FROM THE MOUNTAINS TO THE SEA: SUNLIGHT, ISLAND TOPOGRAPHY AND GIANT KELP

WILLIAM W. BUSHING

StarThrower Educational Multimedia, P.O. Box 849, Avalon, CA 90704; bushing@post.harvard.edu

ABSTRACT—This study utilized a GIS to investigate the influence of terrestrial and submarine topography on the light regime and distribution of giant kelp (*Macrocystis pyrifera*) in the waters around Santa Catalina Island. The island's northwest-to-southeast orientation, rugged topography and highly dissected coastline offer a wide range of micro-habitats with respect to the nearshore light regime. GIS data layers included a kelp distribution map, a digital terrain model, digital bathymetric model, submarine slope, submarine aspect, and two solar insolation models. A model of the relative light levels at the ocean surface incorporated the diurnal path of the sun, and the effect of hillshading on nearshore waters due to the adjacent island topography. Insolation on the sea floor estimated light extinction through the water column utilizing the bathymetric data. Kelp bed distribution was evaluated statistically relative to both insolation models. Definite patterns in kelp distribution were observed relative to surface and bottom insolation, and were especially pronounced during the peak growing season. On the leeward side, shaded from afternoon sun by the island's 450–640 m main ridge, kelp favored the higher light environments around coastal features such as points, offshore reefs, and regions with greater bottom relief. Kelp on the more exposed, windward side of the island favored locations sheltered from the prevailing winter storms despite lower light levels in these sites. Using such methods, light as a limiting factor for giant kelp can now be incorporated with other variables into habitat suitability models and used to consider appropriate regions for designation as marine reserves.

Keywords: giant kelp, GIS, hillshading, insolation, kelp, Macrocystis, Santa Catalina Island

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 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). Dean and Jacobsen (1984) felt irradiance was likely a critical factor influencing growth in *Macrocystis*, especially during winter. Low light levels at specific locations or times may restrict giant kelp distribution by inhibiting growth or sporophyte production (Dean and Deysher 1983). Canopy-forming kelps like *Macrocystis* may also be light-limited during periods of fog or overcast (North et al. 1986, Jackson 1987).

The ecological effects of varying daylength on marine plants due to season or latitude are well-known (see North 1971, Kirk 1983, Jackson 1987, Lüning and Kadel 1993). Site-specific slope-aspect values and hillshading also alter the effective photosynthetic daylength, creating marked spatial heterogeneity in the nearshore marine environment adjacent to high relief landmasses. The seasonal (Kirkpatrick et al. 1988) or diurnal (Miklos et al. 1991) timing of peak insolation in such regions may influence physiological or reproductive functions in a species. Santa Catalina Island offers an excellent opportunity for investigation of such influences. The island is oriented in a northwest-to-southeast direction, has an irregular 87-km coastline, a high (450–600-m) central ridge, rugged topography and varying water depths. These factors result in a wide range of microhabitats with respect to light between the southwest-facing windward side and the northeast-facing leeward side. Afternoon sunlight intercepted by the island's main ridge reduces irradiance in the nearshore waters on the leeward side, reducing the effective photosynthetic daylength. The island's steep offshore slope and narrow shelf force kelp closer to shore where it may be affected more by these variations in the light regime.

Solar radiation is an important ecological parameter for organisms (Brock 1981), especially those that photosynthesize. Terrestrial studies indicate the spatial patterns of net surface radiation and its variability are important in understanding the growth and distribution of individual species (Pearcy 1983), the distribution of plant and animal species within a community (Weiss et al. 1988, Murphy and Weiss 1988), or ecosystem processes such as energy fixation and water balances (Hetrick et al. 1993a, 1993b). Significant variation in the light regime exists in terrestrial regions with high topographic relief due to variations in illumination angle and shading (Dozier and Frew 1990). The importance of slope, aspect and elevation to terrestrial plant distributions has been noted by researchers (Hicks and Franks 1984). The effect of topographic shading is less well known (Hetrick et al. 1993b), but investigations of this factor are becoming more common (Weiss et al. 1988, Murphy and Weiss 1988, Davis and Dozier 1990).

Light has greater variability in aquatic environments due to strong and selective absorption by water (Kirk 1983), differences in sediment loading and turbidity, bottom substrate type (Dean 1985), suspensoids (Kirk 1985), phytoplankton (Woods and Onken 1982, Pennock 1985), and by-products released from kelp (Lüning 1981). Thom and Albright (1990) concluded that solar energy was the principal factor controlling seasonal physiological changes in benthic plants. Yet, this important variable has seldom been measured over extended periods and large spatial scales in the nearshore marine environment (Kain 1982, Dean 1985). Johansson (1982) found differences in the species composition of freshwater algae between shaded and exposed locations and Seapy and Littler (1993) anecdotally mention the role of afternoon shading by steep sea cliffs on neighboring Santa Barbara Island.

Previous island-wide GIS studies by this author have revealed significant differences in kelp distribution around the island due to differing wave energy, turbidity, submarine topography, disturbance regimes, and other factors (Bushing 1994, 1995, 1996a, 1996b, 1997). Field measurements in these studies indicated terrestrial hillshading may reduce surface light levels by physiologically significant levels in the nearshore marine environment on the shaded leeward side. This study utilizes a computer-generated surface and bottom insolation model to investigate the influence of topographic shading (Fig. 1) on the distribution of giant kelp around the island. The extinction of light in the water column as a function of depth and regional turbidity is incorporated to model spatial variability in light on the ocean floor, and its potential influence on the young sporophytes and gametophytes. These models allow regional variability in light to be considered along with other spatial variables such as wave exposure, bottom substrate, and nutrient levels to better understand kelp distribution and persistence.

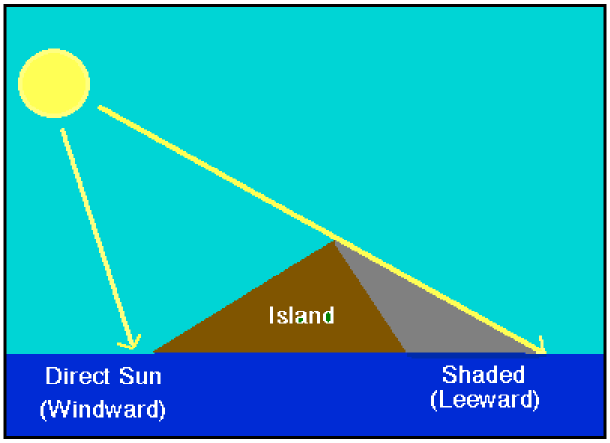

Figure 1. Illustration showing the effect of terrestrial hillshading on the surface waters of Santa Catalina Island.

METHODS

Creation of the Topographic GIS Data Layers and Overlay Masks

Raster GIS data layers required to address the hypotheses in this study included a kelp bed distribution map dated about 1980 provided by Southern California Edison, digital elevation (DEM) and bathymetric (DBM) models, submarine aspect, submarine slope, distance-from-shore, and solar insolation at 20-m resolution. The creation of

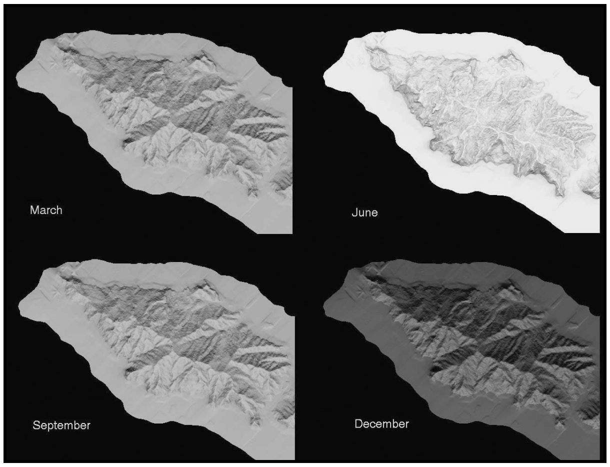

Figure 2. Insolation models of the West End of Santa Catalina Island for the months of March, June, September, and December. Brighter image values indicate higher insolation.

these data layers has been described previously (Bushing 1994, 1995, 1996a, 1997, 2000). The DEM and DBM were integrated to create a continuous topographic surface to model the influence of island topography on light at the ocean surface and floor. The distance-from-shore layer was created by generating the Euclidean distance of each cell from the nearest island coastline. Binary masks representing kelp distribution from the 1980 SCE survey were created for both leeward and windward coasts. The 20-fathom (~40-m) bathymetric contour was chosen to define the maximum expected depth limit for kelp. A second set of binary masks was created between this contour and the shoreline representing the potential habitat of kelp, referred to here as the photic shelf.

TOPQUAD Solar Insolation Model

GIS layers that modeled terrestrial hillshading and light extinction in the water column were required. The TOPQUAD module, developed by Dozier (1980) for integration into the IPW (Image Processing Workbench) software toolkit (Frew 1990), was chosen to generate these. It has been used extensively for modeling light environments in regions of high relief (Dozier et al. 1981, Davis and Dozier 1990).

For physiological or ecological studies only certain regions of the electromagnetic spectrum may be important (Brock 1981). For this study, only photosynthetically active radiation or PAR (400–700 nm) was used. Insolation was modeled for the 21st day of each month to create monthly intervals between solstices and equinoxes (Fig. 2). Similar methods were used by Weiss et al. (1988), Murphy and Weiss (1988) and Hetrick et al. (1993a). Monthly values were averaged in three month intervals to create seasonal images. For example, October, November and December were averaged to create a fall insolation composite. All twelve monthly values were averaged to create an annual model.

A bottom insolation model incorporating regional turbidity and light extinction was created. It assumes the deepest depth for *Macrocystis* occurs at a value of 1% of surface irradiance (PAR), the generally accepted limit of the photic zone (Lüning and Dring 1979, Lüning 1981, Kirk 1983). Relative turbidity was estimated by determining the maximum depth (d_{max}) at which kelp was found on the windward and leeward coasts. Insolation at the ocean floor was generated by multiplying the surface insolation value (I_s) in each cell by a light extinction equation based on Beer's Law (Gates 1980, Kirk 1983, Jackson 1987):

$$I_d = I_s * e\text{^} (-4.61*d/d_{max})$$

where bottom insolation (I_d) is the percent of surface insolation (I_s) at that cell's depth (d), and d_{max} is the maximum depth kelp was found in that region. Monthly, seasonal and annual bottom insolation models were created from the corresponding surface insolation models. Both the I_s and I_d indices assume clear skies.

Insolation as a Function of Aspect and Distance-from-shore

Insolation is strongly dependent on aspect (Holland and Steyn 1975). Bushing (1994, 1995) created kelp frequency distributions for 10° intervals of aspect. Aspects with kelp frequency values greater than 5% were designated typical aspects (0–60° and 330–360° on the leeward coast; 180–270° on the windward side) and are consistent with the island's geographic orientation. Aspects with frequency less than 5% were designated atypical. These atypical aspects represent values different from the prevailing coastal orientation on each side, and have been shown to have higher percent cover of kelp (Bushing 1994, 1996a). Polar graphs of mean surface and bottom insolation relative to aspect were prepared. The frequency distribution, percent cover, and mean values for both kelp and the photic shelf were also plotted as a function of 30° aspect intervals for each of the four seasonal, and the annual, surface and bottom insolation models.

To test the hypothesis that greater observed distances from shore for kelp along the leeward coast were a response to terrestrial hillshading, mean winter surface and bottom insolation values were graphed as a function of distance from shore in 25-m intervals. In a separate analysis, distance was treated as the dependent variable, and mean distance from shore was calculated for 10-unit intervals of annual surface insolation.

DATA ANALYSIS

Coincident data was extracted from the GIS layers for submarine aspect, depth, slope, distance-from-shore, and surface and bottom insolation using the kelp and photic shelf binary masks. These data were imported into Foxpro databases. Each record represented a single geographic location (raster cell) incorporating the associated data in separate fields allowing analysis on a cell-by-cell basis. Two important statistics were evaluated for each data layer. Kelp frequency refers to the percentage of total kelp raster cells along each coastline with a given data value or range (e.g., 5% of all kelp cells had surface insolation values of 150–160). Percent cover refers to the percent of the corresponding photic shelf raster cells covered by kelp for a given value of an environmental variable (e.g., 20% of all 8 m depths were covered by kelp).

Observed kelp distributions were compared against the expected values using the corresponding photic shelf distribution as a probability model (Johnson et al. 1988). Expected probabilities were calculated from the frequencies for the corresponding photic shelf region. Residual values were obtained by subtracting the observed values for kelp from these expected values, indicating parameter values which are preferred (+) or avoided (-). The null hypothesis is that the two distributions do not differ in a statistically significant way. If significant differences exist, topographic influences on light may play a role in effecting *Macrocystis* distribution. Additional statistical methods were based on those of Bishop (1983).

RESULTS

On the leeward coast, raster cells where kelp was present had significantly ($P < 0.050$) higher mean insolation values for the annual and four seasonal models than regions where kelp was not found. However, light levels on the windward side were significantly lower ($P < 0.001$) in all but the fall and winter models for cells with kelp. Kelp frequency relative to spring surface insolation index peaked at the upper end of the insolation range on both coasts (Fig. 3). On the leeward side, kelp frequency exceeded expected values towards the high end of the range while residual values peak at the lower end on the windward side. Kelp percent cover relative to spring surface insolation on the leeward side showed a peak at the upper end of its range, but windward kelp peaked at the lower end.

Kelp Distribution as a Function of Insolation and Aspect

Kelp frequency relative to aspect is dominated by the prevailing orientation on the windward (south-to-west) and leeward (north-northwest -to-northeast) coasts (Bushing 1996a). Only 17.8% of total kelp on the leeward side was found at atypical aspects differing from the prevailing coastal orientation while the value was substantially higher (27.3%) for the windward coast. Mean annual surface insolation (Fig. 4) on the leeward coast was greater at atypical than typical aspects, but lower on the windward side.

Kelp on both sides favored atypical aspects but for different reasons. On both coasts, atypical aspects often represent locations around coastal points, offshore reefs or other features where the irregularity of the coastline provides a wider range of exposures. For the shaded leeward coast protected from severe storm disturbance, surface and bottom insolation was significantly higher ($P <$ 0.050 or greater) at atypical aspects representing sunnier sites for the year, and most seasons except

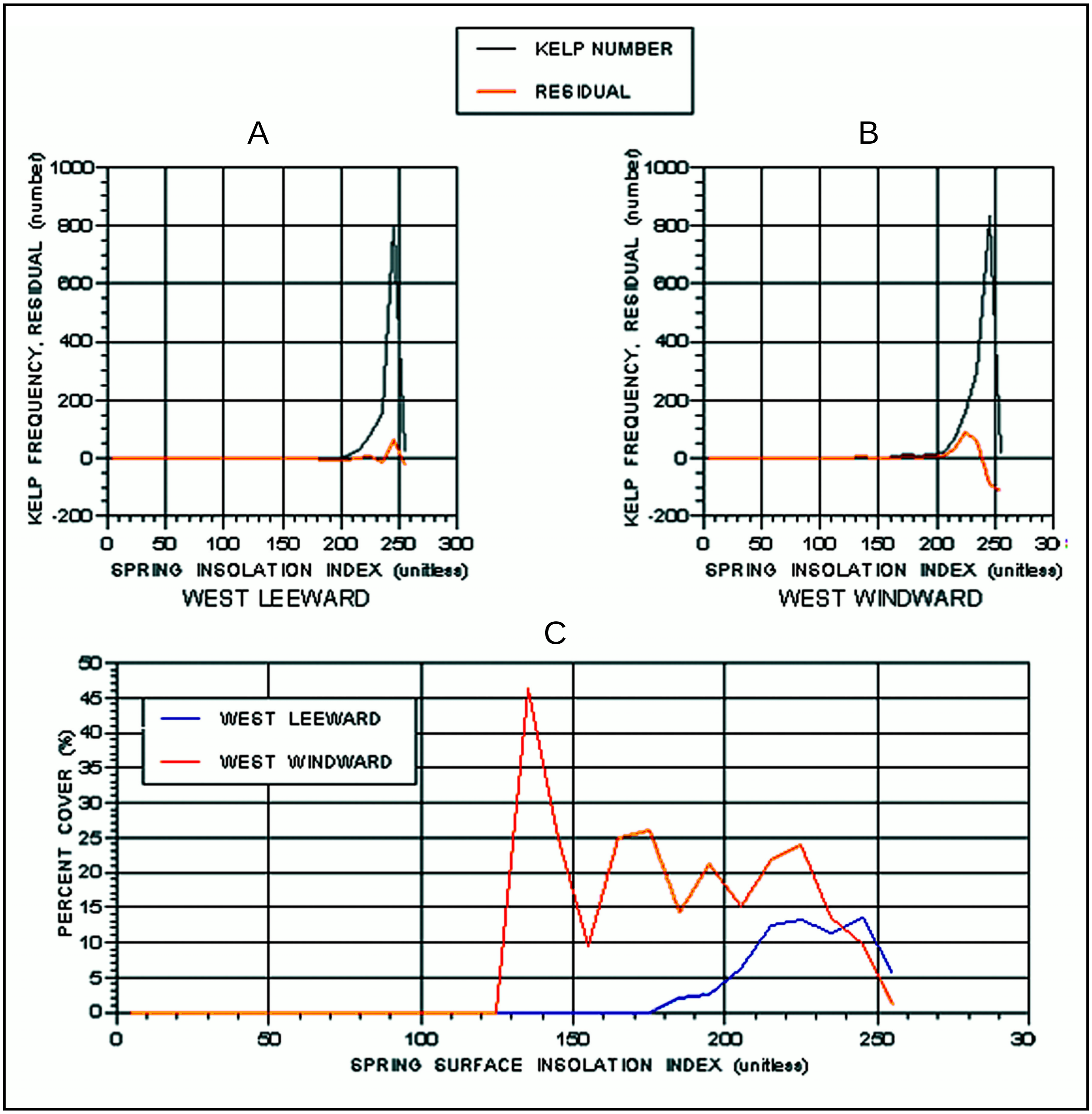

Figure 3. Kelp frequency (A and B) and percent cover (C) relative to spring surface insolation. Graphs illustrate areas where kelp frequency is highest relative to insolation on the leeward (A) and windward (B) sides, and where percent cover is highest relative to insolation for both coasts (C).

spring. On the leeward side, bottom light levels for kelp cells at atypical aspects always exceed those for typical aspects regardless of sun exposure and distribution is optimized for bottom insolation there. On the exposed but well-lit windward side, surface and bottom insolation values were lower at atypical aspects for all seasons, suggesting protection from storms may dominate on a coastline where light levels are generally high, but winter storm disturbance more significant (Bushing 1995). This is consistent with light being a controlling factor on the leeward, and storm exposure on the windward sides.

The difference between typical and atypical aspects defined previously is further explained by plotting mean depth as a function of aspect for the two coasts. On both, kelp is found at deeper depths at atypical aspects (15–35 m vs. 12–15 m on the

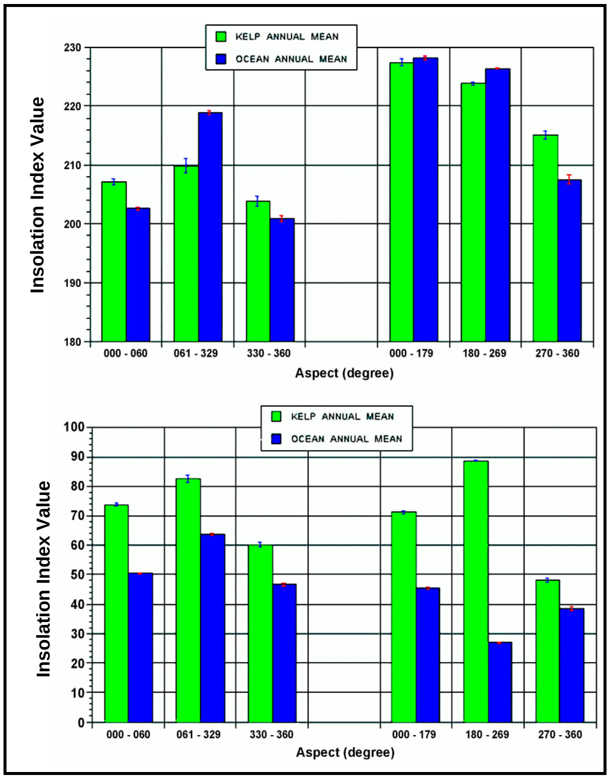

Figure 4. Mean annual surface (a) and bottom (b) insolation a function of aspect, the direction the coastline faces, on both le ward and windward coasts of Santa Catalina Island.

leeward and 12–25 m vs. <10–15 m on the windward). The difference is not statistically significant ($P > 0.050$) on the leeward side, but is ($P < 0.001$) on the windward side.

Kelp Distribution as a Function of Light and Distance-from-shore

Previous work (Bushing 1994) indicated the mean distance-from-shore for kelp was significantly greater on the leeward (91.0 m) than the windward side (66.7 m), but the maximum distances were comparable at 331 m and 340 m respectively. This is noteworthy since the submarine slope on the leeward side is greater than on the windward side. Horizontal displacement of kelp away from shore on the leeward side due to hillshading by the island's main ridge, the focus of this study, may be responsible.

On the leeward side, there is a pronounced increase in insolation out to a distance of about 220 m (Fig. 5). Within this distance, the horizontal displacement of kelp away from the coast may be due to hillshading. Beyond that, the pattern is irregular, suggesting offshore reefs play a role at these distances. On the windward side there is a slight decrease in average surface insolation with increasing distance from shore. Bottom insolation values support this interpretation. Windward side insolation drops exponentially as distance increases, reflecting increasing depth. On the leeward side the drop is less precipitous, especially at distances from about 100–200 m from shore. The unexpected peak in bottom insolation values at distances of 200–300 m appears to confirm the influence of offshore reefs on the light environment at greater distances.

DISCUSSION

This study offers the first evidence of the influence of terrestrial hillshading on the distribution of *Macrocystis pyrifera* on a regional scale. Instantaneous light levels and effective photosynthetic daylength in Catalina's nearshore marine environment exhibit a high degree of spatial variability which appears to influence the distribution of giant kelp. Mature kelp canopies absorb sunlight at its highest intensity near the surface, providing the adult sporophytes with relative immunity from changes in light due to factors like hillshading or absorption in the water column. Kelp's greater average distance from the coast on the steeper leeward side reinforces the interpretation that hillshading plays a factor in influencing distribution. Such horizontal displacement may allow the interception of more light for photosynthesis by the adult sporophyte canopy at the surface.

Macrocystis must recruit and grow as a gametophyte or young sporophyte on the ocean floor, where nutrients are high but irradiance may be limiting (Wheeler 1978, Dean and Jacobsen 1984, Dean and Jacobsen 1990). Dense *Macrocystis* canopies may reduce surface light up to 99% by the time it reaches the bottom (Neushul 1971, Pearse and Hines 1979), so the younger stages at the ocean floor experience diminished, and widely fluctuating bottom insolation values (North et al. 1986). The light requirements of gametophytes may be more critical for the ecological success and persistence of kelp (Harger 1979, Reed and Foster 1984, Deysher and Dean 1984). Values from the TOPQUAD

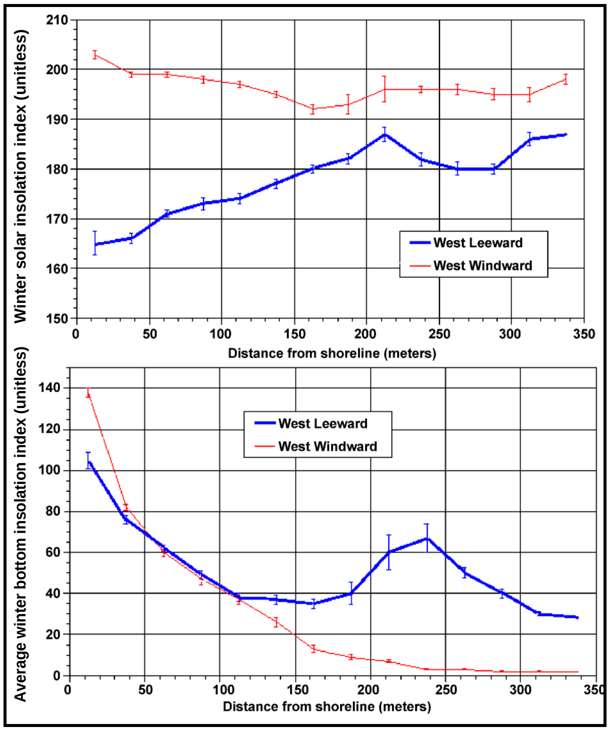

Figure 5. Mean winter surface (a) and bottom (b) insolation as a function of distance from shore around Santa Catalina Island.

model indicate surface insolation in winter varied by nearly 20:1. When light extinction and turbidity are incorporated, variation in bottom insolation exceeds 1,000:1, resulting in real world light levels below compensation range for kelp in this model under clear skies.

The extinction of light in the water column significantly influences the potential habitat for marine vegetation. Light often determines the maximum survival depth at a given site (Lüning 1971, Lüning and Dring 1979, Gerard 1988), and is believed to limit the seaward extent of *Macrocystis pyrifera*, especially in turbid coastal waters (North 1971). Submarine illumination and its extinction through the water column have been discussed by Jerlov (1976), Gates (1980), Kirk (1983), and others. Based on Lüning (1981) and the apparent depth limits (d_{max}), the waters off the West windward coast would be Jerlov type 5 and those off the leeward side Jerlov type 3, comparable to the range observed by Dean (1985) off the mainland coast.

Seasonal and diurnal fluctuations in surface irradiance are generally not a major factor in the variability of bottom irradiance levels compared to changes in water clarity (Harger 1979, Dean and Jacobsen 1984) in regions where hillshading is not an issue. Dean (1985) found that variations in sediment levels related to storm activity, rather than seasonal surface irradiance, were responsible for observed fluctuations in bottom insolation in mainland southern California kelp beds. Seasonal fluctuations in turbidity due to increased winter storm activity, higher rainfall and sediment loading from runoff may be especially important if surface insolation is simultaneously reduced by low sun angles and increased hillshading or higher levels of overcast. Regional differences in seasonal bottom insolation between the windward and leeward coasts off Catalina may be greater due to differing seasonal storm regime and wave energy. The windward side experiences sediment loading not only from runoff, but also from resuspension of sediments in the high energy environment (Bushing 1994). Reduced winter surface light levels on the leeward side due to topographic hillshading may somewhat balance this.

A plant's ability to adapt to a given light regime depends on its genetic flexibility (Wheeler 1978). Plants found in lower light environments, like shaded habitats or deeper depths, may have a higher photosynthetic efficiency (Wheeler 1978, Lüning and Neushul 1978). Such light ecotypes with greater nutrient uptake rates and higher photosynthetic efficience are known from other marine algae (Gerard 1988, 1990). Kopczak et al. (1991) found *Macrocystis* off Catalina's shaded leeward side also was more efficient in its nutrient uptake and utilization.

If *Macrocystis* ecotypes that are adapted to different light regimes exist around the island, this could have consequences for the selection of a marine reserve network around Catalina Island. Gerard (1988) suggested the limited gene flow between kelp populations due to short spore dispersal distances might maintain the geographic isolation of such ecotypes. Individuals adapted to the higher turbidity environments of the windward side would most likely incur a greater metabolic cost involved in maintaining higher pigment concentrations. This could be difficult under the more oligotrophic conditions that prevail on the leeward side of the island.

Reduced growth rates due to lower light levels on the shaded leeward side, or at protected aspects on the windward side, may result in higher mortality and diminished ability to resist the effects of the prevailing disturbance regime on each coast (Steinman et al. 1991). If so, regional persistence in kelp may be affected by the observed spatial variability in the light regime (Bushing 1995, 1996a, 1996b). Those individuals, populations and ecotypes which are able to survive may respond once the light regime increases due to removal of adult canopy by storm, reduced turbidity or other seasonal change. Resilience and persistence should be higher in such populations. Such spatial differentiation in local population characteristics should be incorporated as a factor along with others in the identification of potential new marine reserves around the island (Bushing 1997).

ACKNOWLEDGMENTS

The author would like to acknowledge the following: the Catalina Island Conservancy and the Offield Family Foundation for their support in the development of several elements in this GIS; UCSB's Map & Imagery Lab; Southern California Edison for the contribution of a kelp data layer in ARC/Info format; Dr. M. Neushul, Dr. A. Ebeling, Dr. L. Mertes, Dr. J. Markham, Dr. D. Reed and Dr. K. Lafferty for their encouragement and advice along the way; and Dr. J. Dozier for his suggestion of the TOPQUAD algorithm.

REFERENCES

Abbott, I. and G. Hollenberg 1976. Marine Algae of California. Stanford University Press. Stanford, CA, 827 pp.

Bishop, O.N. 1983. Statistics for Biology. Longman House. Essex, England, 232 pp.

Brock, T.D. 1981. Calculating solar radiation for ecological studies. Ecological Modeling 14:1–19.

Bushing, W.W. 1994. The influence of topography on the distribution of giant kelp (*Macrocystis pyrifera*) beds around Santa Catalina Island using a geographic information system. Pages 70–82. *In*: Halvorson, W.L. and G.J. Maender (eds.), The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Bushing, W.W. 1995. Identifying regions of persistent giant kelp (*Macrocystis pyrifera*) around Santa Catalina Island for designation as marine reserves. Proceedings of the 15th ESRI User Conference, 21–26 May 1995, Palm Springs, CA. Proceedings published on CD-ROM and via World Wide Web (URL: http://www.esri.com).

Bushing, W.W. 1996a. The use of satellite remote sensing and a geographic information system (GIS) to characterize regions of persistent giant kelp (*Macrocystis pyrifera*) around Santa Catalina Island for designation as marine reserves [Ph.D. dissertation]. University of California, Santa Barbara, CA, 719 pp.

Bushing, W.W. 1996b. The influence of island topography on the nearshore light regime and the distribution of giant kelp around Santa Catalina Island. Proceedings of the 16th ESRI User Conference, 19–24 May 1996, Palm Springs, CA. Proceedings published on CD-ROM and via World Wide Web (URL: http://www.esri.com).

Bushing, W.W. 1997. GIS-based gap analysis of an existing marine reserve network around Santa Catalina Island. International Journal of Marine Geodesy 20:205–234.

Bushing, W.W. 2000. Monitoring the persistence of giant kelp around Santa Catalina Island using a geographic information system. Pages 148–160. *In*: Browne, D.R., K.L. Mitchell and H.W. Chaney (eds.), Proceedings of the Fifth California Islands Symposium: Update on the Status of Resources. OCS Study MMS 99-0038. Minerals Management Service, Camarillo, CA.

Davis. F.W. and J. Dozier. 1990. Information analysis of a spatial database for ecological land classification. Photogrammetric Engineering and Remote Sensing 56:605–613.

Dean, T.A. 1985. The temporal and spatial distribution of underwater quantum irradiation in a southern California kelp forest. Estuarine, Coastal and Shelf Science 21:835–844.

Dean, T.A. and L.E. Deysher. 1983. The effects of suspended solids and thermal discharges on kelp *Macrocystis*. Pages 114–135. *In*: Bascom, W. (ed.), The Effects of Waste Water Discharges on

Kelp in Southern California. Southern California Coastal Water Research Project, Long Beach, CA.

Dean, T.A. and F.R. Jacobsen. 1984. 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. and T.A. Dean. 1984. Critical irradiance levels and the interactive effects of quantum irradiance and dose on gametogenesis in the giant kelp, *Macrocystis pyrifera*. Journal of Phycology 20(4):520–524.

Dozier, J. 1980. A clear-sky spectral solar radiation model for snow-covered mountainous terrain. Water Resources Research 16:709–718.

Dozier, J., J. Bruno and P. Downey. 1981. A faster solution to the horizon problem. Computers & Geosciences 7:145–151.

Dozier, J. and J. Frew. 1990. Rapid calculation of terrain parameters for radiation modeling from digital elevation data. IEEE Trans. on Geoscience and Remote Sensing 28:963–969.

Foster, M.S. 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). National Coastal Ecosystems Team. Slidell, LA, 152 pp.

Frew, J.E. 1990. The Image Processing Workbench [Ph.D. dissertation]. Department of Geography, University of California, Santa Barbara, CA, 305 pp.

Gates, D.M. 1980. Biophysical Ecology. Springer-Verlag, New York, NY, 611 pp.

Gerard, V.A. 1988. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. Marine Biology 97:25–36.

Gerard, V.A. 1990. Ecotypic differentiation in the kelp *Laminaria saccharina*: phase-specific adaptation in a complex life cycle. Marine Biology 107:519–528.

Harger, B.W.W. 1979. Coastal Oceanography and Hard Substrate Ecology in a Californian Kelp Forest [Ph.D. dissertation]. Department of Biology, University of California, Santa Barbara, CA, 427 pp.

Hetrick, W.A., P.M. Rich, F.J. Barnes and S.B. Weiss. 1993a. GIS-based solar radiation flux models. Pages 132–143. *In*: Proceedings ASPRS 1993 Annual Conference, Volume 3, New Orleans, LA.

Hetrick, W.A., P.M. Rich and S.B. Weiss. 1993b. Modeling insolation on complex surfaces. Pages 447–458. *In*: Proceedings 13th Annual ESRI User Conference. Environmental Systems Research Institute, Redlands, CA.

Hicks, R.R. and P.S. Franks. 1984. Relationship of aspect to soil nutrients, species importance and biomass in a forested watershed in West Virginia. Forest Ecology and Management. 8:281–291.

Holland, P.G. and D.G. Steyn. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. Journal of Biogeography 2:179–183.

Jackson, G.A. 1987. Modeling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*. Marine Biology 95:611–624.

Jerlov, N.G. 1976. Marine Optics. Elsevier Publishers, Amsterdam, The Netherlands, 231 pp.

Johansson, C. 1982. Attached algal vegetation in running waters of Jämtland, Sweden. Acta Phytogeographica, suecica 71:12–73.

Johnson, L.B., C.A. Johnston and J. Pastor. 1988. Raster and vector data in ecological research applications. Pages 386–94. *In*: Proceedings Third Annual International GIS/LIS '88 Conference, San Antonio, TX.

Kain, J.M. 1982. Morphology and growth of the giant kelp *Macrocystis pyrifera* in New Zealand and California. Marine Biology 67:143–157.

Kirk, J.T.O. 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, New York, NY, 401 pp.

Kirk, J.T.O. 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. Hydrobiologia 125:195–208.

Kirkpatrick, J.B., R.J. Fensham, M. Nunez and D.M.J.S. Bowman. 1988. Vegetation-radiation relationships in the wet-dry tropics: granite hills in northern Australia. Vegetatio 76:103–112.

Kopczak, C.D., 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.

Lüning, K. 1971. Seasonal growth of *Laminaria hyperborea* under recorded underwater light conditions near Helgoland. Pages 347–361. *In*: Fourth European Marine Biological Symposium. Cambridge University Press, Cambridge, England.

Lüning, K. 1981. Light. Pages 326–355. *In*: Lobban, C.S. and M.J. Wynne (eds.), The Biology of Seaweeds. Botanical Monographs, vol. 17. University of California Press, Los Angeles, CA.

Lüning, K. and M.J. Dring. 1979. Continuous underwater light measurements near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgoländer wissenschaftliche Meeresuntersuchungen 32:403–424.

Lüning, K. and P. Kadel. 1993. Daylength range for circannual rhythmicity in *Pterygophora californica* (Alariaceae, Phaeophyta) and synchronization of seasonal growth by daylength cycles in several other brown algae. Phycologia 32(5):379–387.

Lüning, K. and M. Neushul. 1978. Light and temperature demands for growth and reproduction of Laminarian gametophytes in southern and central California. Marine Biology 45:297–309.

Miklos, L., I. Matecny and M. Kozova. 1991. Interpretation of the morphometric relief indices for spatial differentiation of microclimatic conditions. Ekologia (CSFR) 10:223–46.

Murphy, D.D. and S.B. Weiss. 1988. A long-term monitoring plan for a threatened butterfly. Conservation Biology 2:367–374.

Neushul, M. 1971. Submarine illumination in *Macrocystis* beds. Pages 241–254. *In*: North, W.J. (ed.), The Biology of Giant Kelp Beds (*Macrocystis*) in California. Beihefte zur Nova Hedwigia, vol. 32.

North, W.J. (editor). 1971. The Biology of Giant Kelp Beds (*Macrocystis*) in California. Beihefte zur Nova Hedwigia 32, 600 pp.

North, W.J., G.A. Jackson and S.L. Manley. 1986. *Macrocystis* and its environment, knowns and unknowns. Aquatic Botany 26:9–26.

Pearcy, R.W. 1983. The light environment and growth of C3 and C4 tree species in the understory of a Hawaiian forest. Oecologia 58:19–25.

Pearse, J.S. and A.H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. Marine Biology 51:83–91.

Pennock, J.R. 1985. Chlorophyll distributions in the Delaware Estuary: regulation by light limitation. Estuarine, Coastal and Shelf Science 21:711–725.

Reed, D.C. and M.S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65:937–948.

Seapy, R.R. and M.M. Littler. 1993. Rocky intertidal community structure on Santa Barbara Island and the effects of wave surge on vertical zonation. Pages 273–92. *In*: Hochberg, F.G. (ed.), Proceedings of the Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Steinman, A.D., P.J. Mulholland, A.V. Palumbo, T.F. Flum and D.L. DeAngelis. 1991. Resilience of lotic ecosystems to a light-elimination disturbance. Ecology 72:1299–1313.

Thom, R.M. and R.G. Albright. 1990. Dynamics of benthic vegetation standing-stock, irradiance and water properties in central Puget Sound. Marine Biology 104:129–141.

Weiss, S.B., D.D. Murphy and R.R. White. 1988. Sun, slope and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69:1486–1496.

Wheeler, W.N. 1978. Ecophysiological Studies on the Giant Kelp, *Macrocystis* [Ph D. dissertation]. Department of Biology, University of California, Santa Barbara, CA, 179 pp.

Woods, J.D. and R. Onken. 1982. Diurnal variation and primary production in the ocean-preliminary results of a Lagrangian ensemble model. Journal of Plankton Research 4:735–756.