

- Druehl, L. D., P. J. Harrison, K. E. Lloyd, and P. A. Thompson. 1989. Phenotypic variation in N uptake by *Laminaria groenlandica* (Laminariales, Phaeophyta). *Journal of Experimental Marine Biology and Ecology* 127:155-164.
- Espinoza, J., and A. R. O. Chapman. 1983. Ecotypic differentiation of *Laminaria longicuris* in relation to seawater nitrate concentration. *Marine Biology* 74:213-218.
- Gerard, V. A. 1988. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Marine Biology* 66:25-36.
- Gerard, V. A., and K. H. Mann. 1979. Growth and production of *Laminaria longicuris* (Phaeophyta) populations exposed to different intensities of water motion. *Journal of Phycology* 15:33-41.
- Gerard, V. A., and K. R. DuBois. 1988. Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Marine Biology* 97:575-80.
- Herbst, C. C., and G. R. Johnstone. 1937. Life history of *Pelagophycus porra*. *Botanical Gazette* 99:339-354.
- Kopczak, C., R. C. Zimmerman, and J. N. Kremer. 1991. Variation in nitrogen physiology and growth among geographically isolated populations of the giant kelp *Macrocystis pyrifera* (Phaeophyta). *Journal of Phycology* 27:149-158.
- Leman, D. S. 1822. *Laminaria*. In: *Dictionnaire des Sciences Naturelles* (edited by F.G. Levrault) 25:189.
- Lewis, R. J. and M. Neushul. 1994. Northern and southern hemisphere hybrids of *Macrocystis* (Phaeophyceae). *Journal of Phycology* 30:346-353.
- Mathieson, A. C., T. A. Norton, and M. Neushul. 1981. The taxonomic implications of genetic and environmentally induced variations in seaweed morphology. *Botanical Review* 47:313-47.
- North, W. J., E. K. Anderson, and F. A. Chapman. 1989. Wheeler J. North ecological studies at Diablo Canyon power plant: final report. Prepared for Pacific Gas and Electric.
- Parker, B. C., and J. Bleck. 1965. A new species of elk kelp. *Transactions of the San Diego Society of Natural History* 14:57-64.
- Parker, B. C., and J. Bleck. 1966. A contribution to the ecology of *Pelagophycus*. *Annals of the Missouri Botanical Garden* 53:1-16.
- Parker, B. C., and E. Y. Dawson. 1964. Notes on the variability and range in the elk kelp *Pelagophycus*. *Transactions of the San Diego Society of Natural History* 13:303-307.
- Parker, B. C., and M. Fu. 1965. The internal structure of the elk kelp (*Pelagophycus* species). *Canadian Journal of Botany* 43:1293-1306.
- Sanbonsuga, Y., and M. Neushul. 1978. Hybridization of *Macrocystis* (Phaeophyta) with other float-bearing kelps. *Journal of Phycology* 14:214-224.
- Schott, J. W. 1976. Dago Bank and its "Horseshoe Kelp" bed. *Marine Resources Information Bulletin* No. 2. State of California Resources Agency, California Fish and Game. 21 pp.
- Setchell, W. A. 1896. The elk-kelp. *Erythea* 4:179-184.
- Setchell, W. A. 1908. *Nereocystis* and *Pelagophycus*. *Botanical Gazette* 45:125-134.
- Zimmerman, R. C., and D. L. Robertson. 1985. Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island. *Limnology and Oceanography* 30:1298-1302.

The Influence of Topography on the Distribution of Giant Kelp (*Macrocystis pyrifera*) Beds around Santa Catalina Island Using a Geographic Information System

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Abstract. Geographic information systems (GIS) are becoming established tools for analyzing species distributions in relation to environmental factors at various ecological scales. This study utilizes GIS technology to investigate the influence of terrestrial and submarine topography on the distribution of giant kelp, *Macrocystis pyrifera*, (Laminariales, Lessoniaceae) around Santa Catalina Island. For this paper, a single kelp distribution map was chosen to test procedures that will eventually be applied to a series of temporally distinct maps covering a period of about 80 years. A digital elevation model (DEM) and digital bathymetric model (DBM) for the island were generated. Several additional layers were produced from the DEM and DBM including slope, aspect and hillshading images. Kelp distribution was then evaluated statistically relative to several factors influenced by topography including depth, submarine slope, submarine aspect (storm exposure), topographic relief and solar illumination (hillshading) patterns. Clear relationships between observed kelp bed distribution and environmental factors related to topography were apparent. However, it is difficult to isolate the effect of individual factors due to their synergistic nature, the fact that they are often closely linked, and the lack of comprehensive field sampling.

Keywords: Phaeophyta; Laminariales; Lessoniaceae; Channel Islands; sediment; solar irradiance.

Introduction

This study utilizes geographic information systems (GIS) technology to investigate island and submarine topography as factors influencing the distribution of giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island. A GIS is an effective tool for studying the environmental factors responsible for marine species distributions on landscape and other ecological or biogeographic scales (Welch and Remillard 1988; Meaille and Wald 1990). Santa Catalina Island offers an excellent opportunity for investigation due to its varied topography and geographic orientation. The

windward and leeward coasts, combined with locally irregular coastlines, present a wide spectrum of submarine aspects, slopes and depths and corresponding exposures to storms, swell, light, and wind.

Macrocystis plays an important role in the marine environment of our offshore islands by providing food and habitat for a wide range of marine life. Physical factors affecting the distribution of kelp include exposure to storms and other water motion, irradiance and spectral distribution, bottom relief, substrate type, water temperature, nutrients and sediments (North 1971; Dean and Jacobsen 1983; Foster and Schiel 1985). Biological factors include grazing by invertebrates and fish, self shading, encrusting growth, competition from other algae and "black rot" (North 1971; Foster and Schiel 1985).

Macrocystis is found in depths ranging from the shallow subtidal to 120 ft or more, but most commonly in depths less than about 60 ft in turbid coastal waters (Mel 1977; Neushul Mariculture Inc. 1981; Foster and Schiel 1985). *Macrocystis* generally requires rocky substrate along more exposed coasts (North 1991), but may establish on soft substrate in quiet waters where burial by sediment is not a problem (North 1971).

Kelp forests are best developed in areas protected from heavy wave surge or storms (North 1968). Such conditions prevail on the gently sloping mainland continental shelf protected by the offshore islands. The steep submarine slopes off Santa Catalina may be less ideal even though the water is clearer and free from pollution.

North (1991) outlined a seasonal cycle in physical factors influencing kelp distribution such as storm regime, daylength, water temperature, wind, rainfall, and nutrient enrichment due to upwelling or terrestrial runoff. Such changes in the physical environment may affect juvenile and adult stages of *Macrocystis* differently.

The current study focuses on a general description and a multi-variate characterization of some physical factors affecting kelp bed distribution around Santa Catalina Island. The test hypothesis was to investigate the influence of differences due to topography on kelp distribution between the exposed windward and more protected lee-

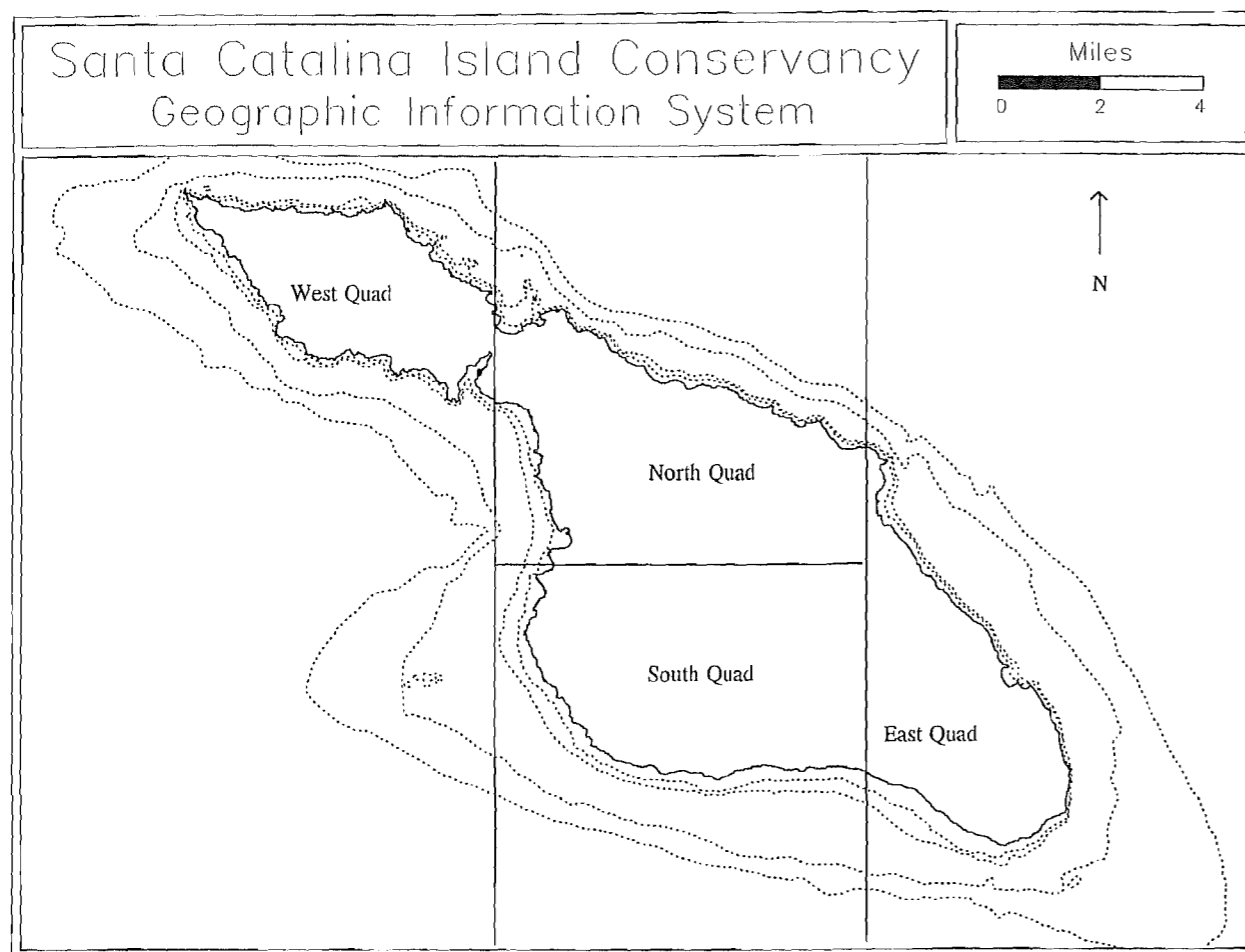


Figure 1. Map of Santa Catalina Island with bathymetry identifying four USGS quads.

ward sides of Santa Catalina using the elements of depth, aspect, slope, topographic variation, and irradiance extracted with the GIS.

Methods

Creation of the geographic information system layers

GIS data layers required to address the hypothesis include kelp distribution, bathymetric depth, submarine aspect, submarine slope, topographic variation, terrestrial elevation and irradiance. To create these data layers, several commercial software packages were employed including ARC/INFO, IDRISI, Atlas*GIS, and ERDAS. Data layers were all registered to base maps manually digitized from the four USGS 7.5' quad maps covering Santa Catalina Island (Fig. 1). Bathymetric contours to a depth of 100 fathoms were digitized from NOAA chart 18757 ("Santa Catalina Island"). A kelp distribution map provided by Southern California Edison was selected for the initial analysis.

A digital elevation model (DEM) and digital bathymetric model (DBM) at 20-m (66-ft) resolution were interpolated for each quad using the topographic and bathymetric contours. Aspect and slope images for the submarine topography were generated from the DEM and DBM layers.

Six data layers incorporating indices of topographic variation were generated by applying 3 separate diversity filters (3x3, 5x5 and 10x10 pixels) to both the depth and aspect layers. These yield an index of the degree of bottom relief at spatial resolutions of about 30–40 (98–132), 50–70 (164–230) and 100–140 m (328–459 ft), respectively.

The influence of island topography on irradiance levels required layers to model the effects of terrestrial hill-shading on the nearshore marine environment and light extinction in the water column. Light index #1 (LI1), modelled light levels at the ocean's surface using a solar azimuth of 225° and solar elevation of 30° corresponding to a simulated late afternoon solar position. Image values resulting from the first index (LI1) were scaled to a range of 0–100 and represent 1 time slice in the diurnal and seasonal variability in the path of the sun across the sky and

Table 1. General characteristics of Santa Catalina kelp beds (number of beds, bed area in square miles; average area per bed in square miles, shoreline in miles, area of beds per mile of shoreline and percent cover of the habitable bathymetric zone).

Region	Number of beds	Kelp bed area (sq mi)	Average area per bed (sq mi)	Shoreline (mi)	Area of beds per mi of shoreline	Percent cover to 120-ft depth
West windward	30	0.2089	0.0070	12.79	0.0163	10.90
West leeward	29	0.1659	0.0057	9.52	0.0174	12.40
North windward	22	0.1051	0.0048	5.94	0.0177	5.88
North leeward	23	0.0633	0.0028	10.44	0.0061	4.29
South windward	29	0.2535	0.0087	11.17	0.0227	6.19
East windward	11	0.1284	0.0117	4.25	0.0302	5.91
East leeward	18	0.0696	0.0039	9.65	0.0072	3.76

its interplay with the island's topography. A second index (LI2), estimating irradiance at the ocean floor, applied a light extinction equation to the LI1 values:

$$LI2 = LI1 * e^{-4.60517 * d / d_{max}}$$

where LI2 is the percent of surface irradiance (LI1) at a given depth (d), and d_{max} is the maximum depth at which kelp was found in each geographic region. This assumes the deepest depth for *Macrocystis* juvenile growth occurs at a value of 1% of surface irradiance (Kirk 1983; Ramus 1983; Walsh et al. 1987). This assumption does not account for differences in water clarity within each geographic region. Both indices assume clear skies and do not account for local variations in cloud cover or fog.

To facilitate data analysis, information was extracted from the data layers using appropriate GIS query masks. Kelp bed masks for the leeward and windward sides of each region were created. Bottom substrate masks were also generated for the vertical depth range (0–120 ft) defined for kelp (Neushul Mariculture, Inc 1981; Shivji 1985). In the following analyses, the phrase "kelp frequency" refers to the percentage of total kelp in each region with a given data value. "Percent cover" refers to the percent of bottom substrate for a given data value covered by kelp (e.g., 20% coverage at a depth of 35 ft), representing the potential occupiable space.

Results

General characteristics of Santa Catalina Island kelp beds

Santa Catalina's kelp beds were grouped geographically into 7 regions defined by the 4 USGS quads and the leeward and windward coasts (e.g., west windward or north leeward). The south quad has no leeward coast. The number of beds, total bed area, average area per bed, length of shoreline, area of beds per mile of shoreline and percent cover of bottom substrate for each region are summarized (Table 1).

Total bed area and the number of kelp beds were highest in the south windward, west windward and west

Table 2. Depth characteristics of Santa Catalina Island kelp beds (average depth [μ_{depth}], standard deviation [σ_{depth}], minimum depth [min_{depth}] and maximum depth [max_{depth}] for beds in all 7 geographic regions).

Region	N	μ_{depth}	σ_{depth}	min_{depth}	max_{depth}
West windward	1,432	23.17	18.14	0	79
West leeward	1,081	38.06	23.06	2	137
North windward	592	30.09	14.41	2	65
North leeward	384	51.58	33.75	4	118
South windward	1,542	12.66	9.70	0	53
East windward	810	14.06	8.41	0	48
East leeward	350	22.83	18.86	0	100

leeward regions, and lowest along the north leeward and east leeward coasts. The regions with the highest average area per bed and the greatest area per square mile of coastline were the east windward and south windward. The regions with the lowest average area and area per mile of coastline were the north leeward and east leeward.

The only other statistic extracted for all 7 regions is depth (Table 2). Kelp beds on the windward coasts were uniformly shallower than the corresponding leeward coasts based on average depth (μ_{depth}) values. Bathymetric ranges on the windward coasts also had uniformly shallower maximum depths (max_{depth}) than the corresponding leeward coast. Standard deviations (σ_{depth}) for the leeward coasts were uniformly higher than on the windward coasts, reflecting the wider bathymetric ranges.

Data characteristics for west end kelp beds

The remainder of the data focuses entirely on the west end where extensive kelp beds along both coasts allow comparisons (Fig. 2). Data were extracted from GIS layers including distance from shoreline, depth, slope, aspect, topographic diversity, and both irradiance indices, which are all linked to terrestrial and/or submarine topography. Mean values, standard deviations, and ranges (minimum/maximum values) are summarized (Table 3).

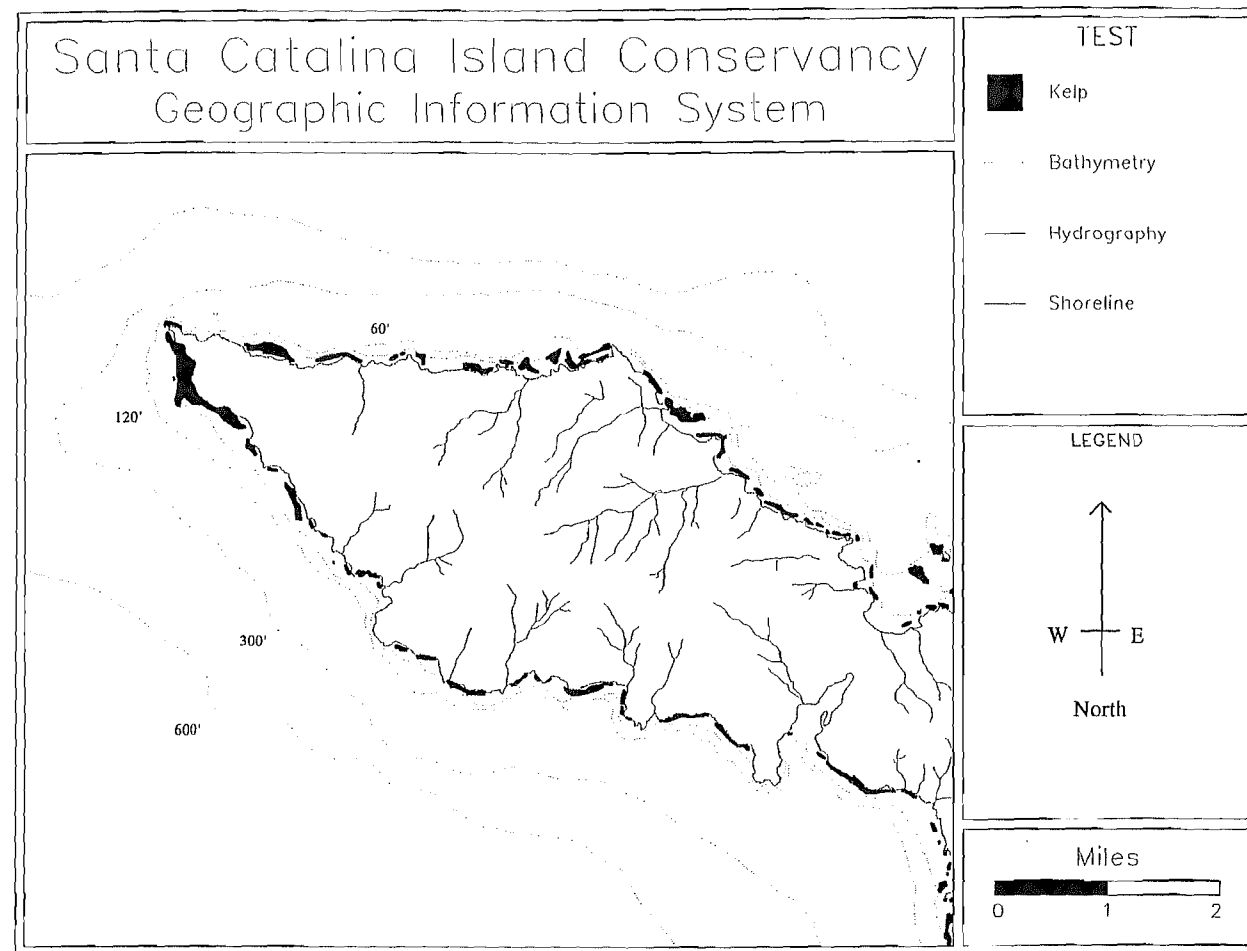


Figure 2. West end of Santa Catalina Island with GIS data layers including kelp distribution, bathymetry, and hydrography registered to base map.

The mean value (μ_{dis}) for distance from shoreline for the west leeward side was 299 ft with a standard deviation (σ_{dis}) of 205, while the windward side showed a very highly significant ($p < 0.001$, $z = 9.87$) lower mean value of 219 ft ($\sigma_{dis} = 194$). Maximum distances for both west end coastlines were comparable at 1,086 ft (leeward side) and 1,115 ft (windward side).

Both kelp frequency and percent cover were analyzed with respect to depth (Fig. 3). The west windward coast beds had a mean depth of 38 ft compared to 23 ft on the leeward coast, a difference that was very highly significant ($p < 0.001$, $z = 17.52$). The west windward side exhibited the highest percent cover from 5 to 20 ft with values 2–3 times greater than those at other depths, while the leeward values showed a more pronounced peak from 15 to 45 ft.

Submarine slope data (Fig. 4) also exhibited differences between leeward and windward sides. Mean slope (μ_{slope}) on the windward side was 5.8° with a standard deviation (σ_{slope}) of 2.9° , while the corresponding values on the leeward side were 7.5° and 3.6° . Percent cover was more uniformly distributed, especially on the leeward side, with values of 5–7° (windward) and 12–16° (leeward).

Average values (μ_{aspect}) for aspect on either side are consistent with the values for the bathymetric zone as a

whole, 217° on the windward side and 17° on the leeward side. Kelp frequency values are influenced by marked peaks at about 225° on the windward and 30° on the leeward sides (Figs. 5a, 5b). When aspect is analyzed in terms of percent cover rather than frequency, a different picture emerges (Figs. 5c, 5d). For all aspect values having at least 10 but less than 100 pixels of occupiable substrate, percent cover exhibits bimodal peaks at about $170\text{--}180^\circ$ and $280\text{--}305^\circ$ on the windward side, and a pronounced peak at about $320\text{--}330^\circ$ on the leeward side. When aspect is grouped in 10-degree intervals (e.g., $0\text{--}9^\circ$) and analyzed relative to intervals with more than 100 pixels, the same pattern is evident.

Graphs of the topographic diversity indices based on aspect reveal discernible differences in percent cover relative to bottom relief on the leeward and windward sides of the west end (Fig. 6). Percent cover on the leeward side had a more uniform distribution (10–20%) without any prominent divergences at any of the 3 spatial resolutions. On the windward side percent cover was lower (0–10%) in regions of low bottom relief but higher (15–45%) in regions of moderate to high relief at all 3 resolutions.

The mean values for ocean surface irradiance (μ_{LI}) on the leeward and windward sides were comparable to those

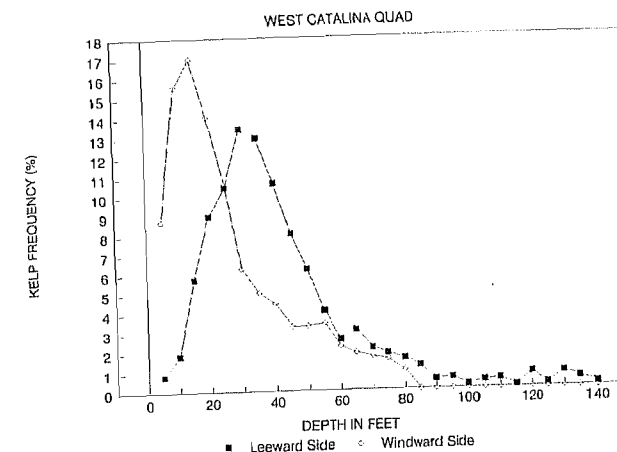


Figure 3. Kelp frequency (percent) as a function of depth (in feet) for the leeward and windward sides of the west end of Santa Catalina Island.

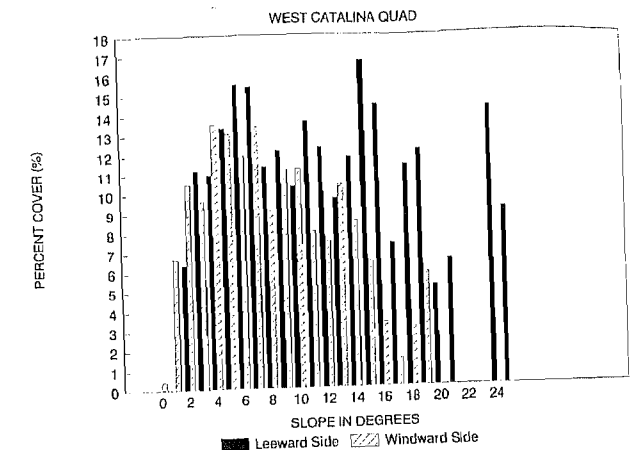
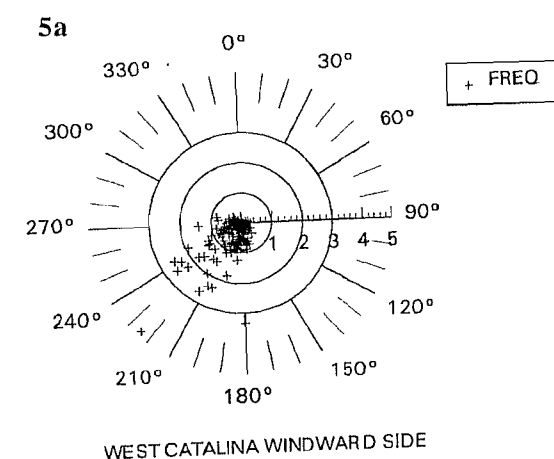
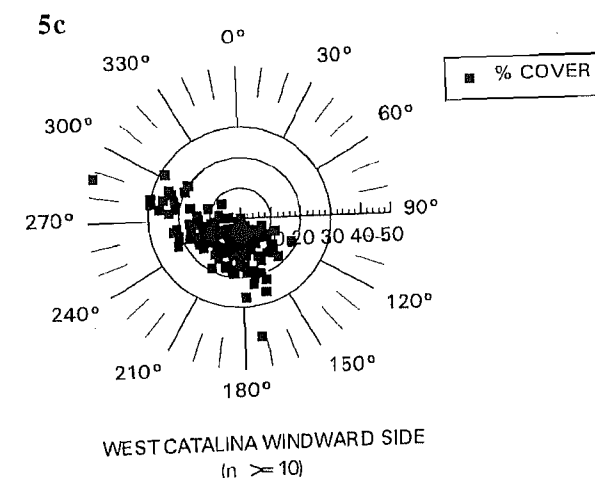


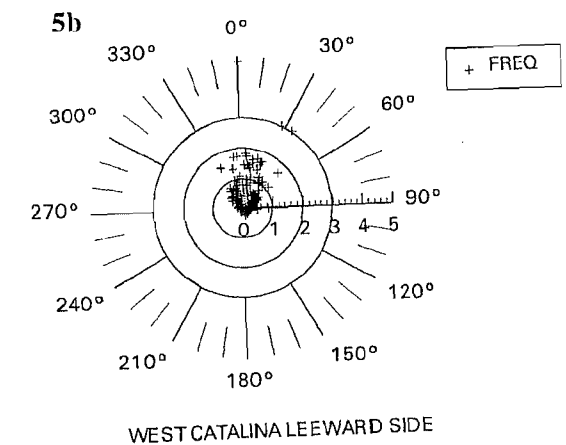
Figure 4. Percent kelp cover as a function of slope (in degrees) for the leeward and windward sides of the west end of Santa Catalina Island.



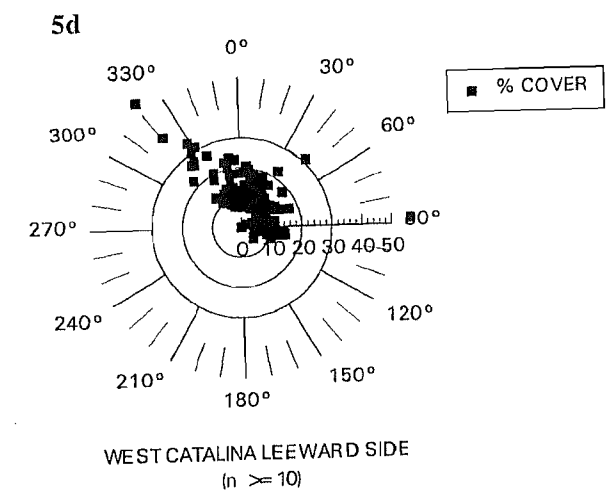
WEST CATALINA WINDWARD SIDE



WEST CATALINA WINDWARD SIDE
($n \geq 10$)



WEST CATALINA LEEWARD SIDE



WEST CATALINA LEEWARD SIDE
($n \geq 10$)

Figure 5. Kelp frequency (percent) and percent kelp cover as functions of aspect (in degrees) for the windward and leeward sides of the west end of Santa Catalina Island.

Table 3. Statistics for depth, aspect, slope, surface irradiance and bottom irradiance data extracted from west windward and leeward regions of Santa Catalina Island (number of pixels [N], average [μ], standard deviation [σ], minimum [min] and maximum [max]).

	N	μ_{depth}	σ_{depth}	min _{depth}	max _{depth}
Depth (in feet)					
West windward kelp	1,432	23.17	18.14	0	79
West windward substrate	13,138	55.61	35.30	0	123
West leeward kelp	1,081	38.06	23.06	2	137
West leeward substrate	8,713	56.50	35.08	0	133
Aspect (in degrees)					
West windward kelp	1,432	217	44	0	319
West windward substrate	13,138	215	42	0	337
West leeward kelp	1,081	17	37	0	358
West leeward substrate	8,713	17	43	0	359
Slope (in degrees)					
West windward kelp	1,432	5.76	2.87	0.44	19.35
West windward substrate	13,138	6.05	3.65	0.00	27.07
West leeward kelp	1,081	7.48	3.61	1.95	24.89
West leeward substrate	8,713	7.57	4.14	0.00	30.91
Surface irradiance (LI1)					
West windward kelp	1,432	40.28	2.66	33	64
West windward substrate	13,138	39.95	2.16	22	72
West leeward kelp	1,081	35.92	1.51	24	41
West leeward substrate	8,713	35.61	2.12	8	49
Bottom irradiance (LI2)					
West windward kelp	1,432	15.50	11.15	0.38	64.00
West windward substrate	13,138	7.24	10.70	0.03	61.41
West leeward kelp	1,081	12.34	6.64	0.39	36.46
West leeward substrate	8,713	9.57	9.30	0.41	40.20

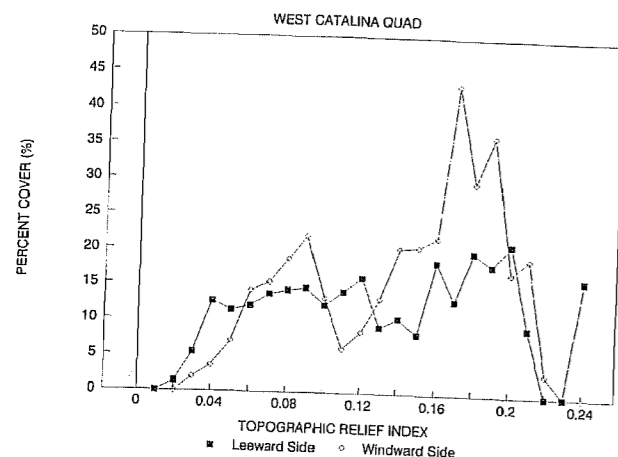


Figure 6. Percent kelp cover as a function of topographic relief index from 10 x 10 filter of aspect values for the leeward and windward sides of the west end of Santa Catalina Island.

extracted from the respective bathymetric zones, yet the ranges (min_{LI1} to max_{LI1}) were noticeably different. As expected, the mean LI1 value for the leeward side is significantly lower ($p < 0.001$, $z = 52.091$) than on the windward side, indicating lower surface irradiance levels in the afternoon (Fig. 7). The maximum windward value (LI1 = 40.28) falls near the low end of its range (33–64) while the maximum leeward value (LI1 = 35.92) is near the upper end of its range (24–41). Percent cover (Fig. 8) shows even greater separation with leeward peaks at 30–40 vs 45–60 on the windward side.

Mean values (μ_{LI2}) for ocean floor irradiance were similar on the windward (15.50) and leeward (12.34)

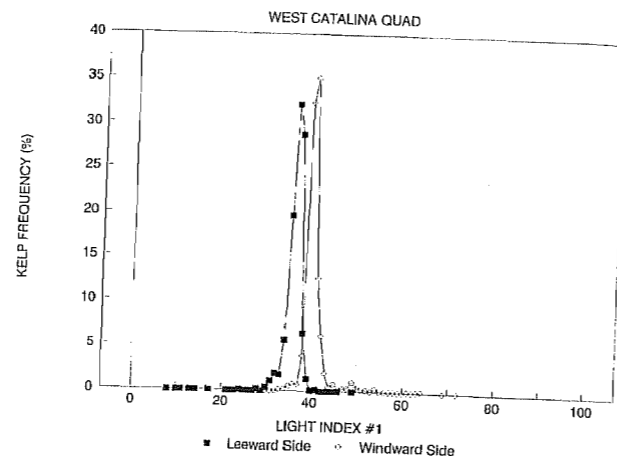


Figure 7. Kelp frequency (percent) as a function of the surface irradiance index (LI1) for the leeward and windward sides of the west end of the Santa Catalina Island.

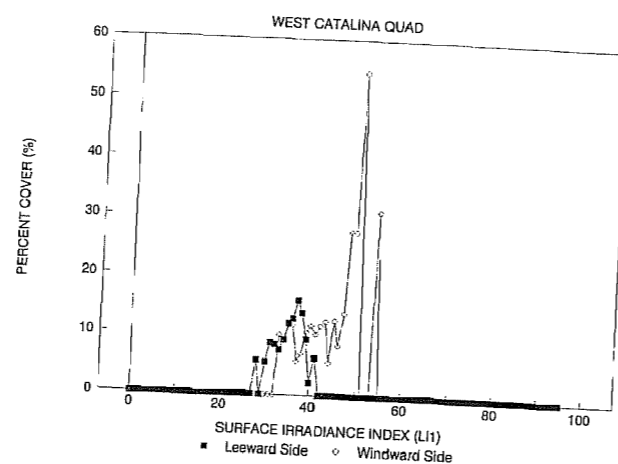


Figure 8. Percent kelp cover as a function of the surface irradiance index (LI1) for the leeward and windward sides of the west end of Santa Catalina Island.

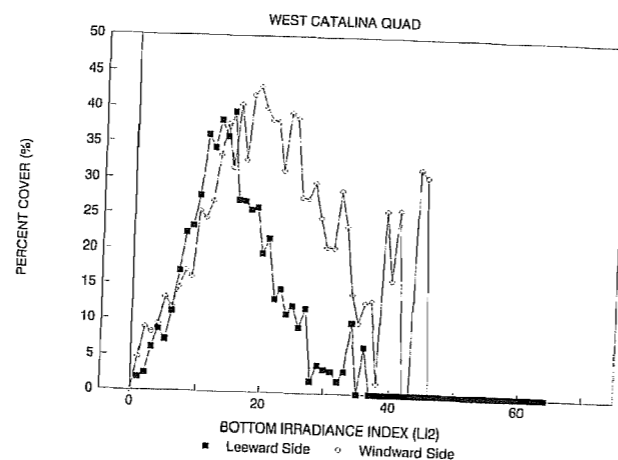


Figure 9. Percent kelp cover as a function of the bottom irradiance index (LI2) for the leeward and windward sides of the west end of Santa Catalina Island.

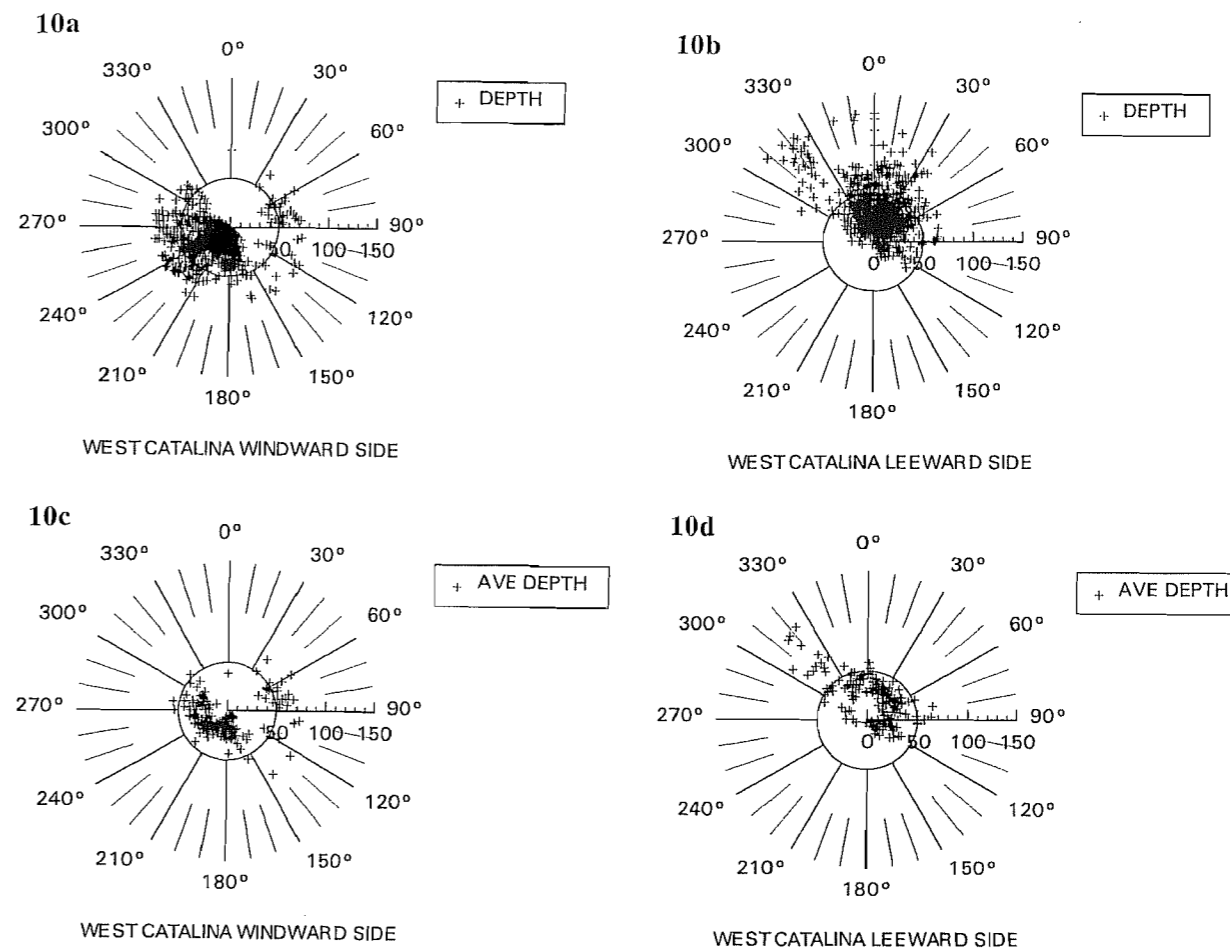


Figure 10. Depth and average depth (in feet) as functions of aspect (in degrees) for the windward and leeward sides of the west end of Santa Catalina Island.

sides, but the standard deviation (σ_{LI2}) and range (min_{LI2} to max_{LI2}) was higher on the windward side. Percent cover plotted against LI2 (Fig. 9) show the leeward side peaking at 10–14 and the windward at significantly higher values of 13–24 ($p < 0.001$, $z = 8.827$).

Multivariate analyses for west end data

To help explain the above results, some initial multivariate analysis was undertaken. Polar plots of depth, and average depth, against aspect (Fig. 10) identified anomalies in the data. Average depths on the windward side were generally less than 30–50 ft for aspects of about 150–315°, but noticeably deeper (40–80 ft) for aspects of 30–100°. Leeward side values averaged less than 40–50 ft at aspects of 330–150°, but 50–120 ft at aspects of 300–330°.

Polar plots of average slope against aspect reveal kelp is generally limited to average slopes $\leq 10^\circ$ on both sides. Windward side aspect values noted as having anomalously high average depths had only slightly higher average slopes, suggesting the deeper depths were not a result of increased slope. Anomalously high slope values ($\geq 10^\circ$) on

the windward side around 180°, 225°, and 270° did not correspond to exposures with abnormally deeper depths. Higher average slope values at 300–330° on the leeward side did correspond to aspects that had higher average depths, suggesting these depth anomalies may result from steeper submarine slope. However, there were also slope anomalies around aspects of 0°, 45°, and 60–90° that do not correspond to anomalous average depth values.

Discussion

Limitations of the GIS model

All data presented in this paper are derived from the GIS and are not field measured data. Therefore, any results must be viewed in terms of the limitations and any associated error imposed by this model.

Mature *Macrocystis pyrifera* may reach lengths of 200 ft from holdfast to the tip of the longest frond, with half floating near the surface as canopy (Neushul Mariculture Inc. 1981; North 1991). The kelp distribution map used in this study is based on kelp canopy, not hold-

fast attachment. A fully extended canopy subjected to differential current, swell or wind on the 2 coasts, could extend 1–2 pixels (66–131 ft) horizontally from the point of attachment.

The “quantization effect” due to spatial resolution may introduce error given the narrow vertical bathymetric range of *Macrocystis*, and steep submarine slopes, off the island. Such error decreases with better registration, shallower slopes, and higher spatial resolution. All data layers were carefully registered using ground control points, but a registration error of only a single pixel could shift depths 8 ft on opposite sides of the island, given the extracted values for nearshore slope (about 7°).

To evaluate error associated with spatial resolution, a subregion around Arrow Point that offered wide ranges in aspect was extracted. A new digital bathymetric model (DBM) and submarine aspect layer were created at 5-m resolution. Two kelp beds on either side of Arrow Point were selected and data extracted for each from both resolutions. Differences in mean depth and mean aspect for the 2 beds at 5- and 20-m resolutions showed no significant difference ($z = 0.004$ and 1.526 for mean depth, $z = 0.530$ and 0.230 for mean aspect) due to spatial resolution. The area of bed 1 was 2.7% less, and that of bed 2 was 2.6% more, at 5-m vs 20-m resolution. The beds had different shapes suggesting canopy configuration plays a role in determining the effect of varying spatial resolution on area estimates.

General characteristics of Santa Catalina Island kelp beds

Differences in total area, average area per region, and average area per bed between the 7 geographic regions may be due to differences in turbidity, in nutrient regime due to the effect of windshadowing on upwelling or reductions in light regime due to hillshading.

In the absence of a suitable substrate map, percent cover values may yield information about the nature of the bottom substrate in each region. The west leeward (12.40%) and windward (10.90%) regions exhibited the highest percent cover while the east leeward (3.76%) and north leeward (4.29%) had the lowest. These differences may indicate a higher proportion of rocky substrate in the west end subtidal, and of sandy bottom on the north and east leeward, consistent with personal field observations.

Differences in depth between the windward and leeward sides appear an important finding of this study. The maximum depth (μ_{depth}) values decrease from northwest to southeast along both the windward (79, 65, 53, 48 ft) and leeward (137, 118, 100 ft) sides. The differences between windward and leeward sides for each quad are greater than might be expected due to “quantization error” or poor registration.

The original hypothesis proposed that beds on the exposed outer coasts would be at deeper depths due to storm exposure, so the 4 windward regions would have deeper average depths (μ_{depth}) than the 3 leeward coasts. The shallower observed μ_{depth} values on the windward

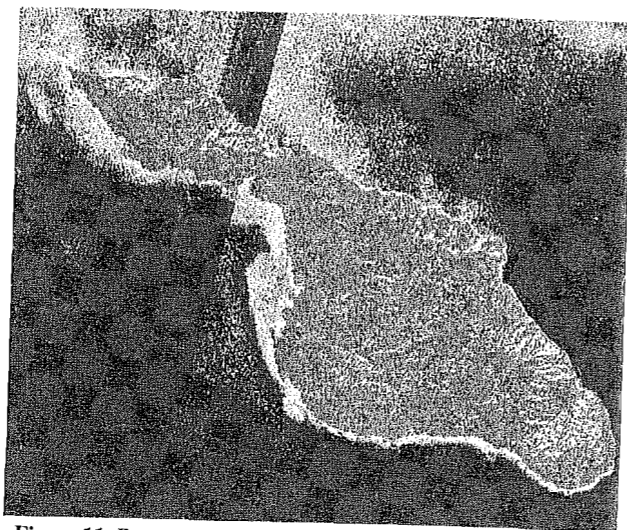


Figure 11. Processed spot satellite image in the visible red (XS2) band acquired 15 March, 1990, showing regions of high reflectance on the windward coasts indicative of higher turbidity.

coasts may indicate higher turbidity, forcing *Macrocystis* into shallower water where irradiance values would be higher. A SPOT satellite image of Santa Catalina Island dated 15 March 1990, provided some ancillary information. In the XS-2 (610–680 nm, visible red) band, regions of uniformly higher reflectance were observed in the waters off the windward side of the island (Fig. 11). These values were attributed to higher turbidity rather than phytoplankton abundance because the wavelengths represent chlorophyll absorption regions (Lobban et al. 1985).

The shallow μ_{depth} values on the southern and eastern windward coasts also suggest higher turbidity in regions with sandy bottom exposed to winter and southern storms, increasing the probability of re-suspension. North (1991) stated there is generally less turbidity observed off high relief rocky coasts than low relief coasts with long stretches of sedimentary bottom.

Increased turbidity could also result from higher sediment input from terrestrial stream drainages. Analysis of weather records (National Climatic Data Center 1990; Times Mirror Corporation 1990) for the 5 days prior to satellite acquisition indicated only 0.08 in. of measurable precipitation. High wind velocities (15–25 knots from the W-NW) and regional wave heights near peak for the month (Scripps Institute of Oceanography 1990) suggest re-suspension of bottom sediments due to exposure and shallower bottom slopes as a cause of the observed turbidity. Depth values on the windward side are comparable to those on exposed, mainland coasts while the leeward side shows the deeper depths “characteristic” of the clearer island waters.

Such re-suspension of sediment may also increase nutrient levels in the upper water column. Zimmerman (1983) found the seasonal cycle of nutrient available in Santa Catalina Island waters was consistent with storm-

induced vertical mixing during winter months. Higher average bed sizes and area per mile of shoreline on the windward sides may reflect higher *Macrocystis* productivity due to nutrient availability. Potential corroboration comes from a study of chlorophyll concentration off the island on 6 March 1979, using Coastal Zone Color Scanner (CZCS) satellite imagery (Smith et al. 1982). Values off the west end of the island ($0.4\text{--}1.5\text{ mg/m}^3$) consistently declined along the windward side to the east end ($0.2\text{--}0.4$) with nearshore values on the leeward side also dropping abruptly from Long Point (0.4) to the east end (0.1). This pattern was also evident in later CZCS images of Catalina studied by Palaez and McGowan (1986). Nutrient levels are also affected by upwelling, which may explain the high abundance of kelp from Arrow Point to Blue Cavern Point on Santa Catalina’s west end leeward coast (State Water Resources Control Board 1979).

Data characteristics for west end kelp beds

On the mainland, *M. pyrifera* beds off San Onofre and San Diego were located between 150 and 2,500 m from shore (Augenstein et al. 1991; Deysher 1993). Beds off the steeper island coasts may be closer to shore, and the island’s topography and geography may exert a greater influence. Differences in mean distance (μ_{dis}) from shoreline may reflect the influence of hillshading on the leeward coasts forcing a horizontal displacement of kelp away from the coastline. This interpretation is also supported by the results from the irradiance index studies.

It was postulated that for protection from the prevailing NW-WNW winter storms, kelp beds on the windward side would favor deeper water, gentler slopes or shorelines with sheltered aspects. Instead, kelp on the windward side occupied consistently shallower depths than on the protected leeward side. The biological significance appears to be in the trade-off between increased irradiance levels necessitated by the higher turbidity in these waters and increased exposure to wave and surge action from storms.

North (1991) stated that the outer edges of mainland coastal kelp beds usually lie at depths of 60 ft or less except where the water may be very clear (such as Santa Catalina) allowing deeper light penetration. This limit also coincides with the surge zone defined by Quast (1971). Kelp on the windward coastlines is almost entirely within this zone subject to more frequent disturbance by storm and swell, suggest higher mortality rates and turnover typical of shallower depths (Dayton and Tegner 1984; Seymour et al. 1989).

The shallower submarine slope on the windward side of the west end, similar to the adjacent mainland, reflects differences in submarine topography resulting from the uplift of the island’s land mass. As a function of slope, percent cover is highest on shallower slopes (less than 5–6°) on the windward side and on steeper leeward side slopes where wave action may be less pronounced. Incoming

waves and surge respond differently to shallow vs steeply sloping bottom topography, and energy may be dissipated more gradually resulting in less destructive water motion at comparable depths.

Storms and surge may impinge upon the island from several directions dependent on season. Winter storms are largely from the NW or WNW with average peak wave heights of 7–9 ft (State Water Resources Control Board 1981). During El Niño years, the swell may be almost directly from the west (Seymour et al. 1984). During the summer months, southern swells may affect the island’s windward coast. Although generally protected from these storms, the leeward side is impacted by Northeast and Santa Ana storms.

The direction of exposure due to aspect is important in determining the size, viability and other characteristics of kelp beds (Hodder and Mel 1978; Harger 1983; Reed and Foster 1984; North 1991). The diversity of storm exposures on Santa Catalina offers a wide range of potential disturbance regimes. Aspect values extracted for the west end are generally consistent with the NW to SE orientation of the island’s main ridge. However, anomalous aspects with high percent cover suggest kelp may be more abundant than expected in potentially sheltered locations that do not receive the full effect of winter or Santa Ana storms.

Kelp beds are directly linked to bottom relief, with areas of higher topographic diversity generally supporting more abundant kelp (Harger 1983). In this study, the relatively uniform distribution relative to the topographic diversity indices on the leeward side suggests substrate occupation without regard to bottom relief. On the windward side, higher percent cover in areas of mid- to high relief suggests a preference for such areas in the face of greater exposure to storms. There were no clear trends using depth-based relief indices, suggesting aspect diversity may be a better indicator of bottom relief. Diversity in depth values may simply indicate regions of steeper slope rather than areas of higher relief.

It has been well-documented that topography affects the distribution of terrestrial plants (Holland and Steyn 1975; Holland et al. 1977; Kirkpatrick and Hutchinson 1980). In regions of rugged relief such as Santa Catalina, the landscape is often a visual mosaic due to the influence of aspect and slope on the interception of solar radiation. Hillshading may also explain differences in kelp distribution between the windward and leeward sides.

The island’s main ridge reaches elevations of about 2,000 ft with generally steeper slopes on the leeward coasts. Afternoon sunlight intercepted by this ridge often creates lower surface irradiance in nearshore leeward waters than on the windward side. Values for LI1 indicate kelp on the shaded leeward side occupies regions of higher than average surface irradiance, while on the windward side kelp is more common at lower surface irradiances. The greater average distance from the coast on the leeward side also supports this interpretation. The uniformly deep-

er depth values for the leeward side may reflect the need to intercept more surface light for photosynthesis. The uniformly larger kelp bed areas on the windward side may be due in part to higher light levels and greater photosynthetic potential.

Macrocystis gametophyte and young sporophyte stages must recruit and grow at the bottom, a relatively high nutrient environment where irradiance may be limiting, whereas the adult plants have most of their tissue in the upper water column where irradiance is high and nutrients may be low (Dean and Jacobsen 1983; Dean and Jacobsen 1990). *Macrocystis* must establish in the first regime before it can grow large enough to benefit from near-surface conditions.

The ocean floor irradiance (LI2) values, incorporating hillshading and light extinction through the water column, better model light levels near the bottom. Light extinction by water molecules, suspended sediments, and phytoplankton affects the depth penetration in different Jerlov water types. The depth of the 1% surface irradiance value in open ocean water may vary from about 85 m (Jerlov Type I) to 25 m (Type III) while in coastal waters penetration depths range from about 22 m in Type 1 to 5 m in Type 9 waters (Holmes 1957). The mean LI2 values suggest that the deeper depths occupied by kelp on the less turbid leeward side have bottom irradiances comparable to shallower depths on the more turbid windward side.

The terms windward and leeward suggest the island's main ridge intercepts more than sunlight. Island topography may also affect upwelling and nutrient regimes through the establishment of windshadows on the leeward side creating more stable thermoclines with less vertical mixing. This may be an overlooked factor in explaining kelp bed distribution on Santa Catalina. The east leeward region is strongly influenced by the 1,400- to 1,500-ft main ridge. Windshadows extending out 1–2 mi from the coast were experienced off Toyon Bay (J. McAleer 1974, pers. comm.). Even where canyons allow wind to funnel through to the leeward side, the bays at their mouths often have sandy substrate inappropriate for kelp attachment. A combination of wind shadowing, hillshading and a higher percentage of sandy substrate in the east region leeward may help explain the low values for kelp in this area.

Multivariate analysis

The average depth values at aspects of 150–315° correspond to "normal" storm exposures on the windward side of the island. Deeper values at aspects of 30–100° indicate the relatively few beds at these aspects were in deeper, potentially clearer water perhaps in the lee of promontories sheltered from the prevailing winter NW and WNW storms. Anomalously deeper average depths on the leeward side coincide with locations sheltered from the NE storms and Santa Ana's impacting that side.

Summary

Santa Catalina Island's geographic orientation, coastal configuration and topography, both terrestrial and submarine, offer a wider variety of physical habitats for *Macrocystis pyrifera* than would be found on the corresponding mainland coast. The often complex coastline creates a wider range of aspect angles and exposure to storms due to the presence of both windward and leeward island coasts. Analysis of *Macrocystis pyrifera* distribution relative to aspect angle indicates higher-than-expected percent cover at values representing locations with greater protection from prevailing storm directions on each coast.

The shallower submarine slopes and direct exposure to prevailing wind, swell and storm patterns on the windward side generate higher levels of turbidity and increased light extinction in the nearshore waters, influencing the depth distribution of kelp around the island.

The high degree of topographic relief in both terrestrial and subtidal environments also affects kelp distribution. Kelp occurs more frequently in regions of greater bottom relief on the exposed windward side, while on the more protected leeward side there is no recognizable pattern.

Hillshading by the terrestrial topography reduces light values in the nearshore waters of some regions on the leeward side. Kelp distribution there favors regions with higher-than-average surface and bottom irradiance values while on the windward side the distribution is more uniform with respect to irradiance. Wind shadowing due to similar topographic effects may alter nutrient availability and temperature by reducing vertical mixing in nearshore environments on the leeward side.

The results from this initial study suggest the need to extend the analysis from the west end into the other geographic regions of the island. Refinement of current irradiance indices may assist in evaluating the effects of seasonal and diurnal changes in irradiance due to topography. Other existing kelp distribution maps will be consolidated to identify the most persistent beds, and an analysis of the factors responsible may help explain the observed distribution.

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Literature Cited

- Augenstein, E., et al. 1991. Evaluation of SPOT HRV-XS data for kelp resource inventories. *Photogrammetric Engineering and Remote Sensing* 57(5):501–09.
- Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Niño and patch stability in a southern California kelp community. *Science* 224:283–285.
- Dean, T. A., and F. R. Jacobsen. 1983. Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. *Marine Biology* 83:301–311.
- Dean, T. A., and F. R. Jacobsen. 1990. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982–1984 "El Niño" in southern California. *Marine Biology* 90:597–601.
- Deysher, L. E. 1993. Evaluation of remote sensing techniques for monitoring giant kelp populations. *Hydrobiologia* 260/261:307–312.
- Foster, M., and D. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.2). 152 pp.
- Harger, B. W. 1983. A historical overview of kelp in southern California. In: *The Effects of Waste Disposal on Kelp Communities*, California Sea Grant Symposium (edited by W. Bascom), pp. 70–83.
- Hodder, D., and M. Mel. 1978. Kelp survey of the Southern California Bight. Esca-Tech Corporation and Science Applications, Inc. Technical Report Volume III, Report 1.4 to the Bureau of Land Management (Year II SCOCs Program), Contract No. AA550-CT6-40, La Jolla.
- Holland, P. G., and D. G. Steyn. 1975. Vegetation responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography* 2:179–183.
- Holland, P. G., D. G. Steyn, and R. F. Fuggle. 1977. Habitat occupation by *Aloe ferox* Mill. (Liliaceae) in relation to topographic variations in direct beam solar radiation income. *Journal of Biogeography* 7:61–72.
- Holmes, R. W. 1957. Solar radiation, submarine daylight and photosynthesis. In: *Treatise on Marine Ecology and Paleoecology*, Volume 1, Ecology (edited by J. W. Hedgpeth), Geological Society of America, Memoir 67, pp. 109–128.
- Kirk, J. 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, New York. 401 pp.
- Kirkpatrick, J. B., and C. F. Hutchinson. 1980. The environmental relationships of Californian coastal sage scrub and some of its component communities and species. *Journal of Biogeography* 7:23–38.
- Lobban, C. S., P. J. Harrison, and M. J. Duncan. 1985. The physiological ecology of seaweeds. Cambridge University Press, New York. 242 pp.
- Meaille, R., and L. Wald. 1990. A geographic information system for some Mediterranean benthic communities. *International Journal of Geographic Information Systems* 4(1):79–86.
- Mel, M. 1977. Aerial remote sensing of subtidal vegetation in southern California. Master's Thesis. University of California at Los Angeles.
- National Climatic Data Center. 1990. NOAA climatological data: California, March, 1990. NOAA National Climatic Data Center Vol. 94, No. 3.
- Neushul Mariculture, Inc. 1981. Historical review of kelp beds in the Southern California Bight. Southern California Edison Company Research Report Series Number 81-RD-98. 74 pp.
- North, W. J. 1968. Foreword. In: *Utilization of Kelp-bed Resources in Southern California*. Department of Fish and Game Fish Bulletin 139, pp. 7–12.
- North, W. J. 1971. Introduction and background. In: *The Biology of Giant Kelp Beds (Macrocystis) in California* (edited by W. J. North), Beihefte Zur Nova Hedwigia 32:1–97.
- North, W. J. 1991. The kelp beds of San Diego and Orange counties. Published by Wheeler J. North, 15 March 1991. 270 pp.
- Palaez, J., and J. McGowan. 1986. Phytoplankton pigment patterns in the California Current as determined by satellite. *Limnology and Oceanography* 31(5):927–950.
- Quast, J. C. 1971. Some physical aspects of the inshore environment particularly as it affects kelp bed fishes. In: *The Biology of Giant Kelp Beds (Macrocystis) in California* (edited by W. J. North), Beihefte Zur Nova Hedwigia 32:228–240.
- Ramus, J. 1983. A physiological test of the theory of complementary chromatic adaptation. II. Brown, green and red seaweeds. *Journal of Phycology* 19:173–178.
- Reed, D. C., and M. S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65(3):937–948.
- Scripps Institution of Oceanography. 1990. Coastal Data Information Program Monthly Report #169, March, 1990, SIO REF 90–14. University of California San Diego.
- Seymour, R., R. Strange, R. Cayan, and R. Nathan. 1984. Influence of El Niños on California's wave climate. In: *Proceedings of the 19th Coastal Engineering Conference*, American Society for Coastal Engineers, September 3–7, 1984, Houston TX 1:577–592.
- Seymour, R., M. Tegner, P. Dayton, and P. Parnell. 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuarine, Coastal and Shelf Science* 28:277–292.
- Shivji, M. 1985. Interactive effects of light and nitrogen on growth and chemical composition of juvenile *Macrocystis pyrifera* (L.) C. Ag. (Phaeophyta) sporophytes. *Journal of Experimental Marine Biology and Ecology* 89:81–96.
- Smith, R. C., R. W. Eppley, and K. S. Baker. 1982. Correlation of primary production as measured aboard ship in southern California coastal waters and as estimated from satellite chlorophyll images. *Marine Biology* 66:281–288.

- State Water Resources Control Board. 1979. California marine waters: areas of special biological significance, reconnaissance survey report, Santa Catalina Island-Subarea I, Los Angeles County. Water Quality Monitoring Report No. 79-6. State Water Resources Control Board, Division of Planning and Research, Surveillance and Monitoring Section.
- State Water Resources Control Board. 1981. California marine waters: areas of special biological significance, reconnaissance survey report, Santa Catalina Island-Subareas II and IV, Los Angeles County. Water Quality Monitoring Report October, 1981. State Water Resources Control Board, Division of Planning and Research, Surveillance and Monitoring Section.
- Times Mirror Corporation. 1990. Los Angeles Times. Issues dated 10, 11, 12, 13, 14 and 15 March 1990. Weather section, pp. B-2, B-4, B-5.

- Walsh, J., D. Dieterle, and W. Esaias. 1987. Satellite detection of phytoplankton export from the mid-Atlantic Bight during the 1979 spring bloom. *Deep Sea Research* 34(56):675-703.
- Welch, R., and M. M. Remillard. 1988. Remote sensing and geographic information system techniques for aquatic resource evaluation. *Photogrammetric Engineering and Remote Sensing* 54(2):177-85.
- Zimmerman, R. C. 1983. Seasonal patterns in productivity of a giant kelp (*Macrocystis pyrifera*) forest: the effect of nutrient availability. Ph.D. dissertation, University of Southern California. 182 pp.

Assessment of Abalone Resources at the Channel Islands

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Abstract. Commercial and recreational landings data for 1983 to 1992 from the Channel Islands were examined to determine the resource condition of 5 abalones: black (*Haliotis cracherodii*), red (*H. rufescens*), green (*H. fulgens*), pink (*H. corrugata*), and white (*H. sorenseni*). Additionally, the results of fishery-independent intertidal and subtidal surveys were compared with landing data. These 3 databases yielded similar information about abalone resources at the Channel Islands, but fishery-independent data provided a more complete understanding of resource conditions. The black abalone has disappeared from most of the islands, a result of withering syndrome mortality. The red abalone has increased recently in commercial fishery and field transect data, but landings are still far below past levels. Green, and pink abalones are declining in the commercial and recreational fisheries, while available data suggest that the white abalone is now rare.

Keywords: California; Channel Islands; red abalone; black abalone; green abalone; pink abalone; white abalone; Assessment; Marine Fisheries Statistics.

Introduction

Abalones are the subject of a valuable commercial and recreational fishery in California. Historically, 5 species comprised the California commercial and recreational abalone fishery: black abalone (*Haliotis cracherodii*), red abalone (*H. rufescens*), green abalone (*H. fulgens*), pink abalone (*H. corrugata*), and white abalone (*H. sorenseni*). Each is found in overlapping but generally distinctive habitats related to prevalent seawater temperatures and depth. While the ranges and local distribution of these large marine gastropods vary along the California coast, all occur around the California Channel Islands.

Two of these abalones occur throughout coastal California. The black abalone lives in rocky intertidal areas of the mainland and throughout the Channel Islands. The red abalone occur intertidally to 33 m along the mainland and along coasts of San Miguel, San Nicolas, and northern Santa Rosa islands, which are

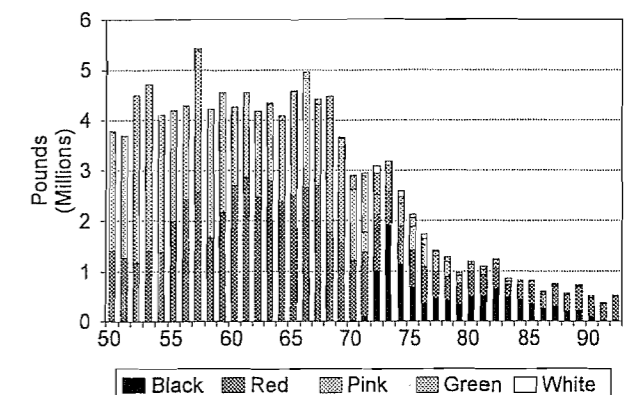


Figure 1. California commercial abalone landings from 1950 to 1992. (Data from CDFG Marine Fisheries Statistical Unit).

under the influence of cooler northern waters. Three species occur only south of Point Conception. The green abalone is a shallow subtidal species; the pink abalone occurs from about 7- to 40-m depths; and the white abalone is found from 20 to 60 m on rocky reefs. These species occur most commonly at Santa Catalina, San Clemente, Santa Barbara, Anacapa, Santa Cruz, and southern Santa Rosa islands, areas influenced by warm temperate waters.

The commercial fishery landed 4 million pounds annually from about 1952 to 1968 (Fig. 1). Since then, landings have dropped; about half a million pounds were landed in 1992. The once large fishery was displaced into southern California waters as sea otters recovered parts of their former range in central California (Hardy et al. 1982). As mainland stocks suffered from increasing impacts of a growing human population, such as habitat degradation and heavy harvesting, divers ranged farther to find abalone. Once protected by their remoteness, the Channel Islands abalone stocks became readily accessible (Table 1) with the development of fast fishing boats and improved diving equipment.

The availability of scuba diving equipment stimulated the recreational diving industry and provided the public access to deep water marine resources, including abalones. Large commercial passenger recreational dive