MONITORING THE PERSISTENCE OF GIANT KELP AROUND SANTA CATALINA ISLAND USING A GEOGRAPHIC INFORMATION SYSTEM

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ABSTRACT

Geographic information systems (GIS) facilitate the monitoring and analysis of population distributions at spatial and temporal scales differing from those conventionally employed in field monitoring. This study utilizes a GIS to perform a gap analysis on an informal network of marine reserves around Santa Catalina Island relative to the regional ecology, disturbance regime, metapopulation biology, and persistence of giant kelp (*Macrocystis pyrifera*), a keystone species in the nearshore marine environment. Catalina's NW-to-SE orientation and highly-dissected leeward and windward coastline create diverse microhabitats with respect to storm exposure, temperature, depth, slope, aspect, bottom relief, light regime, and other factors quantified as GIS data layers. GIS overlay methods applied to multi-temporal kelp distribution maps spanning nearly 60 years generated a model representing the spatial "persistence" of kelp. Correlations between the kelp distributions, persistence, the disturbance regime and the physical variables that permit kelp to resist or recover from it were drawn. Geographic patterns were observed relative to the disturbance regime, topographic variables, and insolation. This gap analysis identified regions of persistent kelp under disturbance regimes markedly different from those in the existing reserves, suggesting the designation of additional reserves may be necessary in these currently unprotected areas.

Keywords: Geographic information system, GIS, gap analysis, marine reserves, *Macrocystis pyrifera*, giant kelp, persistence, sea surface temperature, insolation, Santa Catalina Island, California.

INTRODUCTION

Giant kelp (*Macrocystis pyrifera*) is a marine alga found along the Pacific coast of North America from central California to Baja California (Abbott and Hollenberg 1976). Although it begins life as a microscopic spore at the ocean floor, this species may grow to lengths of 60 meters (m) with its upper fronds forming a dense canopy at the surface. Giant kelp prefers depths less than 40 m, temperatures less than 20°C, hard substrate, and bottom light intensities above 1% that of the surface (North 1971; Foster and Schiel 1985). *Macrocystis* plays an important role in the marine environment by providing food and habitat for a wide range of marine invertebrates and fishes in southern California. Forests of giant kelp may support millions of individual organisms and more than 1,000 species of marine plants and animals (North 1971; Earle 1980; Foster and Schiel 1985).

Santa Catalina Island is one of the eight Channel Islands located off the southern California coast. The island is oriented in a NW-to-SE direction relative to the prevailing westerly and northwesterly swell and wind (Figure 1). This orientation results in a high energy exposed coastline on the southwest-facing windward side and a lower energy, more protected environment on the northeast-facing leeward side. In addition, the island's 87 kilometer (km) coastline is highly dissected with small bays, points, and other coastal features. Combined, these geographic characteristics result in a wide range of microhabitats with respect to storm exposure, temperature, light, and other environmental parameters.

Gap analysis (Scott et al. 1993) has become a popular method of evaluating the degree of protection afforded a species, or a habitat, by an existing network of protected areas (e.g., parks, reserves). The geographic distribution of the species or potential habitat is compared with the spatial configuration of reserves, and gaps in the coverage relative
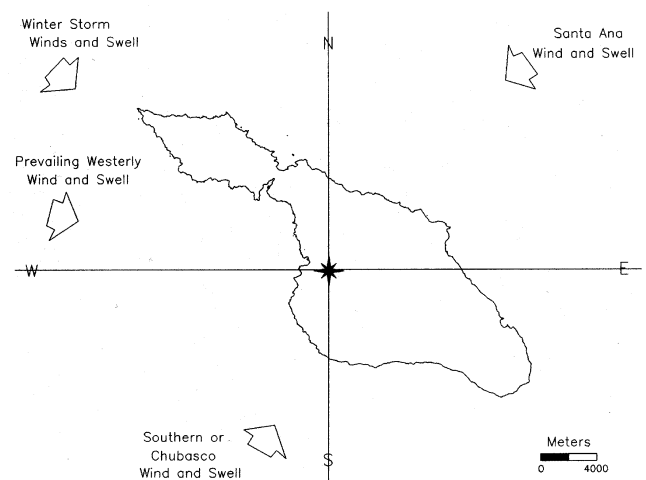

Figure 1. Santa Catalina Island is oriented in a NW-to-SE direction relative to the prevailing westerly and northwesterly winds and swell which directly impact its southwest-facing windward side. Occasional summer chubasco storms strike this coast from the south to southwest. The more protected leeward coast may also be impacted by seasonal Santa Ana and northeasterly storms.

to the characteristics of the landscape and the target's ecology are identified. This study evaluates the degree of protection afforded by existing reserves relative to ecosystem dynamics or processes such as disturbance. Geographic information systems (GIS) are tools often employed in such analyses.

Most of southern California's giant kelp is found along the coasts of the offshore Channel Islands, including Catalina. Anecdotal and personal observations suggest reductions in the distribution of *Macrocystis* around this island over the past 25 years. Similar trends have been noted elsewhere in the region, and have been attributed to sewage pollution, sea otter hunting, sea urchin grazing, elevated temperatures associated with El Niño events, and other causes (Hodder and Mel 1978; Neushul Mariculture, Inc. 1981; Harger 1983; North 1991).

The loss of kelp, and the important marine habitat that it represents, has been one factor stimulating interest in the establishment of marine reserves around Catalina Island. Several existing reserves have already been designated based largely on recreational or educational access. These include Lover's Cove and Casino Point designated by the City of Avalon, Toyon Bay (Catalina Island Marine Institute), Blue Cavern Point (USC's Wrigley Marine Science Center at Big Fisherman Cove) and the West End Invertebrate Reserve (Figure 2).

These reserves are all located on the leeward side of the island near existing population centers. Island-wide studies using a GIS have indicated the island's most productive kelp beds are located on the more exposed windward coast (Bushing 1994, 1997). This suggests that selection of future
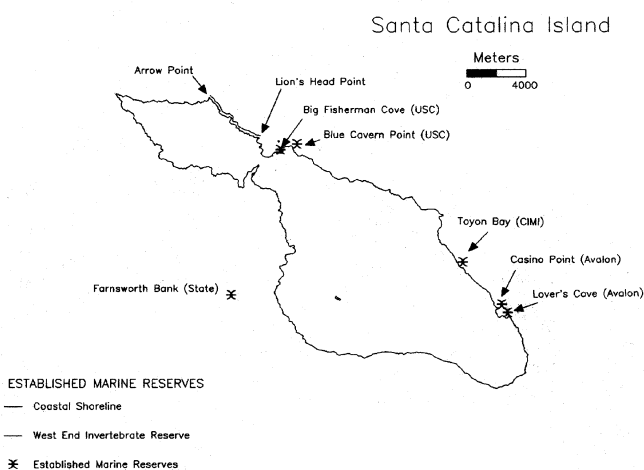

Figure 2. Existing marine reserves are located almost entirely on the island's leeward coast. These include Lover's Cove and Casino Point (designated by the City of Avalon), Toyon Bay (Catalina Island Marine Institute), a reserve from Big Fisherman Cove to Blue Cavern Point (University of Southern California's Wrigley Marine Science Center) and the West End Invertebrate Reserve from Lion's Head Point to Arrow Point. Some additional protection has been afforded by the Areas of Special Biological Significance (ASBS) designated by the State of California Water Resources Control Board.

marine reserves should be done on the basis of ecological processes such as disturbance or criteria such as metapopulation characteristics and persistence, rather than strictly on issues of access or recreational value.

This study utilizes the same GIS to elaborate on the preliminary research referenced above. New data layers include models of swell and storm exposure, solar insolation and the persistence of kelp around the island which offer a better understanding of ecological disturbance and the ability of kelp to recover from it. The persistence layer incorporates multi-temporal kelp maps allowing the analysis of kelp distribution over time relative to the other variables.

Ecologically, the term disturbance has been defined as the discrete removal of individual organisms from a biological population, a detectable change in population response to sudden changes in resources, or an event causing a community or ecosystem characteristic (e.g., species diversity) to diverge from its normal range (Forman and Godron 1983; Bazzaz 1983; Wallace 1990; Gore et al. 1990). Removal of kelp plants by storms is an example of the first, reductions in growth or biomass due to elevated El Niño temperatures the second, and decreases in species diversity of the marine invertebrates associated with kelp the third. The "disturbance regime" includes the type, areal extent, magnitude, frequency, predictability, and turnover rate of disturbance events through time within a given landscape (Forman and Godron 1983; Sousa 1984), and is relative to the characteristics of both the local landscape, and the species of interest. Environmental factors influencing the disturbance of *Macrocystis* may be biological or physical in nature.

Biological factors include grazing by invertebrates or fish, competition from other algae, encrusting growth and diseases (North 1971; Foster and Schiel 1985). Sea urchins are often cited as agents of disturbance in kelp bed systems globally (e.g., Mann and Breen 1972; Lawrence 1975; Hagen 1983) and in southern California (e.g., Leighton et al. 1966; North and Pearse 1970; Tegner 1980), and several species are known from Catalina waters. Based on other studies (Harrold and Reed 1985; Ambrose et al. 1993), conditions around Catalina are generally favorable for sea urchin overgrazing due to low nutrients, warm temperatures, and exposure to storms on the windward side. However, overgrazing events noted on the other Channel Islands (Ambrose et al. 1993; Richards et al. 1993) are rarely observed in Catalina waters based on published reports (Engle 1994; McAlary and McFarland 1994) and personal observations. *Macrocystis pyrifera* exhibits such strong competitive advantage over other local algae that competition is rarely a problem (Dayton et al. 1992).

The absence of significant local biotic disturbance makes physical factors of primary importance (North 1968, 1971; Foster and Schiel 1985). Warm water episodes such as El Niño have serious effects on the growth and survival of giant kelp (e.g., Dayton and Tegner 1984; Gerard 1984). These large-scale events play a role in the disturbance regime directly through the physiological stress associated with

elevated temperature, or indirectly due to associated phenomena (e.g., reduced nutrients or strong storms). On a local scale, exposure to wind, waves, swell and storm events plays an important role in Catalina's disturbance regime. Storms impact the island's windward side primarily from the NW or W during winter, but may also strike from the south during summer or on the leeward side during seasonal Santa Ana or NE winds.

A species' response to such disturbance events determines its ability to persist locally through time. Ecological persistence may be simply defined as the absence of local extinction (Rabinowitz et al. 1989) or the continued existence of a species over time (Connell and Sousa 1983). Two components of a species' stability are resistance, the ability to withstand disturbance, and resilience, the ability to return to its pre-disturbance state (Connell and Sousa 1983). The spatial heterogeneity of the physical habitat may play a significant role through the presence of microhabitats serving as refugia (Sousa 1984), high complexity (Pearsons and Li 1992), high nutrient supplies (Steinman et al. 1991), and other factors.

This study utilizes a GIS to identify environmental factors that appear to confer higher persistence for kelp around Catalina. The physical disturbance regime is characterized based on available data and models. Multi-temporal kelp distribution maps are used to generate a model of persistence, and statistical correlations are drawn to determine the environmental factors which may contribute to kelp's stability geographically. It is hypothesized that in regions of higher storm-related disturbance kelp will favor sites in protected coastal aspects, deeper water, shallower slopes and higher bottom relief and show higher persistence there. Finally, this information will serve to identify gaps in the existing marine reserve system relative to ecosystem dynamics, and generate guidelines for identifying optimal kelp beds suitable for designation as future marine reserves.

MATERIALS AND METHODS

GIS data layers required to address the issues in this study include topographic data (bathymetry, submarine aspect, submarine slope, and bottom relief), significant wave height, sea surface temperature (SST), solar insolation, and several kelp bed distribution maps. Data layers were all registered to base maps of the island's shoreline manually digitized (using UTM-11 coordinates) from the four U.S. Geological Survey (USGS) 7.5' quad maps covering Santa Catalina Island at a scale of 1:24,000. Software employed included PC ARC/Info (version 3.4.2), ARC/View 2.1 and 3.0 for Windows, IDRISI (version 4.1) and ERDAS (version 7.5).

Topographic GIS Data Layers (Depth, Aspect, Slope and Bottom Relief)

The methods used to generate the topographic GIS data layers have been detailed previously (Bushing 1994, 1996a, 1996b, 1997). To summarize, topographic contours were manually digitized from the same base maps at 15 to 76 m (50-250') intervals depending on local topography. Bathymetric contours to a depth of 183 m (100 fathoms) were digitized from National Oceanic and Atmospheric Administration (NOAA) chart 18757 ("Santa Catalina Island"). A digital terrain model (DTM) was interpolated from the combined topographic and bathymetric contours at 20 m resolution to coincide with the spatial resolution of the French SPOT (Systéme Probatoire l'Observation de la Terre) satellite imagery used. Submarine aspect and slope data layers were generated from the resulting DTM.

Because bottom relief is a potentially important factor for kelp distribution, GIS layers representing indices of relief were generated. The submarine aspect layer was re-classed into twenty-four 15-degree categories (e.g., 0-14°). Rectangular "diversity" or "texture" (Star and Estes 1990) filters were applied at several pixel dimensions (3 x 3, 5 x 5, and 10 x 10) to model the heterogeneity in the region of each raster cell. The variable dimensions of the spatial filters permitted the incorporation of a bottom relief index at three separate spatial scales (30 to 40 m, 50 to 70 m, and 100 to 140 m, respectively) from the subject cell.

Kelp Bed Distribution and Persistence Levels

This research updates previous work in which a single kelp distribution map (Bushing 1994) and a series of four maps (Bushing 1995) were employed. The distribution map used in the initial studies, dated about 1980, was provided by Southern California Edison (SCE). Distribution data for 1934 were obtained from NOAA's National Ocean Survey (NOS) database and converted to GIS vector point format. Polygon buffers were created at a distance of 60 m from each point in this data. Kelp bed polygons were manually digitized from a 1977-1978 kelp distribution map identified in a field survey (SWRCB 1979). Distribution for 1989 was established using a hard copy map based on an aerial photographic survey conducted by the California Department of Fish and Game (CDF&G) provided by Kelco, Inc. Kelp presence in 1990 was generated using a raster-to-vector conversion of a SPOT satellite image in the near infrared (NIR). Kelp's high reflectance and water's strong absorption in the NIR allowed the delineation of kelp canopy in the satellite image using image processing techniques to create a distribution map. Satellite imagery has been employed for kelp surveys, but it is difficult to detect beds smaller than 10 hectares and canopy of low density or entirely submerged (see Jensen et al. 1976, 1979, 1980, 1987; Belsher and Mouchot 1990, 1992; Augenstein et al. 1993; Deysher 1993). McAlary and McFarland (1994) have noted distinct differences in the degree of surface canopy formation at selected sites around Catalina Island.

All five distribution maps (Figure 3) were converted to binary raster data layers indicating presence (1) or absence (0) of kelp in each. The five layers were then composited using GIS overlay methods so each cell in the resulting "persistence" layer represented the number of survey years in which kelp was found at that geographic
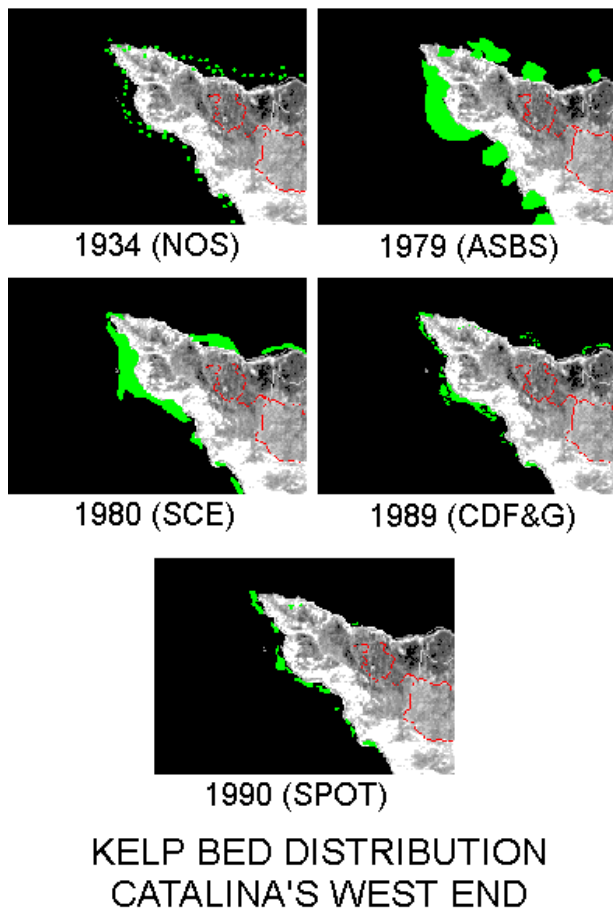
KELP BED DISTRIBUTION
CATALINA'S WEST END

Figure 3. Individual kelp distribution maps for five survey years are shown above for the region surrounding the extreme West End of the island. These data cover the years 1934 (National Ocean Survey, point vector data, courtesy NOAA); 1977-1978 (Areas of Special Biological Significance survey, mapped product); 1980 (Southern California Edison, vector polygon data, courtesy SCE); 1989 (California Department of Fish & Game, mapped product) and 1990 (SPOT satellite image, 20-m raster data, image courtesy SPOT Image Corp.)

position. The resulting values ranged from 0 (kelp present in no survey years) to 5 (kelp present in all five survey years). A similar method has been used by SCE to look at the persistence of kelp near its San Onofre generating station (A. Lin, pers. comm. 1992).

Disturbance Layers: Storm Exposure and Sea Surface Temperature

Storm exposure was incorporated into the GIS from a model developed by O'Reilly and Guza (1993) employing submarine bathymetry and swell characteristics to estimate significant wave heights (H_s) in the Southern California Bight. H_s is defined as the mean height of the largest 1/3rd of observed waves (Pond and Pickard 1983). An image modeling H_s at 200-m resolution for a peak storm event on March 12, 1995, (1048 PST) was used for this analysis. The image was then printed in color at a scale that permitted digitization of the boundaries between H_s values into vector polygons encoded with the corresponding H_s value. These

polygons were registered to the base layers and incorporated into the GIS, and also converted to raster data for cell-by-cell analysis.

Because kelp canopy responds to wave energy as well as wave height, H_s (m) was also quantized into three wave energy levels based on the following equation from Pond and Pickard (1983):

$$E = (\rho * g * H_s^2)/8$$

where E is wave energy in Joules/m^2, ρ is density and g is 9.8 m sec^{-2}. Since wave energy is proportional to the square of H_s, values of $H_s < 1.40$ were assigned to energy level 1, $1.40 < H_s < 2.00$ to level 2, and $H_s > 2.0$ to level 3. These classes permitted statistical analysis of differences in slope and depth as a function of H_s and wave energy.

Sea surface temperature (SST) data was incorporated using Advanced Very High Resolution Radiometer (AVHRR) imagery archived by NOAA (Coastwatch 1995). The coarse resolution (1.1 km) of this data made registration to the existing GIS data layers impractical, so visual comparisons and extracted regional data were employed.

Data Analysis

Many of the data layers were stored both as polygon and raster data to facilitate the analyses in this study at differing spatial scales. Although analysis was conducted using the vector polygon layers, much of the information presented here looked at the data on a cell-by-cell basis due to the influence of smaller-scale (~20 m) heterogeneity on kelp distribution. Binary raster masks representing kelp distribution from the individual temporal surveys were created at 20 m resolution from the original polygon data for both leeward and windward coasts. Unless otherwise stated, all statistics for single year distributions reference the 1980 SCE data set. The 36.6 m (20 fathom) bathymetric contour was chosen to define the maximum expected depth limit for kelp. The region along the ocean floor between this depth contour and the shoreline represents the potential area that might be occupied by kelp. For this study it is referred to as the "photic shelf" since its lower limit is generally considered to be light-limited. A second set of binary masks, corresponding to the "photic shelf" on the leeward and windward coasts, was created.

Coincident data was extracted from the raster GIS data layers for submarine aspect, depth, slope, bottom relief, and significant wave height using the kelp and photic shelf binary masks and GIS overlay techniques. These data were analyzed within the GIS, and imported into Foxpro databases representing the windward and leeward sides. Each data layer (e.g., binary kelp distribution mask, extracted aspect, persistence) was imported as a separate field in the database so each record represented a single 20 x 20 m geographic location incorporating the associated data in multiple fields. Several computer programs were written to further analyze the data on a cell-by-cell basis.

Two important statistics were evaluated for each data layer: kelp frequency and kelp percent cover. In this paper the phrase "kelp frequency" refers to the percentage of total kelp along each coastline with a given data level (e.g., 5% of all kelp on the West leeward coast was found at a depth of 18 m). The phrase "percent cover" refers to the percent of the corresponding "photic shelf" covered by kelp for a given value of an environmental variable (e.g., 20% of all 8 m depths on the West windward coast were covered by kelp).

Data were also imported into SYSTAT (version 5.02) for further analysis and graphical presentation. Statistical tests were run on the data to determine which environmental factors were correlated with the persistence of kelp on the two coasts (Pearson correlation matrices), and whether there were statistically significant differences between persistence levels (pairwise mean Tukey HSD comparisons) based on the methods of Wilkinson et al. 1992. Simple means testing between populations was based on Bishop (1984).

RESULTS

Topographic GIS Data Layers (Submarine Aspect, Depth, Slope and Bottom Relief)

Results from the analysis of kelp distribution relative to the topographic variables have been detailed previously (Bushing 1994, 1996a, 1996b, 1997). Due to the prevailing NW-to-SE trend of the island, the frequency distribution (Figure 6a in Bushing 1997) of kelp relative to submarine aspect shows strong peaks at 0 to 40° on the north- and northeast-facing leeward side, and 210 to 250° on the south- to southwest-facing windward side. When distribution relative to aspect is analyzed in terms of percent cover, a different picture emerges (Figure 6b in Bushing 1997). Marked peaks are observed at ~120° and 300 to 330° on the leeward side, and 50 to 90° on the windward side.

Kelp frequency distribution relative to depth (Figure 7a in Bushing 1997) on the leeward side peaked at statistically significant ($p < 0.001$) deeper depths than on the windward side. Mean and maximum depth values were 11.6 and 41.8 m on the leeward side versus 7.1 and 24.1 m on the windward side. Percent cover (Figure 7b in Bushing 1997) also indicated the same pattern with maximum values at deeper depths on the leeward side (8 to 9 m) than the windward (3 to 5 m).

Figure 8 in Bushing (1997) depicts the results for kelp frequency and percent cover relative to submarine slope. Kelp frequency also shows statistically significant differences ($p < 0.001$) with kelp found on shallower slopes on the windward side than the leeward. Mean values were 5.8° ± 2.9° on the windward side and 7.5° ± 3.6° on the leeward. Percent cover shows generally higher values at lower slopes on both coasts, but an avoidance of steep slopes on the windward side.

Visually, kelp appeared to have a strong affinity for regions of increased bottom relief such as offshore reefs and areas around coastal points and headlands (Figure 10 in Bushing 1997). Although the mean values relative to bottom relief were lower on the windward side, kelp frequency peaked at higher values (6-8) there than on the leeward side (4-7). The mean values were significantly higher for kelp than for the corresponding shelf on both sides, but test statistics indicate the relationship was stronger for the windward side ($p < 0.001$) than the leeward side ($p < 0.010$). There were also detectable trends in average bottom relief relative to aspect (Figure 11a in Bushing 1997).

The presentation of kelp percent cover data is more revealing (Figure 11b in Bushing 1997). The leeward side exhibits a more uniform distribution (10 to 20%) relative to bottom relief. No prominent peaks are noted, although there is a slight trend for increasing percent cover with increasing bottom relief. On the windward side, percent cover was low (0 to 10%) in regions of low bottom relief (1-5), quite variable (7 to 22%) at moderate relief (6-16) and exhibited strong peaks (30 to 45%) in regions of high relief (17-19). Similar trends were noted at all three spatial scales.

Kelp Bed Distribution and Persistence Levels

The five-year persistence model is illustrated in Figure 4 showing the results on the extreme West End of the island. It can be seen from the legend that very few 20-m raster cells had kelp present in all five survey years. In previously reported results (Bushing 1995) results from a four-year persistence model were presented. In the five-year persistence model, windward and leeward persistence was compared for each of the five survey years, and for all raster cells in which kelp was present in at least one survey year (i.e., persistence level ≥ 1). In each of the five survey years, mean persistence on the windward side was significantly higher ($p \ll 0.001$) than that of the leeward side. Considering all cells with persistence values ≥ 1, mean persistence on the windward side ($\mu = 1.71$) was significantly higher

Kelp Persistence (5 survey model)
Catalina's West End

Persistence Level 1
Persistence Level 2
Persistence Level 3
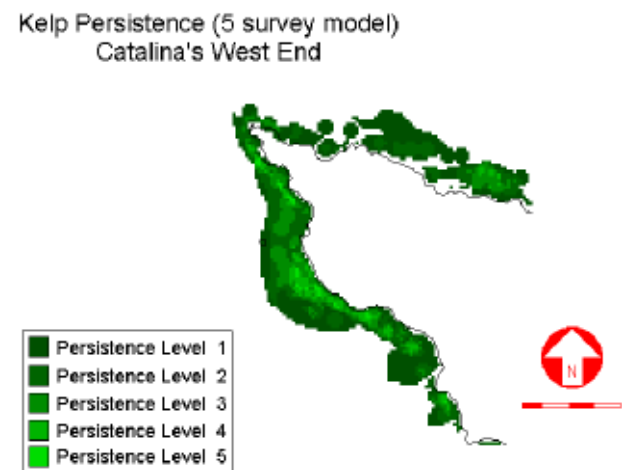Persistence Level 4
Persistence Level 5

Figure 4. The 5-survey persistence model for the extreme West End of the island is illustrated above. Each cell represents a 20-m x 20-m region of the nearshore shelf. Cells with lower persistence (kelp present in fewer survey years) are darker grey, while those representing higher persistence (kelp present in 4 or 5 survey years) are lighter grey.

(p << 0.001) than that of the leeward side (μ = 1.41). In this analysis, 18.9% of kelp on the windward side exhibited persistence values ≥ 3 whereas only 8.7% of kelp on the leeward side fell into these categories.

Swell and Storm Exposure

The significant wave height (H_s) image for March 12, 1995, confirms the expected difference between the exposed windward and protected leeward coasts. It also reveals the development of strong "swell shadowing" on the southern portions of the windward coast, and to a lesser extent along that portion of the West windward coast that faces almost directly south.

Initial results from the GIS analysis of kelp distribution relative to H_s were reported in Bushing (1995 and 1997). To summarize, the frequency distribution for kelp on the windward and leeward sides relative to H_s is consistent with the observed visual patterns. About 90% of kelp on the leeward side was found at lower values of H_s (0.24 to 1.41 m). On the windward side, the distribution fell into two ranges (1.41 to 1.70 m and 2.21 to 2.62 m), reflecting the south and southwest exposures along this coastline, with nearly 70% of the kelp in the upper range.

Percent cover of kelp showed some significant divergence from the frequency distribution. On the leeward side, values were higher (11 to 32%) at moderate (0.77 to 1.41 m) and high (3.61 m) values of H_s while on the windward side the highest percent cover (17%) was near the lower H_s range (1.41 m).

Very revealing patterns emerged when the mean value for H_s was graphed as a function of depth (Figure 5) and

MEAN SIGNIFICANT WAVE HEIGHT Hs
AS A FUNCTION OF SLOPE
(Error Bars = 1 S. E.)
March 12, 1995

Figure 6. The mean value for significant wave height (H_s, in meters) graphed as a function of submarine slope (degrees) for kelp in the 1980 SCE survey on both West leeward and windward coasts (error bars equal one standard error). On the protected leeward side there appears to be a general trend towards higher wave energy at steeper slopes, but the magnitude of the error bars suggests a wide range of values and therefore possible site conditions. Trends on the exposed windward side are more consistent with expectations. Mean H_s declines with increasing slope suggesting that wave energy is dissipated at sites with shallower slopes.

slope (Figure 6). In the first graph, mean H_s steadily increases on both the windward and leeward sides with increasing depth. Plotted against slope, mean H_s steadily declined on the windward side as slope increased, but the reverse trend was noted on the leeward side. Statistical tests were applied to the frequency distributions for depth and slope at the three levels of swell energy. Significant differences (p < 0.001) existed between all three swell energy classes for both depth and slope on the protected leeward side, but only between energy classes 2 and 3 on the exposed windward side.

Multivariate Data Analysis

Analysis of persistence as a function of storm exposure, represented by wave energy (αH_s^2), generated results consistent with expectations. Persistence exhibited a statistically significant difference for each of the three wave energy levels (0.00 to 1.40 m; 1.41 to 1.99 m, and 2.00 to 4.00 m) on the exposed windward side, mirroring patterns in previous work using the four-year persistence model (Bushing 1995). On the leeward side some significant differences were noted between energy classes 1-2 and 2-3, unlike the previous study in which no significant differences were detected. Table 1 presents the current data in the form of pairwise comparison probabilities.

Looking at depth as a factor in persistence (Table 2), there appears to be little significant influence on either side of the island, mirroring results in the earlier study. On the windward side the only highly significant difference was noted between persistence level 1 and levels 2-5. On the leeward side none of the pairwise comparisons in the probability matrix showed any significant difference.

MEAN SIGNIFICANT WAVE HEIGHT (Hs)
AS A FUNCTION OF DEPTH
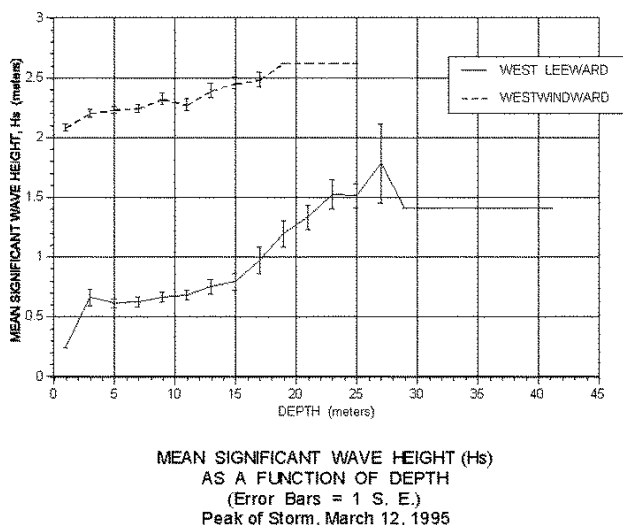(Error Bars = 1 S. E.)
Peak of Storm, March 12, 1995

Figure 5. The mean value for significant wave height (H_s, in meters) graphed as a function of depth (meters) for kelp in the 1980 SCE survey on both West leeward and windward coasts (error bars equal one standard error). Wave height, and therefore energy, increases with deeper depths on both coasts. This suggests that kelp may survive in higher energy environments when its holdfasts are anchored at deeper depths, while holdfasts attached in shallower depths may be torn loose by the energy exerted on the surface canopy.
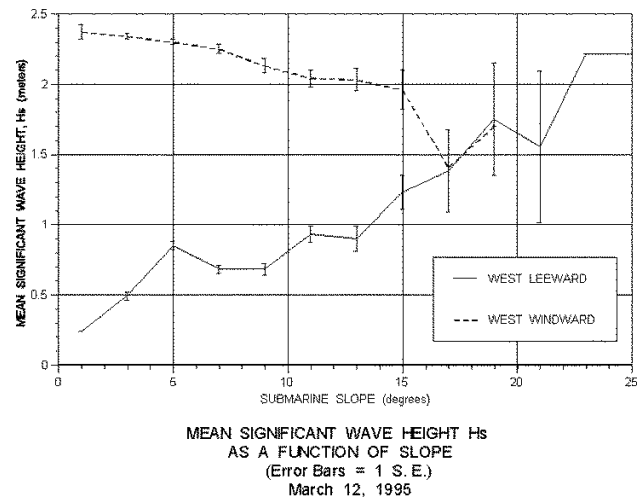
Slope appears to play a more important role in determining persistence. Based on the calculated probabilities (Table 3), differences in slope have a high statistical significance between all five levels of persistence on the windward side except levels 4-5. Pair-wise differences on the leeward side show significance only between persistence level pairs 1-2, 1-3 and 3-4.

The last topographic variable investigated relative to persistence was the 10x10 bottom relief index (Table 4). The patterns follow similar trends to those for slope and swell. Kelp distributions on the windward side generally show statistically significant differences except for three pairings (1-4, 1-5 and 4-5). The leeward side pairwise probability matrix shows no significant difference between any of the persistence levels.

DISCUSSION

The Disturbance Regime Around Catalina

The response of *Macrocystis pyrifera* to the disturbance regime around Santa Catalina Island, and therefore its persistence in the face of disturbance, is a complex issue due to the varying geographic impact of disturbance events, and the wide range of microhabitats afforded by the island's coastline. The spatial heterogeneity of the physical environment appears to be a major factor in determining where giant kelp survives. Coupled with this is the seasonally and

Table 1. Pairwise comparison matrix of statistical significance in differences between kelp persistence as a function of swell energy on the west windward and leeward coasts (shaded pairs significant at p<0.050).

Wave Height	West Windward		
	0.00-1.40 m	1.41-1.99 m	2.00-4.00 m
0.00-1.40 m	1.000		
1.41-1.99 m	0.000	1.000	
2.00-4.00 m	0.000	0.000	1.000
Wave Height	West Leeward		
	0.00-1.40 m	1.41-1.99 m	2.00-4.00 m
0.00-1.40 m	1.000		
1.41-1.99 m	0.000	1.000	
2.00-4.00 m	0.918	0.002	1.000

Table 2. Pairwise comparison matrix of statistical significance in differences between kelp distributions as a function of persistence on the west windward and leeward coasts (shaded pairs significant at p<0.050).

	West Windward				
	1	2	3	4	5
1	1.000				
2	0.000	1.000			
3	0.000	0.997	1.000		
4	0.000	0.556	0.411	1.000	
5	0.000	0.488	0.389	0.977	1.000
	West Leeward				
	1	2	3	4	5
1	1.000				
2	0.990	1.000			
3	0.974	0.871	1.000		
4	0.965	0.924	0.994	1.000	
5	***	***	***	***	1.000

Table 3. Pairwise comparison matrix of statistical significance in differences between kelp slope distributions as a function of persistence on the west wondwartd and leeward coasts (shaded pairs significant at p< 0.050).

	West Windward				
	1	2	3	4	5
1	1.000				
2	0.000	1.000			
3	0.000	0.042	1.000		
4	0.000	0.000	0.000	1.000	
5	0.000	0.000	0.000	0.957	1.000
	West Leeward				
	1	2	3	4	5
1	1.000				
2	0.001	1.000			
3	0.000	0.861	1.000		
4	0.921	0.077	0.036	1.000	
5	***	***	***	***	***

Table 4. Pairwise comparison matrix of statistical significance in differences between kelp bottom relief distributions as a function of persistence on the west windward and leeward coasts (shaded pairs significant at p< 0.050).

	West Windward				
	1	2	3	4	5
1	1.000				
2	0.000	1.000			
3	0.025	0.036	1.000		
4	0.800	0.000	0.000	1.000	
5	0.926	0.000	0.013	1.000	1.000
	West Leeward				
	1	2	3	4	5
1	1.000				
2	0.997	1.000			
3	0.949	0.979	1.000		
4	0.929	0.952	0.988	1.000	
5	***	***	***	***	***

geographically variable nature of disturbance events on the island.

El Niño effects have established the influence of temperature as a major disturbance factor for *Macrocystis* over large spatial scales. The waters surrounding Catalina are the warmest in the Channel Islands region, and temperatures regularly exceed 20°C during the warmer months. Thus kelp around the island is near the limits of its preferred temperature range. In earlier studies (Bushing 1996a, 1997), sea surface temperature (SST) data from AVHRR satellite imagery (CoastWatch 1995) revealed patterns in the local distribution of ocean temperature of potential significance for *Macrocystis*. Temporal and spatial variability (both regional and local) in temperature was highest during the summer months, while winter values were more uniform. Average summer temperatures on the leeward side were uniformly warmer than on the windward side with a significant (p < 0.050) difference between the NW and SE ends of the island. Warm water bodies were observed frequently on the leeward side, and cooler water regions were apparent on the windward side in images.

The temperature differences between the windward and leeward sides of the island suggest possible implications relative to the recovery of kelp from regional El Niño disturbances. Reductions in kelp canopy noted for the leeward side began about 1976, coinciding with a mild El Niño. Ocean temperatures since that time have remained above normal (Norton et al. 1985; Stevens 1994). The consistently higher temperatures on the island's leeward side, the attendant reduction in nutrients and the resultant physiological stress may be factors in explaining why kelp has not recovered there, yet appears to be doing well on the windward side.

However, at smaller scales surge and waves associated with storms may be the most important cause of adult mortality, and therefore a prime disturbance factor, for *Macrocystis*. The exposed outer coastline of the island's windward side receives the incoming storm energy with little protection. Catalina's steep submarine slopes compared to the mainland may accentuate the impact of incoming storms. For a given wavelength, wave energy is released as a function of depth, being stronger in shallower water. Along steep coasts, wave energy may be dissipated closer to shore where kelp usually grows, rather than farther away as on the more gently-sloping mainland shelf. Regions of higher bottom relief may offer some refuge by breaking up the incoming swell. Therefore its location relative to storm direction (aspect), depth, the slope and relief of the ocean floor may all play a role in determining the ability of a kelp bed to resist storm disturbance on the windward side.

Univariate Factors And Storm Exposure

Many authors have stressed the importance of coastal aspect in determining the size or viability of kelp beds (Hodder and Mel 1978; Harger 1983; Reed and Foster 1984; North 1991). The analysis of kelp distribution around Catalina relative to aspect appears to validate the hypothesis that kelp favors regions offering some shelter from the prevailing storm or swell direction. Anomalously high percent cover at aspects facing away from the prevailing coastal directions on both windward and leeward sides suggest kelp may have higher survivorship there. Such regions in the lee of points or headlands, offshore reefs or other coastal features may serve as micro-refugia from storm impact.

Contrary to expectations, kelp on the exposed windward side did not favor deeper water where surge effects would be minimized. Instead, its distribution was in uniformly shallower depths than on the corresponding leeward side. This finding has been interpreted as a result of reduced light environments caused by increased turbidity on the windward coast due to the re-suspension of bottom sediments in the higher energy environment (Bushing 1994). North (1991) stated that the outer edges of mainland kelp beds usually lie at depths of 18 m or less except where the water may be very clear, allowing light to penetrate deeper. This also coincides with the surge zone defined by Quast (1971). Kelp on the windward side falls almost entirely within this vertical zone subject to more frequent disturbance by storm, suggesting higher mortality and turnover typical of shallower depths (Dayton and Tegner 1984; Seymour et al. 1989).

Differences in topography resulting from the uplift of the island's land mass have resulted in shallower submarine slopes on the windward side. The photic shelf there is more like that of the adjacent mainland than the island's steeper leeward side. Incoming waves and surge respond differently to the shallow and more steeply-sloping bottom topography. Energy may be dissipated more gradually on shallow slopes resulting in less destructive water motion at comparable depths. The higher observed percent cover at shallow slopes on the windward side supports the hypothesis that kelp would favor such regions in the face of storm exposure.

Geographic relief due to topography has long been known to influence the distribution of terrestrial plants (e.g., Holland and Steyn 1975; Krcho 1991). Kelp beds are also linked directly to submarine topography, with areas of greater bottom relief generally supporting more kelp (SWRCB 1979; Harger 1983). In this study the more uniform distribution of kelp relative to bottom relief on the leeward side suggests substrate occupation without regard to bottom relief. On the windward side, higher percent cover in areas of moderate to high relief suggests a preference for such regions in the face of increased exposure to storms.

The incorporation of storm exposure, as measured by significant wave height, offers an improvement over the preliminary research reported earlier (Bushing 1994). Without this element, only subjective statements could be made about the relationship between environmental variables and the potential disturbance regime. Although the storm event selected represents but one of a wide range of events due to varying wave heights and swell directions, it does allow quantitative data to be used in this analysis. The findings from this study suggest kelp on the leeward side favors

regions of moderate rather than low H_s, indicating a preference for some water motion. The high percent cover at lower values of H_s on the windward side strongly suggests that regions protected from direct storm impact are favored there.

Multivariate Interpretations of Disturbance and Persistence

The evaluation of mean H_s as a function of depth and slope also confirms the original hypotheses regarding disturbance. Steadily increasing values of H_s with increasing depth on both leeward and windward coasts may be interpreted as a result of higher mortality in shallower waters due to storm exposure. Kelp may persist in regions of shallow water only when wave and storm exposure is low. At deeper depths, the energy of an incoming swell is felt less strongly so kelp may persist there despite increased values of H_s.

The results relative to slope suggest responses to it are more regional in nature. The decreasing H_s values with increasing slope on the exposed windward side also confirm the original hypotheses. In regions of shallow slope, where wave energy may be dissipated gradually, kelp may persist in areas of higher H_s while on steeper slopes they require calmer waters. The reverse trend on the leeward side suggests that, on this more protected coast, other environmental factors may be more significant.

Using these same variables (aspect, depth, slope, bottom relief, and storm exposure) to evaluate "persistence" first necessitates a consideration of resistance and resilience relative to the model used. *Macrocystis* is a perennial alga, with individual plants surviving for several years and entire kelp beds potentially even longer. Another factor is the differential ability of adult sporophytes near the surface, and the microscopic stages near the bottom, to survive in the face of disturbance. A storm which detaches the adult plant due to the force applied to its canopy may leave the young stages relatively undisturbed. The subadult stages at the bottom may also remain vegetative until conditions are appropriate for their growth, just as plant seeds remain in the soil seed bank for several years. In addition *Macrocystis* is a strong competitive dominant compared to most algae. Kelp beds are known to fully recover from disturbance within 14 months (Kennelly and Underwood 1993).

The "persistence" model employed in this study utilized often widely-separated (1934, 1978-1979, 1980, 1989 and 1990) temporal data. Individual kelp beds are ephemeral, often disappearing between survey years and reappearing much later. This reflects the dynamics of the marine environment (e.g., storm disturbance, bottom sediment transport). The time gaps between some surveys are too great to determine whether the levels of "persistence" represented in this model measure the resistance of kelp, and therefore its ability to withstand disturbance, or its resilience, the ability to recover from it. In the future, additional temporal maps will be incorporated into the model to better evaluate this. Given these limitations, the model can be used to evaluate the following trends.

The influence of storm exposure on kelp persistence is consistent with expectations. On the higher energy windward coast, significant differences in persistence were noted for differing levels of wave energy. Locations that offer more protection may serve as refuges and exhibit higher survivorship. Kelp in such refugia may help re-populate nearby sites where more direct storm exposure has eliminated kelp beds. The absence of significant differences in persistence on the protected leeward side relative to wave energy may simply reflect the smaller amplitude in H_s observed there. Reice et al. (1990) argued that the most frequently and predictably disturbed sites should demonstrate the highest resilience. The findings in this study are consistent with that hypothesis.

Depth did not appear to be a highly significant factor in persistence based on the pairwise probability matrix in Table 2. The restricted depth distribution on the windward side due to turbidity may mask any linkage with survivorship as suggested by the presence of some measurable differences. On the more protected leeward side, where storms may be less of a factor than large-scale disturbance due to elevated ocean temperatures, the value of deep water refugia may be diminished since canopy can't persist in the warmer surface waters.

The strong relationship between persistence and submarine slope (Table 3), especially on the windward side, adds further confirmation to its importance as a physical habitat factor. All persistence levels exhibited significant differences in slope on that coast. Although not as important a factor on the leeward side, slope still appears to play a role in conferring greater stability in kelp beds. However, slope data interpolated from digital terrain data may be subject to significant error (Eastman 1993).

Finally, bottom relief also appears to be a determining factor in the stability of kelp on the windward side (Table 4). In the face of higher wave energy, the protection afforded in regions of greater relief on the windward side may confer sufficient advantage to allow kelp to resist storms. The absence of any significant difference on the leeward side is equally informative. On this more protected coast, the absence of strong storm exposure may minimize the value of bottom relief.

Additional Factors Affecting Persistence

As suggested in the introduction, the ability of kelp to recover from disturbance may depend on the physical heterogeneity of the environment relative to topographic factors, and the presence of refugia from direct storm effects. Given comparable disturbance regimes, kelp may persist in one site and not another if resources allow it to repair damaged tissue or grow at rates sufficient to keep up with losses due to disturbance (Jackson 1977). Additional resource factors which may influence this are temperature, light, and nutrients. Temperature was addressed above. The latter two factors, both essential for photosynthesis, have been

addressed in detail previously using the GIS (Bushing 1994, 1995, 1996a, 1996b, 1997), but will be summarized for consideration here.

In earlier studies (Bushing 1994, 1996a, 1996b), kelp distribution was evaluated relative to the light regime using models of solar insolation (Figure 17 in Bushing 1997). The windward side had uniformly higher levels of surface insolation throughout the year while the light regime on the leeward side was lower due to shading of the nearshore waters by the island's high central ridge. Kelp on the leeward coast favored sites with higher insolation. Higher light levels on the windward side during critical growth periods, which also coincide with seasonal storms, may permit kelp to regenerate faster there. However, light is also correlated with factors related to the island's topography making its influence difficult to isolate.

The spatial distribution of kelp, and its ability to recover from disturbance, may be affected by the availability of nutrients such as nitrates (NO_3). Large scale field-measured nitrate levels are not economically feasible for a region as extensive as the nearshore environment of Catalina Island, and there are no remotely-sensed sources of such data. A strong correlation between temperature and nitrate levels (Zimmerman and Kremer 1984) allowed SST to be used as a surrogate for NO_3 levels. Sea surface temperatures from AVHRR satellite images were color-encoded to represent physiologically significant levels: regions of adequate nutrients, borderline nutrient levels, and depleted nutrients but acceptable temperatures (Bushing 1995, 1996). Warmer temperatures on the leeward side result in lower surface nutrient levels, often to the point of depletion, whereas colder water on the windward side means nutrients may exist at higher levels in the surface waters where the kelp canopy is found. This suggests that higher nutrient levels on the windward side may also enhance kelp's persistence, even in the face of greater disturbance.

SUMMARY

This research substantiates the value of GIS in looking at larger-scale, longer-term ecological phenomena in the marine environment. Field experiments usually entail limited geographic and temporal scope due to logistics problems, limited time or funding, and the data volumes required. GIS is an appropriate tool for addressing ecological issues on a regional scale, and an excellent means to identify issues and sites for more intensive field work.

The specific findings in this study indicate the physical complexity and diversity of nearshore marine habitats surrounding Santa Catalina Island may be of great importance in determining the ability of *Macrocystis pyrifera* to persist. Regionally, distinct differences in disturbance regime (storm exposure and SST) between the windward and leeward sides, result in large-scale differences in the disturbance regime experienced by kelp. On the windward side, suitable micro-refugia allowing resistance to disturbance may be found in protected sites with aspects sheltered from direct storm impact, on shallower slopes where wave energy is dissipated more gradually, at deeper depths where wave energy is felt less intensely, or in regions of higher bottom relief which may also offer some protection. On those coasts where disturbance level is high, increased levels of light and nutrients, may contribute to the resilience of populations by enhancing their ability to repair damaged tissue or successfully recruit. However on the leeward side, where larger-scale thermal events dominate and both nutrients and sunlight are lower, there are few such refugia due to the lack of significant upwelling (Bushing 1996b).

The kelp beds surrounding the island should be viewed as a metapopulation, or population of populations (*sensu* Levins 1970). The geographic differentiation of persistence has important consequences relative to metapopulation characteristics, and therefore the designation of appropriate marine reserves to protect both giant kelp and the many marine species that utilize it for habitat or food. Disturbance events may decimate or remove protected kelp beds if they are restricted to a limited range of site conditions, as is presently the case around Catalina. Existing reserves, located almost entirely along Catalina's leeward coast, are characterized by a disturbance regime dominated by large-scale, short- and long-term temperature events. The short-term, winter storm-dominated disturbance regime and higher mean persistence on the windward side, suggests there are gaps in this reserve system. New marine reserves should be designated on the windward side to complement existing ones on the leeward side. Then, in the event of large-scale disturbance such as elevated El Niño temperatures, "remnant patches" (*sensu* Forman and Godron 1981) of kelp persisting in refugia may provide "seed stock" for the re-establishment of populations around the island.

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