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Habitat mapping of giant kelp (*Macrocystis pyrifera*) and devil weed (*Sargassum horneri*) off the coast of Santa Catalina Island, California

Abstract

Background: *Macrocystis pyrifera*, commonly known as giant kelp, is a fast-growing brown alga that typically inhabits temperate waters. In southern California, *M. pyrifera* provides many ecologically and economically significant ecosystem services. *Sargassum horneri*, a non-native brown macroalga commonly known as devil weed, often outcompetes *M. pyrifera* while providing fewer ecological or economical benefits. Examining potential areas of species overlap is key to understanding the invasion potential of *S. horneri* and essential to the implementation of removal efforts. This study aims to map the suitable habitat of *M. pyrifera* and invasive *S. horneri* in the coastal waters of Santa Catalina Island, California, and to quantify any overlapping habitat between the two macroalgae.

Methods: Broadly defined potential habitats were characterized around Santa Catalina Island using an unsupervised approach to habitat mapping based on a series of abiotic surrogates mapped at a 2 m spatial resolution. *In situ* substrate data were then overlaid onto the unsupervised classification to identify spatial associations between substrate type and potential habitats, and to interpret the classes. To predict the distribution of *M. pyrifera* and *S. horneri* around Santa Catalina Island based on their respective association with the environment, maximum entropy (MaxEnt) was used to produce species distribution models. The resulting models for *M. pyrifera* and *S. horneri* were overlaid to identify potential areas of conflict based on suitable habitat overlap.

Results: The unsupervised approach to habitat mapping resulted in a map of four potential habitats around Santa Catalina Island based on substrate cover. Sand was the most dominant type of substrate. The supervised approach using MaxEnt identified 10.27% of the study area as suitable habitat for *M. pyrifera* and 7.37% as suitable habitat for *S. horneri*. A total of 33.56% of the suitable habitat for *M. pyrifera* was found to also be suitable for *S. horneri*.

Limitations: The characterization of habitats and the species distribution modeling were limited to the study of benthic terrain characteristics due to the unavailability of other high-resolution environmental data (*e.g.*, hydrodynamics and chemical data) around Santa Catalina Island. In addition, data were not available for the very shallow waters near the coast, where giant kelp is often found. Given the complexity of this ecosystem, the addition of other variables and data coverage closer to the coast would potentially make the maps and models more representative of the actual distribution of *M. pyrifera* and *S. horneri* and provide a more complete understanding of their environmental preferences.

Conclusion: This study provides insight into the kelp forest ecosystems found in California's Channel Islands; it is a vital first step in order to understand the potential areas for invasion of *M. pyrifera* by *S. horneri*, thus supporting decision making and efforts to control *S. horneri* abundance.

Introduction

Macrocystis pyrifera, commonly known as giant kelp, is a fast-growing brown alga normally found in temperate, nutrient-rich waters off the west coast of the Americas and the southern coast of Australia. It is most well-known for its massive size and plant-like appearance. Giant kelp begins its growth cycle by anchoring itself to a suitable substrate with a root-like holdfast that does not absorb nutrients from the benthic environment (1). From there it grows towards the ocean surface, reaching anywhere from 14 to 40 m using gas-filled sacs – the pneumatocysts – along the stipe to remain upright in the water column (2). Blades sprouting from the pneumatocysts maximize the area available for photosynthesis. The combination of this complex structure and the rapid growth rate of *M. pyrifera* makes it a foundational species in its ecosystem. For instance, it provides a three-dimensional habitat for other species, and the high rate of photosynthesis that takes place along the thallus incorporates large amounts of inorganic carbon into the food-web (3). In southern California, *M. pyrifera* supports a complex food-web consisting of nearly 300 species, many of which are ecologically and economically significant (4). Some significant markets include the recreational rockfish, the kelp bass *Paralabrax clathratus*, and the

commercial lingcod fisheries (4).

Santa Catalina Island, which is located about 40 km from the Los Angeles shoreline in the Pacific Ocean (Fig.1), is one of California's most well-known rocky Channel Islands. Although some development has allowed Santa Catalina Island to capitalize on fisheries and tourism, a large majority of the island remains uninhabited, with a large population of its residents living within a small area. Santa Catalina Island possesses several unique ecosystems (*e.g.*, mountainous habitats, grasslands, oak woodlands), including a variety of coastal ecosystems such as sand dunes, beaches, and giant kelp forests. Many of the 900,000+ annual visitors to Santa Catalina Island – compared to the 4,000 residents of the island – come to dive, fish or take a boat tour in the kelp forests (5). These activities, which translate into $167 million in annual spending and over 1,200 jobs on the island (5), put disproportionate pressures on the kelp ecosystem and its species: in the waters surrounding Santa Catalina Island, more than 150 recorded fish species spend a portion of their life cycle in kelp forests using it either as a food source or habitat (4).

A suite of stressors, namely sea star wasting disease, warmer waters, and

rising sea urchin populations have recently threatened southern California's giant kelp population (6). Aerial surveys demonstrate that the combination of these factors has led to a decline in the distribution of *M. pyrifera*, leading to a loss of carbon fixation and suitable habitat for other species (7). On Santa Catalina Island, these stressors are exacerbated by the non-native *Sargassum horneri*, which often outcompetes *M. pyrifera*. Similar to *M. pyrifera*, *S. horneri* is a brown macroalga that establishes a
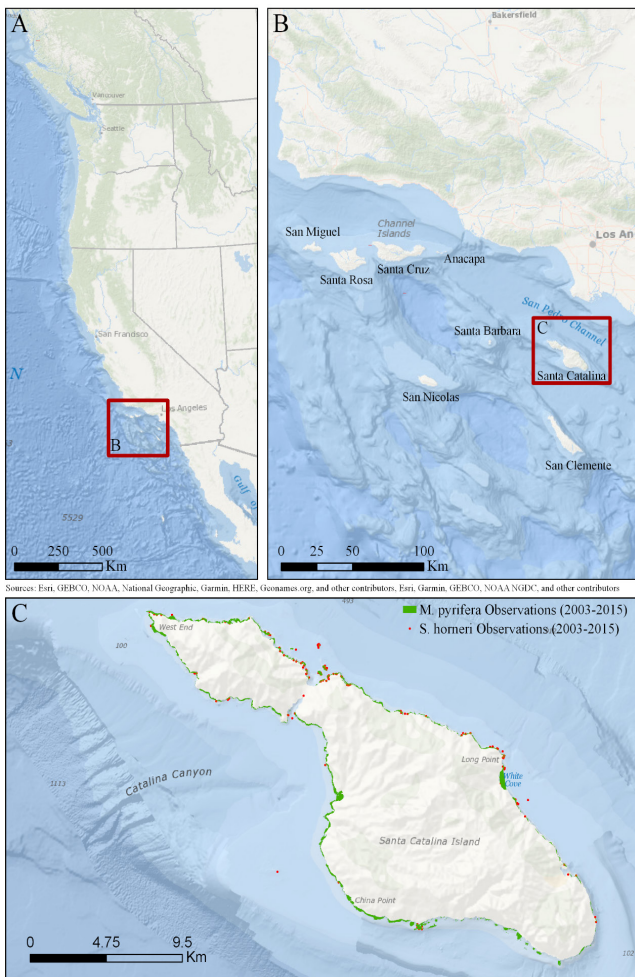

Figure 1. West Coast of the United States of America (A), with the location of the eight Channel Islands (B) and Santa Catalina Island with *M. pyrifera* and *S. horneri* observations from 2003 to 2015 (C)

holdfast on the ocean floor and uses pneumatocysts to remain upright in the water column. *Sargassum horneri* is native to temperate regions off of Korea and Japan. It was first discovered in the Baja region of California in 2003 and in waters surrounding Santa Catalina Island in 2006. A common hypothesis used to explain the macroalga's arrival is that it was transported by commercial vessels (*e.g.*, in ballast water) (8). Its rapid expansion from the South to the North is partly attributed to its prolific reproductive strategy; *S. horneri* generates and sheds hundreds of germinating embryos that can settle or survive the journey to neighboring ecosystems (8).

In an already stressful environment for *M. pyrifera*, the faster growth rate of *S. horneri* inhibits the recovery of *M. pyrifera* population to its historical abundance and distribution by outcompeting it for space and light (9). Within the first year of its discovery, *S. horneri* has spread along the leeward side of Santa Catalina Island before progressing to the windward side of the island in 2007, consistently forming dense groves of roughly 100 adult individuals and 1,000 immature individuals per square meter (8,10). *Sargassum horneri* cannot provide the same habitat as the tall, canopy-forming *M. pyrifera*, and thus the recruitment of fish species such as kelp bass is negatively impacted by the non-native *S. horneri* invasion (9). While current management of the marine habitats surrounding Santa

Catalina Island includes nine marine conservation areas (11), spatially-explicit approaches to *S. horneri* removal based on distribution and invasion patterns have not been included in management practices (12). The production of both giant kelp and devil weed habitat suitability maps are needed to identify specific areas to focus devil weed removal efforts or isolate and protect giant kelp. Spatial analysis of *M. pyrifera* and *S. horneri* can provide preliminary information on the likelihood of invasion in vulnerable areas by identifying overlap in suitable habitats for both species. The information gained about the habitat distribution of each species could be used to develop a comprehensive response effort. This study aims to map the suitable habitats of *M. pyrifera* and *S. horneri* in the coastal waters of Santa Catalina Island and to quantify overlapping suitable habitats in order to provide a decision-making tool to aid efforts and resource allocation in the control of *S. horneri* abundance.
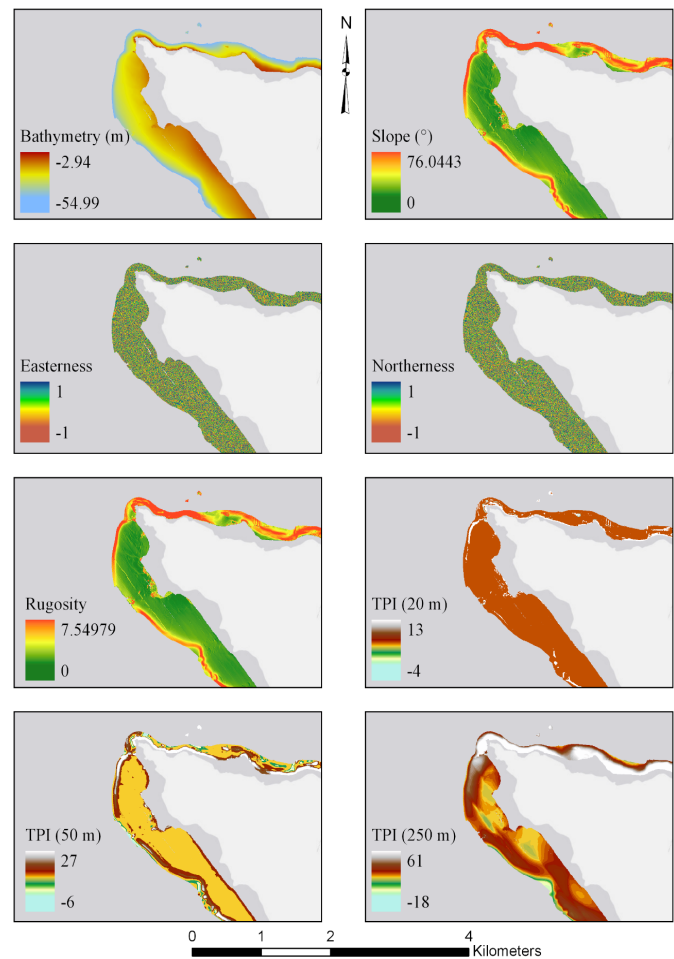
Methods

Figure 2. Example of each variable used in this study, from the northwestern tip of Santa Catalina Island. TPI stands for topographic position index.

Abiotic data of the seafloor were accessed through the Seafloor Mapping Lab at California State University Monterey Bay (13), and included bathymetry (*i.e.*, depth of the seafloor), which was collected in 2008 using acoustic remote sensing technologies. Bathymetry derivatives, namely slope, aspect, topographic position indices (TPI), and rugosity, were also provided by the Seafloor Mapping Lab at California State University Monterey Bay (13). Aspect, which represents the compass orientation of the slope and can be a proxy for hydrodynamics, was converted to northerness (cosine of aspect) and easterness (sine of aspect) to remove circularity in the data and make them statistically valid (14). TPIs, which indicate whether a given location is higher or lower than its immediate surroundings, was available at three different spatial scales, 20 m, 50 m, and 250 m, thus potentially capturing seafloor features at different scales and of

different sizes. Because the deepest occurrence of *M. pyrifera* was found at a depth of 55 m (15), we masked all the data corresponding to waters deeper than that threshold. We note, however, that most often, giant kelp is found in waters between 10 and 40 m, depending on water clarity and light penetration (15). The total area covered by the data was about 35.5 km². An example of each variable is shown in Fig. 2. Correlations between the data layers were quantified to inform data selection.

We used two different strategies for habitat mapping according to Brown *et al.* (16) to model suitable habitats for giant kelp and devil weed. First, to characterize broad potential habitats around Santa Catalina Island based on abiotic environmental characteristics, we used an unsupervised approach to habitat mapping (16). The selected data were inputted into a modified k-means classification tool in the Whitebox GAT v. 3.4.0 software (17). K-means is the most commonly used clustering algorithm that partitions datasets into meaningful classes (18). The maximum number of iterations and the cluster merger distance were set to 10, the pixel class change threshold was set to 10%, and the minimum allowable class size was set to 10 pixels. The cluster centers were initialized with maximum dispersion along the diagonal. The resulting unsupervised classification differentiates broad potential habitats based on abiotic surrogates. *In situ* data of substrate surrounding Santa Catalina Island provided by the National Oceanic and atmospheric Administration (NOAA) were then overlaid onto the unsupervised classification to identify spatial associations between substrate type and abiotic classes using the "multi-values to points" tool in ArcGIS Pro v. 2.3.0 (19). Those substrate data were collected in 1975 using grab samples, which were then classified based on material and grain size. To simplify the analysis, the thematic scale of those data was coarsened by regrouping similar classes together. For example, in NOAA's classification, sand classes were differentiated based on color. We grouped all sand colors into one class of sand for our analysis. These substrate data provided environmental context to the unsupervised classification. Classes were then compared with the occurrences of giant kelp and devil weed (see below).

The second approach to habitat mapping enables the prediction of the potential habitat distribution of *M. pyrifera* and *S. horneri* around Santa Catalina Island based on their respective association with the environment. *Sargassum horneri* occurrences were obtained from Marks *et al.* (2015) (8), who made their dataset available through a long-term repository (20). This dataset includes compiled records of *S. horneri* observations recorded during ecological surveys by trained observers, from 2003 to 2015. The dataset was filtered to keep only the occurrences surrounding Santa Catalina Island and to remove duplicate locations, resulting in 349 occurrences. However, due to the presence of a littoral gap in the abiotic data (see discussion), only 57 occurrences were overlapping the abiotic data. Giant kelp occurrences were provided by the California Department of Fish and Wildlife, which has performed aerial surveys most years since 2002. The main survey data are multispectral imagery (red, green, blue, near-infrared) at 0.3 m resolution and target both submerged and exposed kelp beds. Giant kelp coverage is extracted from the imagery and provided yearly as polygons representing the extent and distribution of kelp. In order to ensure comparability with *S. horneri* data, we compiled only the *M. pyrifera* coverage for the years 2003 to 2015. A set of random points was then created using ArcGIS Pro in order to maximize within-polygon coverage while keeping a minimum distance of 50 m between sample points to prevent autocorrelation. A total of 347 point samples were created as a result. Of those points, 38 overlapped the abiotic data. The point occurrence data of each species were then used in MaxEnt to produce two maximum entropy habitat distribution models – one for each species. Maximum entropy modeling is a machine learning method for species distribution modeling that is often used to model geographic distributions of suitable habitats from presence-only data (21). Models were cross-validated 30 times each with the final model representing the average of those 30 models. Jacknife measures of variable importance and response curves were also generated to identify which environmental variables drive the species distribution and contribute to the models. The area under the curve (AUC) of the receiver operating characteristic curve (ROC) was used as a performance measure for the MaxEnt models. The ROC illustrates the discrimination ability of a model by plotting the true positive rate against the false positive rate at various thresholds. The two habitat distribution models were overlaid to identify the areas corresponding to suitable habitat for both

species. The habitat suitabilities for each pixel of the resultant maps were multiplied by each other to develop a map indicating the probability of the species co-occurring at every pixel, on a scale from zero to one. Additionally, a binary dataset was developed for both species, classifying any pixel that had a suitability greater than 50% as highly suitable habitat, as commonly done in habitat suitability modeling (22). The two binary datasets were then added together in ArcGIS to quantify the area that corresponded with an overlap of suitable habitat.

Results

The analysis of correlation among variables identified two pairs of covarying variables: slope and rugosity, and TPI (20 m) and TPI (50 m) (Table 1). Thus, the selection of variables for the remaining analyses was bathymetry, easterness, northerness, slope, TPI (20 m), and TPI (250 m).

	Bathymetry	Easterness	Northerness	Rugosity	Slope	TPI20	TPI50
Easterness	-0.002						
Northerness	0.000	0.001					
Rugosity	-0.100	0.003	0.002				
Slope	-0.110	0.003	0.003	0.984			
TPI20	0.123	0.001	0.001	0.329	0.299		
TPI50	0.238	0.002	0.002	0.444	0.429	0.712	
TPI250	0.395	0.003	0.002	0.541	0.556	0.358	0.628

Table 1. Correlation matrix between the different variables available for the analysis. Slope and rugosity, and TPI20 and TPI50, were highly correlated (r ≥ 0.700). Rugosity and TPI50 were thus not used in the analyses.
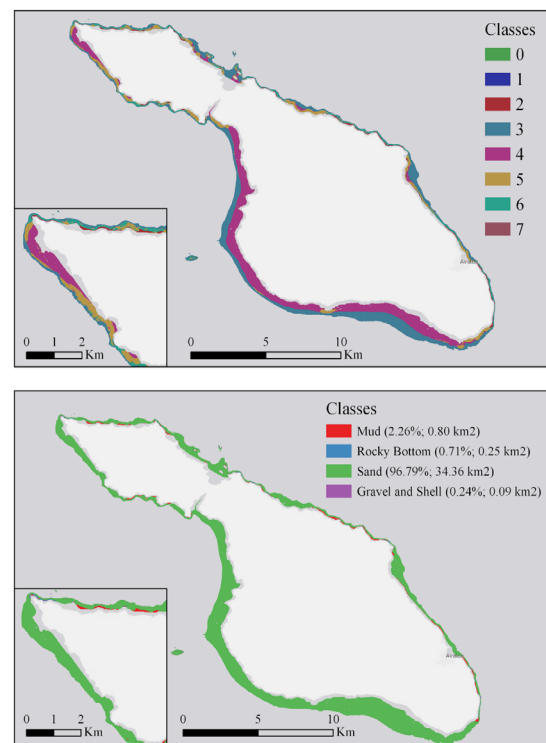

Figure 3. Results of the unsupervised classification, which defined eight potential habitat classes. Those classes were spatially compared to ground-truth data to interpret them as four substrate classes. The insets show the northernmost part of the island.

Using a k-means classification, we created a map of undefined potential habitat classes that are statistically distinct. Eight distinct classes were determined for the benthic area surrounding Santa Catalina Island (Fig. 3). This habitat map based on abiotic surrogates was then validated with *in*

situ substrate data from NOAA to be regrouped into classes representing the actual habitats. This resulted in the eight undefined but distinct classes being regrouped into four defined classes with unique substrate types: sand, mud, rocky bottom, and gravel and shells (Fig. 3). The overall accuracy of this map was relatively low yet acceptable at 58%. Most of the area was identified as being sand (96.79%), although the shallowest areas along the coastline were often predicted to be either mud (2.26% of the surveyed area), rocky bottom (0.71% of the area) or gravel and shells (0.24%), potentially providing insights into the benthic composition in the littoral gap (see discussion). Most of the *M. pyrifera* (78.9%) and *S. horneri* (52.6%) samples were found in sandy areas. The remaining giant kelp samples were found on mud and rocky bottom (10.5% each). The remaining devil weed samples were found on mud (26.3%), rocky bottom (15.8%), and gravel and shells (5.3%).

For the application of the supervised approach to habitat mapping to produce habitat suitability maps of giant kelp and devil weed, both models performed well: the mean AUC (of the 30 models used for cross-validation) for the giant kelp model was 0.89 and the mean AUC for the devil weed model was 0.90, which are considered excellent (models with an AUC greater than 0.50 are better than random and those with AUC greater than 0.75 are considered to provide a useful amount of discrimination; see 23).

	Percent Contribution		Environmental Preference	
	M. pyrifera	*S. horneri*	*M. pyrifera*	*S. horneri*
Bathymetry	78.2%	2.6%	Shallower waters	Shallower waters
Easterness	1.8%	2.5%	No discernable pattern	No discernable pattern
Northerness	4.3%	1.5%	No discernable pattern	No discernable pattern
Slope	6.6%	4.3%	Higher slopes	Higher slopes
TPI20	0.0%	0.0%	Elevated seafloor features	No discernable pattern
TPI250	9.1%	88.9%	Elevated seafloor features	Elevated seafloor features

Table 2. Results from the MaxEnt models, including the average percent contribution of each variable to the 30 models (*i.e.*, cross-validation) for both species, and the environmental characteristics more suitable for each species' settlement.

In terms of variable importance, which corresponds to the percentage contribution of each variable to the models (and thus in explaining species distribution), giant kelp was largely driven by depth, a likely proxy of light availability, and to a lesser extent slope (Table 2). Devil weed habitats were largely driven by broad-scale topographic features (*i.e.*, TPI-250 m) and slope (Table 2). The analysis of species-environment relationships highlights many similarities between *S. horneri* and *M. pyrifera*: both species were more readily found in shallow waters, on higher slopes, and in elevated areas of higher TPI values.

Fig. 4 shows the habitat suitability maps that were produced with MaxEnt for giant kelp and Fig. 5 shows the habitat suitability models for devil weed. Those maps show that 10.27% (about 3.65 km²) of the sampled area surrounding Santa Catalina Island (in waters shallower than 55 m) is suitable habitat for *M. pyrifera* and 7.37% (about 2.62 km²) is suitable habitat for *S. horneri*. Of the area suitable for giant kelp, 33.56% was also suitable for devil weed (Fig. 6). Most of the area of high probability of overlap was located in the northern section of the island and the northeastern side (Fig. 6). The southwestern side of the island was suitable for giant kelp but not for devil weed (Fig. 4 to 6).

Discussion

Both types of habitat maps produced in our study show that the two species of macroalgae seem to thrive in similar environmental conditions. Our map of potential habitats (Fig. 3) suggest that they mainly settle in sandy environments and that *S. horneri* might be more of a habitat generalist than *M. pyrifera* by inhabiting other types of benthic environment like mud and rocky bottoms. Those results are to be interpreted with care as the overall accuracy of this map was not very high, and the area covered by the abiotic data may not be fully representative of
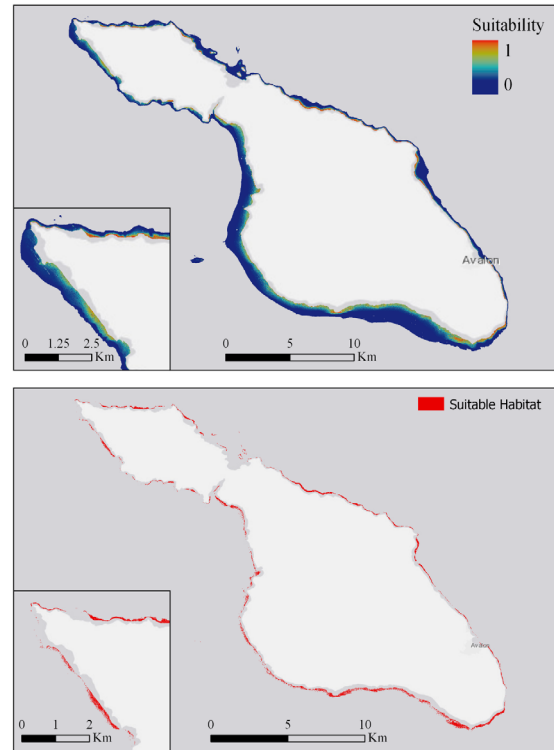
Figure 4. Maximum entropy model for *M. pyrifera* identifying the suitable habitat for this species. The bottom panel represents the areas with a suitability higher than 0.50 (considered highly suitable (22)). The insets show the northernmost part of the island.
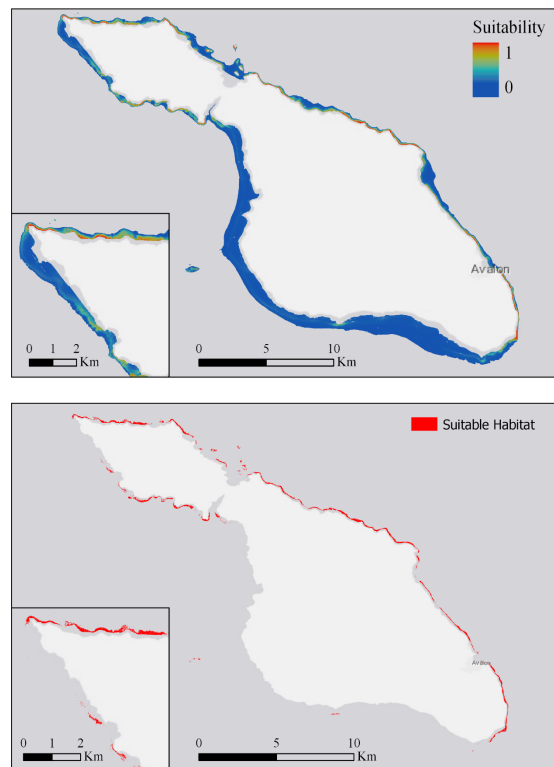

Figure 5. Maximum entropy model for *S. horneri* identifying the suitable habitat for this species. The bottom panel represents the areas with a suitability higher than 0.50 (considered highly suitable (22)). The insets show the northernmost part of the island.
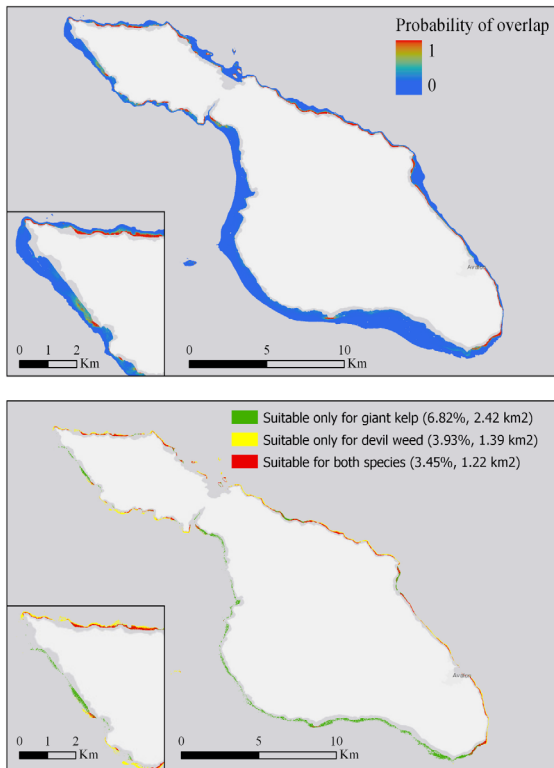
Figure 6. Probability that both species overlap, based on the multiplication of their habitat suitability. The insets show the northernmost part of the island.

S. horneri's association with more positive topographical features (*i.e.*, positive TPI) might be a mechanism that allows it to move higher in the water column to absorb more light. *Macrocystis pyrifera*'s size does not require such elevated features since its growth into the water column places it in a more optimal position for photosynthesis. In addition, giant kelp is more capable of succeeding with low light situations (26). The alga is largely self-shading, with its leaves reducing the light available for photosynthesis at 1 m depth (26). The sub-canopy of the plant can thrive from high-intensity sunflecks that occur when wave-action shifts the plant in the water column. Thus, shading could potentially be used as a more cost-effective, but still targeted, approach to *S. horneri* removal.

The results of this study provide insight into the interactions between kelp forest ecosystems and devil weed in the waters surrounding California's other Channel Islands. The relationships that were established between benthic terrain and the distribution of both species may be used to predict suitable habitats for *S. horneri* and their overlap with suitable habitats for *M. pyrifera* around other Channel Islands and in coastal waters. Such habitat suitability maps could inform monitoring on other islands and enable the eradication of devil weed as soon as it appears in other locations. Our study demonstrated the potential for habitat mapping and species distribution modeling to be used as spatial decision-support tools for Santa Catalina Island and in other areas that require similar map products. However, we note that the extent of our study area was limited by the presence of a littoral gap in the dataset used to produce the maps and models. An example of that littoral gap can be seen in Fig. 2, where data coverage does not reach the coastline – land is represented in white in the figure. In remote sensing, a littoral gap, or white ribbon, refers to the shallow areas where it is difficult to collect data (26): data collected from acoustic remote sensing cannot be collected due to the inability of the surveying vessels to navigate in shallow waters, and terrestrial remote sensing techniques are often not adequate to study the seafloor (27). In our study area, the littoral gap was varying from 35 to 700 m from the coast. The latter measurement reflects Isthmus Cove, a wide and shallow bay on the northeast side of the island. Given how close to shore giant kelp populations are commonly found (Fig. 1C), this littoral gap prevented our models from capturing the entire suitable habitat for giant kelp. A more comprehensive coverage of kelp habitat would improve the accuracy of the predicted distributions around Santa Catalina Island and elsewhere. Future studies could look into using bathymetric LiDAR, or laser altimetry, to fill the littoral gap and collect seafloor data close to shore (28), thus covering the entire range of kelp habitats. The temporal gap between the substrate data collected in 1975, the abiotic data collected in 2008, and the biotic data compiled from 2003 to 2015 is another limitation to consider, as habitat and environmental conditions might have changed to some extent over this timeframe. While remote sensing techniques can fill the littoral gap, *in situ* data collected by grab samples or visual observation by divers or towed video data would also result in more informed maps. Given Santa Catalina Island's active diving community, it would be feasible to employ citizen science as a method to obtain more robust validation data, for instance to collect different types of seafloor data and capture images to document and later interpret benthic composition.

Conclusion

Non-native algae such as *S. horneri* must compete with native algae species for space, understory, and resources such as light (11). Studies have shown reduced recruitment and survivorship of non-native sargassum species in communities containing native algae that cover ground space such as turfing algae and tall canopy-forming kelp (29). Thus, if removal efforts were targeted toward areas where *M. pyrifera* is still prevalent, the native algae species could re-exert biotic control on the ecosystem and reduce the threat of *S. horneri* re-establishment (12). This study identified areas of suitable habitat for giant kelp that are also likely to eventually be invaded by devil weed and is a vital first step to identifying areas that would be most effective for removal.

Acknowledgements

the range of environmental characteristics preferred by the two species (see discussion on littoral gap below). Our species distribution models show that about a third of the suitable habitat for native giant kelp off the coast of Santa Catalina Island is also suitable for non-native devil weed, thus highlighting a high potential of invasion. Based on the generated map, giant kelp seemed to thrive in northward and southward facing areas, which is consistent with seasonal current patterns in the area (24). By positioning itself on a slope parallel with the currents, *M. pyrifera* places itself in the optimal position for gathering upwelling nutrients as the seafloor grows shallower. However, we note that El Niño events shift patterns of upwelling and introduce warmer waters into the ecosystem (25). This, in turn, can reduce native kelp growth and allow *S. horneri* to thrive, and highlights the need for adaptive management techniques (12, 26). More research is needed to understand the more consistent distribution across slopes for *S. horneri*.

Our maps can be paired with current research that examines strategies for patterns of *S. horneri* removal as it can provide additional knowledge about its invasive capabilities. There has been little work done on identifying the ecological variables that allow *S. horneri* to invade kelp forests. Consequently, management practices currently rely on managing giant kelp populations and targeted removal of devil weed. Understanding the spatial dynamics of *S. horneri* and *M. pyrifera* habitat is a necessary first step to identifying these features and provides decision-makers with the necessary tools to reduce further loss of kelp forests via *S. horneri* occupation. The efficiency of *S. horneri* removal is based on several factors, including time of year and methods (12). Understanding the temporal dynamics of these species and producing temporally-explicit species distribution models might offer new insights on management and removal approaches. Removal of new generations is more effective in autumn when *S. horneri* are juveniles and intra-specific competition is at its highest than in winter when they have matured to adulthood (12). The most appropriate technique for removal of the non-native species is dependent upon the budget and staff available. Focusing on areas with a lower chance of *S. horneri* re-establishing and selecting efficient time periods and methods of removal (*e.g.*, suction) will maximize results. Marks *et al.* (2017) demonstrated that light availability is a contributing factor to *S. horneri*'s invasion fitness (12). It is therefore possible that

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