptive management process that greatly expanded the size of, and increased restrictions within, the Pūpūkea MLCD. This process incorporated traditional ecological knowledge (TEK) and scientific advice to develop a strategy aligned with the unique environmental conditions, specific resources, and the cultural and historical context of the area.

The integration of ecological and cultural seascape analyses revealed the interdependence between ecological recovery and cultural reconnection. Many of the species identified as abundant in moʻolelo were also among those showing strong biomass increases within the MLCD. This convergence suggests that ecological restoration is simultaneously enabling the revival of culturally important species. Cultural seascape knowledge can therefore illuminate management priorities that are both ecologically functional and socially meaningful. By combining TEK with 2D and 3D seascape metrics derived from remote sensing and in situ data, the Pūpūkea case demonstrates that eco-cultural recovery can be tracked across both biophysical and cultural dimensions, providing a model for adaptive, community-driven management.

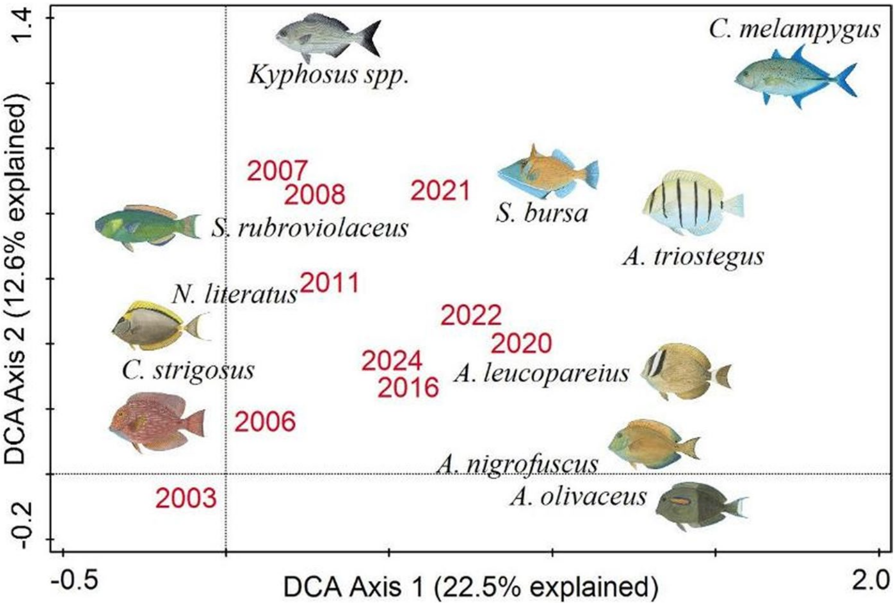

Fig. 6 Fish assemblage structure within the MLCD among years based on Detrended Correspondence Analysis. Taxa biomass (g m^{-2}) was log-transformed and rare species were downweighted. The top 10 species by response weight were plotted for visualization

Similar seascape-based assessments of MPAs have been applied in other parts of the world, such as Puerto Rico (Pittman et al. 2009), the Florida Keys (Bartholomew et al. 2008), and Tanzania (Berkström et al. 2013), where spatial configuration and habitat connectivity were linked to fish diversity and ecosystem recovery. However, these studies have tended to emphasize biophysical habitat structure and rarely incorporate the cultural and historical dimensions of human–marine systems. The present study extends this body of work by advancing a cultural seascape ecology framework that explicitly integrates TEK with spatial pattern metrics. This allows a more holistic understanding of how seascape structure influences both ecological processes and cultural reconnection, offering a transferable model for community-based marine management elsewhere. The Pūpūkea case further illustrates that ecological and cultural recovery within MPAs is closely linked to land-based management. Watershed activities influence nearshore water quality and benthic condition, emphasizing the need for integrated ridge-to-reef management that connects terrestrial stewardship with marine protection. Considering terrestrial pressures within seascape analyses strengthens the evaluation of MPA performance and enhances understanding of the full land–sea continuum.

Traditional ecological knowledge and cultural seascapes

The stories gathered through the cultural seascape ecology research illustrate the deep spiritual and social relationships tied to this place and the historical abundance of marine resources within the Pūpūkea MLCD. Sustaining these resources required diverse fishing techniques and management strategies, underscoring the area's long-standing role as a center of skilled subsistence fishing. Historical kapu (prohibitions) on species such as *Naso unicornis* (1857) and uhu (parrotfishes; 1850) exemplify a governance system in which resources from mauka to makai (mountain to sea) were carefully tended and regulated, paralleling principles of contemporary adaptive management. These same species, together with *Kuhlia* spp. and *Acanthurus triostegus* that remain important in the Kapoʻo tidepools (Shark's Cove) (Rosinski 2012), continue to be abundant today, reflecting continuity between traditional stewardship and ecological recovery.

Increasingly, contributions from local communities and holders of TEK are enriching our understanding of coupled social–ecological systems (Stori et al. 2019), providing holistic perspectives grounded in close relationships with the natural world (Colorado 1996). TEK—an evolving body of knowledge, beliefs, and practices transmitted through oral traditions and cultural rituals (Berkes et al. 2000) —should be integrated within seascape ecology to broaden perspectives and balance the historically Western emphasis in marine science (Wedding et al. 2025).

Overlooking the socio-cultural and qualitative dimensions of seascapes can hinder efforts to decolonize conservation and often lead to low compliance with management measures. In contrast, participatory processes that engage stakeholders throughout planning and implementation have been shown to increase the success of local management initiatives (Ban et al. 2009). Management frameworks built primarily on top-down enforcement should therefore be coupled with long-term, bottom-up approaches emphasizing local education and economic development to address the underlying causes of seascape degradation. Where the needs and knowledge of Indigenous communities are disregarded, MPAs frequently fail to achieve intended outcomes (Cinner et al. 2009). For example, a non-participatory national-park model in the Peixe Lagoon region of southern Brazil ignored Indigenous fishing practices and violated the rights of traditional fishers (Almudi and Kalikoski 2010). In contrast, conservation efforts such as those in this study demonstrate how the inclusion of Indigenous knowledge and cultural values can enhance both ecological effectiveness and social legitimacy.

Effective marine protection and restoration strategies depend on strong community engagement. At Pūpūkea, a community-based stewardship organization—Mālama Pūpūkea-Waimea (MPW)—was established in 2005 to sustain the area's natural and cultural resources through active stewardship, education, and partnerships. MPW's "makai watch" program supports compliance with MLCD regulations, assists enforcement officers, raises awareness, and conducts biological and human-use monitoring. Involving local stakeholders at every stage of protected-area governance has been shown to increase compliance and foster shared responsibility for marine resources (Ban et al. 2009).

Despite the proven benefits of MPAs, less than 1% of nearshore waters around the main Hawaiian Islands are fully protected (Friedlander et al. 2019), and the establishment of new MPAs continues to face social resistance (Pala 2007). Ancient Hawaiian systems of community-based management offer instructive precedents, and several communities are now adapting these practices for contemporary contexts (Friedlander et al. 2014; Winter et al. 2023). For instance, moon calendars refined over generations of Hawaiian fishers document spawning cycles and guide the timing of harvests (Poepoe et al. 2007). Applying traditional closures (kapu) during peak spawning periods reflects a time-tested strategy to align human activity with the natural rhythms of reef species.

Because knowledge about the complexities and processes of ecosystems is always incomplete and coupled human-natural systems change over time, management needs to adapt to these uncertainties (Holling 1978). MPAs are considered one of the best hedges against uncertainty in marine ecosystems because they protect biodiversity and ecosystem services in the face of a changing climate, and complement conventional fisheries management activities (Sala et al. 2021; Grorud-Colvert et al. 2021). The complexities of coral reef ecosystems require a new precautionary approach to management that incorporates TEK with spatial management in the form of MPAs to prevent further declines in these ecosystems (Johannes 1978; Aswani et al. 2007).

The rezoning of the Pūpūkea MLCD not only improved ecological conditions but also reestablished protection for places and species of deep cultural significance. The inclusion of Waimea Bay and the surrounding wahi pana within the expanded boundaries corresponds with traditional resource zones historically governed by kapu and konohiki systems. Thus, rezoning effectively restores aspects of traditional governance by safeguarding both ecological integrity and cultural heritage. This eco-cultural alignment represents a tangible outcome of community-led adaptive management and supports the persistence of biocultural resilience. In 2024, DAR staff in collaboration with Mālama Pūpūkea Waimea developed a management framework for the Pūpūkea MLCD with a strong integration of culture and management in a coordinated effort to adaptively manage the MLCD for present and future generations (Hawaiʻi Division of Aquatic Resources 2024).

Seascape ecology and conservation planning

Building on these eco-cultural outcomes, a seascape ecology framework provides an effective means of evaluating how spatial patterns within the marine environment influence both ecological and cultural processes (Wedding et al. 2025). To design MPAs more effectively, seascape ecology offers tools to characterize ecosystem patterns and processes at scales commensurate with the distribution and movement of resources and their users (Carr et al. 2017). The seascape perspective also positions MPAs within the broader landscape, recognizing that ecological and social processes extend beyond protected boundaries (Wiens 2009). The landscape pattern analyses applied in this study demonstrate how such metrics can inform MPA design and evaluation, both within reserves and across adjacent seascapes (Hogg et al. 2018).The perimeter-to-area ratio of the Pūpūkea MLCD decreased nearly fourfold following expansion, an important improvement because fishes with small home ranges are less likely to move outside protected boundaries where they are vulnerable to fishing (Bartholomew et al. 2008). This reduced ratio also increases the effective core area of protection, minimizing edge effects and enhancing the likelihood of ecological spillover into surrounding fisheries. Expansion of the MLCD incorporated a broader diversity of habitats, including the addition of sand areas absent from the original boundary. These habitats function as corridors among hard-bottom environments and serve as important feeding areas for many reef species (Friedlander et al. 2007a). Inclusion of a greater range of depth and habitat types increased both species richness and biomass, particularly of culturally important herbivores. Following expansion, the MLCD protected approximately 0.08 km^2 of coral habitat (10–50% cover), encompassing deeper reef zones less affected by winter swell events that strongly shape reef structure in Hawai‘i (Grigg 1983). Structural complexity derived from high-resolution bathymetry was strongly correlated with fish assemblage metrics. Variables such as slope, aspect, and variance in depth explained much of the variation in fish abundance and richness within the MLCD. Similar relationships between topographic complexity and faunal diversity have been documented elsewhere (Wedding and Friedlander 2008; Pittman et al. 2009), underscoring the utility of seascape metrics in predicting biological patterns across coral reef systems.

Changes in benthic composition following MLCD expansion

The North Shore of O‘ahu experiences exceptionally large winter surf, which strongly influences benthic community structure (Grigg 1983). Over the study period, benthic functional group composition remained relatively stable except for a ~ 12% decline in scleractinian coral cover (2007–2024) and an increase in crustose coralline algae from 10.0% to 17.3%. The long interval between sampling years makes it difficult to attribute these shifts to specific events although climate change is certainly having an effect on marine ecosystems throughout Hawai‘i (Winston et al. 2022) and the world (Hoegh-Guldberg et al. 2017). Coral cover overall was relatively low, consistent with other wave-exposed north shore reefs (Jokiel et al. 2004). Robust species such as *Pocillopora meandrina* and *Porites lobata* dominated, displaying branching and encrusting morphologies that confer resistance to physical disturbance. Large-scale structural complexity provided by boulders, ledges, and other geomorphic features exerted a stronger influence on associated fish assemblages than coral cover itself, reflecting the reduced topographic complexity of coral morphologies in high-energy environments (Friedlander et al. 2003).

Enhanced fish population dynamics following MLCD expansion

Increases in fish biomass within the MLCD since expansion have been driven largely by resource species such as schools of surgeonfishes (e.g., *Acanthurus. leucopareius*, *A. olivaceus*) and large parrotfishes (e.g., *Scarus rubroviolaceus*). Earlier regulations established in 1983 permitted several extractive activities, limiting the effectiveness of protection. The 2003 rezoning expanded the area and introduced stricter regulations, resulting in greater biomass, species richness, and overall ecosystem health.

Despite these gains, the MLCD faces persistent pressures from recreational overuse, including high visitation, harassment of marine life, trampling of reef habitats, and pollution from adjacent land development. Although commercial activities such as guided snorkel and dive tours were banned from Pūpūkea and Waimea Beach Parks in 2021, the absence of regulations for non-commercial recreational use continues to pose challenges. Strengthening stewardship, monitoring, and education programs led by community groups such as Mālama Pūpūkea-Waimea remains essential for sustaining ecological and cultural benefits.

Conclusions

Integrating cultural and ecological seascape ecology provides a practical framework for assessing the eco-cultural outcomes of MPA design and rezoning, demonstrating that adaptive management rooted in local knowledge can achieve both ecological and cultural restoration. However, for political, ethical, and historical reasons, direct implementation of traditional practices in contemporary contexts remains constrained without concurrent changes in governance, policy, and legal frameworks (Shackeroff and Cambell 2007). The adaptive, community-driven approach taken at Pūpūkea offers a viable model for balancing these realities—effectively managing human use while improving ecosystem health.

This study integrates seascape ecology theory and techniques with in situ and remotely sensed data to quantify spatial patterns and ecological responses at management-relevant scales, offering an approach broadly applicable across marine systems. Strengthening the links between ecological metrics and cultural priorities can guide the development of Indigenous- and community-led MPAs that align conservation goals with local values (Tran et al. 2020). The Pūpūkea experience demonstrates that participatory rezoning, grounded in both scientific and traditional knowledge, can produce improved and resilient, ecosystem-based management outcomes that foster reconnection between communities and the seascapes that sustain them.

Acknowledgements We would like to extend our deepest appreciation to the local community who spearheaded the efforts to improve the health of the ocean on the north shore of O‘ahu. The use of trade names or products does not constitute endorsement by the U.S. Government. This project was funded by NOAA's Coral Reef Conservation Program and National Centers for Coastal Ocean Science-Center for Coastal Monitoring and Assessment. Numerous people participated in the collection of field data including Kosta Stamoulis, Mark E. Monaco, Allan Ligon, Will Smith, Kim Peyton, Greta Aeby, Maile Coberly, Ellie Jones, and Whitney Goodell.

Author contributions A.M.F. and L.M.W. conceived and designed the study. A.M.F, L.M.W, E.K.B, and C.S. collected the data. A.M.F, L.M.W, C.S., and C.E.S. analyzed the data. A.M.F, L.M.W, and C.E.S. prepared the figures. A.M.F. and L.M.W. wrote the first draft of the manuscript, and all authors contributed to the final version of the manuscript.

Funding This work was originally supported by a grant from NOAA/NOS/NCCOS/CCMA, Biogeography Branch.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

References

Almudi T, Kalikoski DC (2010) Traditional fisherfolk and no-take protected areas: The Peixe Lagoon National Park dilemma. Ocean Coast Manage 53:225–233

Anthony KRN, Helmstedt KJ, Bay LK et al (2020) Interventions to help coral reefs under global change—a complex decision challenge. PLoS ONE 15:e0236399

Aswani S, Ruddle K (2013) Design of realistic hybrid marine resource management programs in Oceania. Pac Sci 67:461–476

Aswani S, Albert S, Sabetian A, Furusawa T (2007) Customary management as precautionary and adaptive principles for protecting coral reefs in Oceania. Coral Reefs 26:1009–1021

Ban NC, Picard CR, Vincent ACJ (2009) Comparing and integrating community-based and science-based approaches to prioritizing marine areas for protection. Conserv Biol 23:899–910

Bartholomew A, Bohnsack JA, Smith SG et al (2008) Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. Landscape Ecol 23:55–65

Battista TA, Costa BM, Anderson SM (2007) Shallow-water benthic habitats of the main eight Hawaiian Islands. NOAA/NOS/NCCOS/Biogeography Branch, Silver Spring, MD

Beijbom O, Edmunds PJ, Roelfsema C et al (2015) Towards automated annotation of benthic survey images:

variability of human experts and operational modes of automation. PLoS ONE 10:e0130312

Berkes F, Colding J, Folke C (2000) Rediscovery of traditional ecological knowledge as adaptive management. Ecol Appl 10:1251–1262

Berkes F, Colding J, Folke C (2004) Navigating social-ecological systems: Building resilience for complexity and change. Cambridge University Press, Cambridge

Berkström C, Lindborg R, Thyresson M, Gullström M (2013) Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. Biol Conserv 166:43–53

Berkström C, Eggertsen L, Goodell W et al (2020) Thresholds in seascape connectivity: the spatial arrangement of nursery habitats structure fish communities on nearby reefs. Ecography 43:882–896

Beyer HL (2004) Hawth's analysis tools for ArcGIS

Boström C, Pittman S, Simenstad C, Kneib R (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32:269–276

Carr MH, Robinson SP, Wahle C et al (2017) The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. Aquat Conserv 27:6–29

Christie P, Bennett NJ, Gray NJ et al (2017) Why people matter in ocean governance: incorporating human dimensions into large-scale marine protected areas. Mar Policy 84:273–284

Cinner JE, McClanahan TR, Daw TM et al (2009) Linking social and ecological systems to sustain coral reef fisheries. Curr Biol 19:206–212

Claudet J, García-Charton JA, Lenfant P (2011) Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area: species-habitat relations and MPAs. Conserv Biol 25:105–114

Colorado P (1996) Indigenous science. ReVision 18:6–10

Delevaux JMS, Whittier R, Stamoulis KA et al (2018) A linked land-sea modeling framework to inform ridge-to-reef management in high oceanic islands. PLoS ONE 13:e0193230

DeMartini EE, Friedlander AM, Holzwarth SR (2005) Size at sex change in protogynous labroids, prey body size distributions, and apex predator densities at NW Hawaiian atolls. Mar Ecol Prog Ser 297:259–271

ESRI (2011) ArcGIS Desktop (Release 10)

Fletcher CH, Bochicchio C, Conger CL et al (2008) Geology of Hawaii Reefs. Coral Reefs of the USA. Springer, Netherlands, Dordrecht, pp 435–487

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–326

Friedlander AM, Parrish JD (1998) Temporal dynamics of fish communities on an exposed shoreline in Hawaii. Environ Biol Fish. https://doi.org/10.1023/A:1007497210998

Friedlander AM, Brown EK, Jokiel PL et al (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305

Friedlander AM, Brown E, Monaco ME (2007b) Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. Mar Ecol Prog Ser 351:221–233

Friedlander AM, Brown EK, Monaco ME (2007a) Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. Ecol Appl 17:715–730

Friedlander AM, Wedding LM, Caselle JE, Costa BM (2011) Integration of remote sensing and in situ ecology for the design and evaluation of marine protected areas: examples from tropical and temperate ecosystems. Remote Sensing of Protected Lands. CRC Press, pp 245–280

Friedlander AM, Stamoulis KA, Kittinger JN et al (2014) Understanding the scale of marine protection in Hawai'i. Advances in Marine Biology. Elsevier, pp 153–203

Friedlander AM, Donovan MK, Stamoulis KA et al (2018) Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. Aquat Conserv Mar Freshw Ecosyst 28:146–157

Friedlander AM, Donovan kM, Koike H et al (2019) Characteristics of effective marine protected areas in Hawai'i. Aquat Conserv Mar Freshw Ecosyst 29:103–117

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci U S A 107:18286–18293. https://doi.org/10.1073/pnas.0906473107

Gardner JPA, Lausche B, Pittman SJ, Metaxas A (2024) Marine connectivity conservation: guidance for MPA and MPA network design and management. Mar Policy 167:106250. https://doi.org/10.1016/j.marpol.2024.106250

Grigg RW (1983) Community structure, succession and development of coral reefs. Mar Ecol Prog Ser 11:1–14

Grigg RW (1998) Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. Coral Reefs 17:263–272. https://doi.org/10.1007/s003380050127

Grorud-Colvert K, Sullivan-Stack J, Roberts C et al (2021) The MPA guide: a framework to achieve global goals for the ocean. Science 373:eabf0861. https://doi.org/10.1126/science.abf0861

Harvey BJ, Nash KL, Blanchard JL, Edwards DP (2018) Ecosystem-based management of coral reefs under climate change. Ecol Evol 8:6354–6368. https://doi.org/10.1002/ece3.4146

Hawai'i Division of Aquatic Resources (1992) Marine life conservation district plan. Hawai'i Department of Land and Natural Resources, Honolulu, Hawaii

Hawai'i Division of Aquatic Resources (2024) Pūpūkea marine life management district management plan. Honolulu, Hawaii

Hoctor TS, Carr MH, Zwick PD (2000) Identifying a linked reserve system using a regional landscape approach: the Florida Ecological Network. Conserv Biol 14:984–1000

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci 4:158

Hogg OT, Huvenne VAI, Griffiths HJ, Linse K (2018) On the ecological relevance of landscape mapping and its application in the spatial planning of very large marine protected areas. Sci Total Environ 626:384–398

Holling CS (ed) (1978) Adaptive environmental assessment and management. International Institute for Applied Systems Analysis; Wiley, [Laxenburg, Austria] : Chichester ; New York

Hughes TP, Barnes ML, Bellwood DR et al (2017) Coral reefs in the Anthropocene. Nature 546:82–90

Irish JL, Lillycrop WJ (1999) Scanning laser mapping of the coastal zone: the SHOALS system. ISPRS J Photogramm Remote Sens 54:123–129

Johannes RE (1978) Traditional marine : conservation methods in oceania and their demise. Annu Rev Ecol Syst 953:349–36417

Johannes RE (2002) The renaissance of community-based marine resource management in Oceania. Annu Rev Ecol Syst 33:317–340

Jokiel PL, Rodgers KS, Brown EK et al (2015) Comparison of methods used to estimate coral cover in the Hawaiian Islands. PeerJ 3:e954

Kamakau SM (1961) Ruling chiefs of Hawaii. Kamehameha Schools Press

Kendall MS, Miller T (2008) The influence of thematic and spatial resolution on maps of a coral reef ecosystem. Mar Geod 31:75–102

Kimmerer WJ, Durbin WW (1975) The potential for additional marine conservation districts on Oahu and Hawaii. NOAA Office of Sea Grant, Honolulu, Hawaii

Lepczyk CA, Wedding LM, Asner GP et al (2021) Advancing landscape and seascape ecology from a 2D to a 3D science. Bioscience 71:596–608

Lubchenco J, Grorud-Colvert K (2015) Making waves: the science and politics of ocean protection. Science 350:382–383

Ludwig JA, Reynolds JF (1988) Statistical ecology: a primer on methods and computing. Wiley, New York

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

The MathWorks, Inc. (2011) MATLAB (Version R2011b)

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR

McLeod K, Leslie H (eds) (2009) Ecosystem-based management for the oceans. Island Press, Washington

Moilanen A, Wilson KA, Possingham HP (eds) (2009) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press, Oxford

Mulrennan M, Scott C (2000) *Mare nullius*: indigenous rights in saltwater environments. Dev Change 31:681–708

Nadon MO (2017) Stock assessment of the coral reef fishes of Hawaii, 2016. https://doi.org/10.7289/V5/TM-PIFSC-60

Noormets R, Felton EA, Crook KAW (2002) Sedimentology of rocky shorelines: 2. Sediment Geol 150:31–45

Obura DO, Aeby G, Amornthammarong N et al (2019) Coral reef monitoring, reef assessment technologies, and ecosystem-based management. Front Mar Sci 6:580

Olds AD, Connolly RM, Pitt KA et al (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. Glob Ecol Biogeogr 25:3–15

Opdam P (2020) Implementing human health as a landscape service in collaborative landscape approaches. Landsc Urban Plann 199:103819

Pala C (2007) Conservationists and fishers face off over Hawaii’s marine riches. Science 317:306–307

Pielou EC (1977) Mathematical ecology, 2nd edn. Wiley, New York

Pittman S (ed) (2018) Seascape ecology. Wiley, Hoboken

Pittman SJ, Caldow C, Hile SD, Monaco ME (2007) Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. Mar Ecol Prog Ser 348:273–284

Pittman SJ, Costa BM, Battista TA (2009) Using Lidar bathymetry and boosted regression trees to predict the dversity and abundance of fish and corals. J Coast Res 10053:27–38

Poepoe K, Bartram P, Friedlander A (2007) The use of traditional Hawaiian knowledge in the contemporary management of marine resources. In: Haggan N, Neis B, Baird I (eds) Fishers’ knowledge in fisheries science and management. United Nations Educational, Scientific and Cultural Organization, pp 119–143

Pungetti G (2012) Islands, culture, landscape and seascape. J Mar Isl Cult 1:51–54

Puniwai N (2020) Pua ka wiliwili, nanahu ka manō: Understanding sharks in Hawaiian culture. Hum Biol 92:11

Randall JE (2007) Reef and shore fishes of the Hawaiian Islands. Sea Grant College Program, University of Hawai‘i, Honolulu

Rosinski A (2012) Creating comprehensive protected arteas: The ecology of the Pūpūkea tide pools and their value to the Pūpūkea Marine Life Conservation District. Master of Professional Science, University of Miami

Sala E, Mayorga J, Bradley D et al (2021) Protecting the global ocean for biodiversity, food and climate. Nature 592:397–402

Shackeroff JM, Cambell LM (2007) Traditional ecological knowledge in conservation research: problems and prospects for their constructive engagement. Conserv Soc 5:343–360

Stori FT, Peres CM, Turra A, Pressey RL (2019) Traditional ecological knowledge supports ecosystem-based management in disturbed coastal marine social-ecological systems. Front Mar Sci 6:571

Tran TC, Ban NC, Bhattacharyya J (2020) A review of successes, challenges, and lessons from Indigenous protected and conserved areas. Biol Conserv 241:108271

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Turner MG, Gardner RH, O’Neill RV (2001) Landscape ecology in theory and practice: Pattern and process. Springer, New York

Wedding LM (2025) Five ways seascape ecology can help to achieve marine restoration goals. Landsc Ecol. https://doi.org/10.1007/s10980-025-02099-9

Wedding LM, Friedlander AM (2008) Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. Mar Geod 31:246–266

Wedding LM, Friedlander AM, McGranaghan M et al (2008) Using bathymetric lidar to define nearshore benthic habitat complexity: implications for management of reef fish assemblages in Hawaii. Remote Sens Environ 112:4159–4165

Wedding L, Lepczyk C, Pittman S et al (2011a) Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. Mar Ecol Prog Ser 427:219–232

Wedding LM, Gibson BA, Walsh WJ, Battista TA (2011b) Integrating remote sensing products and GIS tools to support marine spatial management in West Hawaii. J Conserv Plan 7:60–73

Wedding LM, Pittman SJ, Lepczyk CA et al (2024) Integrating the multiple perspectives of people and nature in place-based marine spatial planning. NPJ Ocean Sustain 3:43

Wedding LM, Stuart CE, Govers LL et al (2025) Five ways seascape ecology can help to achieve marine restoration goals. Landsc Ecol 40:115

Wiens JA (2009) Landscape ecology as a foundation for sustainable conservation. Landsc Ecol 24:1053–1065

Williams ID, Walsh WJ, Schroeder RE et al (2008) Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. Environ Conserv 35:261–272

Winston M, Oliver T, Couch C et al (2022) Coral taxonomy and local stressors drive bleaching prevalence across the Hawaiian Archipelago in 2019. PLoS ONE 17:e0269068

Winter KB, Beamer K, Vaughan MB et al (2018) The Moku system: managing biocultural resources for abundance within social-ecological regions in Hawaiʻi. Sustainability 10:3554

Winter K, Vaughan M, Kurashima N, et al (2023) Indigenous stewardship through novel approaches to collaborative management in Hawaiʻi. E&S 28:art26. https://doi.org/10.5751/ES-13662-280126

Young MA, Wedding LM, Carr MH (2018) Applying landscape ecology for the design and evaluation of marine protected area networks. Seascape Ecology, 1st edn. Wiley, Hoboken, pp 429–462