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Spatial and temporal variability of kelp forest canopies in central California

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SPATIAL AND TEMPORAL VARIABILITY OF KELP FOREST CANOPIES IN CENTRAL CALIFORNIA

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and the Department of Marine Science
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In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
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ABSTRACT

SPATIAL AND TEMPORAL VARIABILITY OF KELP FOREST CANOPIES IN CENTRAL CALIFORNIA

by Michael D. Donnellan

Recent advances in computer hardware and software have spurred a renewed look at historical datasets of kelp canopies. Using a time series of aerial photographs spanning 65 kilometers and 6 years, the spatial and temporal patterns of kelp canopy coverage in *Macrocystis*-dominated kelp forests were described offshore of Monterey, California. The principal findings of this work were that: 1) canopy dynamics were much more predictable in central California than previously thought; 2) the size of the spatial window through which temporal patterns of canopy abundance are perceived is a critical determinant of the observed results; 3) canopies exhibited typical "patch sizes" of approximately 1.6 kilometers, suggesting that an important process or processes occur at a similar scale; and 4) kelp forests may be classified by their canopy dynamics over large spatial scales using time series of remotely sensed images, provided the classification scheme is validated by focused *in situ* work.

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INTRODUCTION

Giant kelp (*Macrocystis pyrifera* (L.) C. A. Agardh) and bull kelp (*Nereocystis luetkeana* (Mertens) Postels & Ruprecht) supply the majority of the biomass, primary production, and three-dimensional structure in rocky, nearshore (<30 m depth) marine environments of central California. The "forests" formed by aggregations of individual plants provide food and habitat for hundreds of species (North 1971, Foster and Schiel 1985). Understanding the biology of these forests, however, presents a challenge because of their extensive geographic distribution, substantial variability in space and time across a wide range of temporal and spatial scales, and the logistical difficulty and expertise needed for subtidal research.

Fortunately, the fronds and blades of adult *Macrocystis pyrifera* (hereafter, *Macrocystis*) and *Nereocystis luetkeana* (hereafter, *Nereocystis*) float on the ocean surface, and surface canopies can be surveyed efficiently and cost-effectively using remote sensing techniques. Using remote sensing, all-inclusive studies of kelp forests are possible at scales which are logistically unfeasible using conventional *in situ* sampling techniques (e.g., SCUBA). Since the 1960s, low-altitude aerial photography with infrared-sensitive film (e.g., Jamison 1971, Deysher 1993) has been used for resource assessment and management (reviewed in Larson and McPeak 1995) and ecological research (e.g., Kimura and Foster 1984, Reed and Foster 1984, North et al. 1993, Bushing 1996, Tegner et al. 1996, Graham et al. 1997).

While aerial surveys are indeed a powerful tool for studying kelp canopies, the limitations and inferential pitfalls of the technique are considerable. In brief, the utility of infrared aerial surveys is hindered by: 1) poor water penetration (Jamison 1971); 2) the inability to distinguish among species or individuals (for southern California, North et al. 1993; for central California: Donnellan personal observation; M. H. Graham and R. F. Van Wagenen personal communication); and 3) a lack of strong relationship between the amount of canopy on the surface and the density or size (i.e. number of stipes per plant) of the individual plants that produce the canopy (Foster 1982, Kimura and Foster 1984, Tegner et al. 1996, Graham et al. 1997).

Considering the limitations described above, why study canopies at all? First, the near-infrared signature of canopies in survey imagery is an effective indicator of the location, geographic distribution, and spatial extent of kelp forests when kelp forests attain their maximal development and biomass is concentrated at the sea surface. Time series of canopy surveys have been used to document changes in the geographic and spatial extent of kelp canopies, and the populations that produce them (e.g., North et al. 1993, Tegner et al. 1996). Further, comparisons of geographic and spatial distributions of extant canopies with historical canopy data (McFarland 1912, Crandall 1915) revealed that canopy area may have declined by 30-70% in southern California (Hodder and Mel 1978, Neushul 1981), and substantial differences in geographic distribution and relative abundance of *Macrocystis* and *Nereocystis* in central California (Miller and Geibel 1973, Yellin et al. 1997, Van Blaricom 1984). Such differences can, however, occur interannually in kelp forests as a result of natural disturbances such as El Niño (e.g., Foster and Schiel 1985), so it is not clear from the available historical data that they represent long-term trends (Foster personal communication).

Secondly, canopies are important aesthetically, economically, and ecologically (reviewed in North 1994, Foster and Schiel 1985). Approximately 35% - 60% of giant kelp biomass is present in the upper 1-2 m of surface canopy (McFarland and Prescott 1959, North 1971, Gerard 1984), and more than 98% of *Macrocystis*' primary production occurs within the upper 3 m of water column (Towle and Pearse 1973). Canopy fronds serve as food for grazers (e.g., snails, invertebrates) and are an important, potentially limiting habitat (at least during certain times of the year) for various animal species, including sea otters and fish (reviewed in Foster and Schiel 1985). The seasonal loss of kelp canopies results in drift kelp that is consumed within the kelp forests and exported to adjacent habitats (e.g., beaches, deep sea) (Harrold et al. 1998, reviewed in Foster and Schiel 1985 and Graham et al. 2003). Experimental removals of kelp canopies have clearly demonstrated that surface canopies strongly mediate inter- and intra-specific competition for light and space among benthic algal communities (e.g., Dayton 1975, Pearse and Hines 1979, Reed and Foster 1984, Kimura and Foster 1984, Edwards 1998, Dayton et al. 1999) and influence fish densities (Anderson 1994, Carr 1989, Holbrook et al. 1990).

For the reasons described above (in part), the distribution and dynamics of kelp canopies and the forests they represent are of considerable interest. Several knowledge gaps exist, however. Most canopy-related studies to date have assessed canopy variability by calculating the surface area within a given area of interest, plotting values as a function of time, then relating the time series to independent or dependent variables (but see Bushing 1996, 1997; Strampe 2001). While this strategy has proven fruitful (e.g. North et al. 1993, Graham 1997), a substantial amount of potentially important and useful spatial information is lost in the process of summarization. Some knowledge gaps are particular to central California. For example, canopy studies in this region are hindered by a lack of large-scale and long-term perspective, unlike the relatively well-studied kelp canopies in southern California (e.g., North et al. 1993, Tegner et al. 1996). Additionally, canopy abundance may vary substantially from month to month in central California (Graham et al. 1997), making comparisons of interannual changes in canopy abundance sensitive to the precise time of annual sampling. Nevertheless, description of fine-scale temporal patterns over broad areas has not been done.

To standardize comparisons of kelp canopies among years, surveyors have attempted to record the maximum surface area occupied by kelp canopy within a year (hereafter, "maximum canopy"). Surveying during maximum canopy maximizes the chances that the kelp plants producing the canopy are detected because near-infrared aerial photography cannot detect plant tissue greater deeper than a few centimeters (Jamison 1971). Accurately predicting the timing of maximum canopy is especially important in central California for scheduling surveys, where the large amplitude of canopy seasonality can easily mask interannual trends. Canopies in this region have been reported as generally increasing due to growth in spring and summer, leading to maximum canopy in early fall, then a decline coincident with storms in late fall and winter (Miller and Geibel 1973, Gerard 1976, Cowen et al. 1982, Foster 1982, Kimura and Foster 1984, Reed and Foster 1984, Harrold et al. 1988). Some of this evidence was qualitative, however, and/or temporal resolution was too coarse to precisely determine the actual timing of maximum canopy.

Timing of maximum canopy development for *Macrocystis* has been determined quantitatively or semi-quantitatively for only four local areas in central California, all of which fringed the Monterey peninsula (Kimura and Foster 1984, Graham et al. 1997). Despite the proximity of these study sites, the timing of maximum canopy and the patterns of interannual abundance were variable between and within studies. To complicate matters, Foster (1982) observed *Nereocystis* canopies attaining maximum development 1-2 months later than *Macrocystis*. Furthermore, large interannual differences in canopy abundance have also been reported in addition to differences in timing (Cowen et al. 1982, Foster 1982, Reed and Foster 1984, Graham et al. 1997, Strampe 2001). However, it was unclear how the location, spatial scale of observation (i.e. sample unit size), and timing of canopy surveys (within a year and among different study periods) affected the observed patterns of interannual variability in these studies.

Using the same dataset of canopy surveys originally reported by Harrold et al. (1988) and used, in part, by Graham et al. (1997), I retrospectively assessed the relationships among location, spatial scale of observation, survey timing, and the resulting patterns of canopy seasonality and abundance in *Macrocystis*-dominated kelp forests near Monterey, California. This dataset was uniquely suited to address this question because of its spatial and temporal extent and resolution (ca. 65 kilometers at meter-scale, six years at monthly to quarterly intervals, respectively). Specifically, I evaluated the following questions using descriptive spatial statistics, time series analysis, and visual assessment: 1) what were the temporal and spatial patterns of canopy abundance at the largest spatial scale for which data were available? 2) How were canopies correlated in time and space? 3) Could canopy dynamics be modeled in terms of an underlying "probabilistic" process? 4) How does temporal variability of kelp canopies change across spatial scales? 5) Is there an "optimal" scale at which to study kelp canopies that maximizes spatial resolution and minimizes stochastic variation (i.e. the "scale of non-trivial determinism" *sensu* Rand and Wilson 1995)? 6) Were temporal patterns of canopy abundance spatially variable at scales smaller than the study area?

The spatial extent of this study was imposed more by logistic constraints than biological considerations. This artificial imposition naturally led to the desire to delineate more biologically-relevant boundaries that would be more meaningful for subsequent analyses of canopy patterns. At large spatial scales, the most obvious natural groupings for kelp forests south of Oregon are the regions of Baja, southern, central, and northern California (reviewed in Foster and Schiel 1985). Within-region variability of canopy abundance has not been well-studied, however (but see Foster 1982, North et al. 1993).

For central California, Foster and Schiel (1988) and Foster and Van Blaricom (2001) proposed the existence of four characteristic types of kelp forests in central California based on general patterns of: 1) wave exposure, 2) depth, 3) substrate type and relief, 4) benthic species composition and abundance, and 5) variability of kelp surface canopies. Of these factors, determination of surface canopy variability, geology/substrate type, and wave exposure does not require expensive *in situ* surveys or vessel-based remote sensing (e.g., multibeam bathymetry). However, temporal variability of surface canopies in central California appears to be correlated with wave exposure (Harrold et al. 1988, Graham et al. 1997), and to a lesser extent, substrate type/geology (Foster 1982), therefore may serve as a proxy for these variables to some extent. Further, canopies can greatly influence the benthic communities beneath them (Dayton, 1975, Pearse and Hines 1979, Reed and Foster 1984, Kimura and Foster 1984; Dayton et al. 1999); therefore spatially discrete canopies with consistent patterns of temporal variability may be correlated with characteristic species assemblages or functional groups. Therefore, patterns of canopy variability may be an effective indicator of kelp forest "types" in central California that can be assessed over large spatial scales in a logistically feasible manner.

Using cluster analysis, I classified discrete kelp forests in the Monterey Bay area into types based on temporal patterns of canopy abundance. Although determining the validity of this classification method would be premature prior to adequate *in situ* ground-truthing, I used internal validation measures to assess the likelihood of effective classification. I presented the time series of classified groups with relevant physical variables for environmental context, and then used the results to refine the probabilistic process model developed in the first section of this paper.

STUDY AREA

The study area was located in the northern portion of central California, spanning approximately 65 kilometers from the Monterey breakwater to Cooper Point

(Fig. 1). Rock in the region is primarily granodioritic, and much of the shallow subtidal is rocky. Large expanses of sandy beach are rare, but pocket beaches are common throughout the area (McLean 1962). Coastal aspect ranges from northeast (inside Monterey Bay) to south (Stillwater Cove), but most of the study area faces west/ northwest, the predominant incident angle for incoming waves and wind. The shallow subtidal shelf is generally steep, except for portions of the Monterey Peninsula and south of Point Sur. The subtidal zone is bisected by the Carmel submarine canyon at the head of Carmel Bay, which is also the mouth of the Carmel River.

Oceanography of the area is characterized by high upwelling (Breaker and Broenkow (1994), and sea surface temperatures between 9º and 17º C (National Oceanic and Atmospheric Administration unpublished data). Nutrient concentrations in this area generally do not fall below levels inhibitory to kelp growth (Foster and Schiel 1985), although Foster and Schiel (1985) reported late-summer canopy deterioration for two sites in central California during 1979 and 1982. Subtidal assemblages in kelp forests within this area have been described by many workers (e.g., Andrews 1945, McLean 1962, Foster 1982, Harrold et al. 1988, Foster and Van Blaricom 2001).

METHODS

Data Collection and Processing

Fifty-eight aerial surveys of kelp canopies were done in the study area from November 1985 - December 1991. Surveys were approximately monthly from 1985 - 1989, bimonthly in 1990, and quarterly in 1991. The spatial extent of the surveys was reduced incrementally over time (delineated as Zones A-C in Fig. 1). Aerial surveys were conducted by R. F. Van Wagenen of Ecoscan Resources Data (Watsonville, CA) at an altitude of 2500 meters with infrared-sensitive film and standardized to similar conditions of tidal range, sea state, and weather conditions (Graham et al. 1997), although metadata were not available. The developed film was projected onto blank, hardcopy maps of the coastline within the study area that were displayed at a scale of 1: 9,400 (as determined directly from the hardcopy map size and scale), and imagery interpreted as algal canopy was traced onto the map with a fine-point pen. This process was repeated for each of the contiguous map series spanning the study area (29 series for Zone C, 24 for Zone B, and 13 for Zone C).

Canopy-forming species were not reliably distinguishable in survey imagery, therefore canopies of all species were recorded indiscriminately. Canopies were assumed to represent primarily *Macrocystis pyrifera,* but other species were also known to be present (in order of relative abundance): *Macrocystis pyrifera* >>> *Nereocystis luetkeana* >> *Cystoseira osmundacea* > *Egregia menziesii* > *Macrocystis integrifolia* (Foster personal communication). *Cystoseira osmundacea* is a Fucalean alga; therefore the term "kelp canopies" is used loosely in this paper, but was felt justified by the areal dominance of canopy produced by true kelps (i.e. members of the order Laminariales).

The hardcopy maps were photocopied and reduced in size by 33% to a scale of 1:12,000, then individually scanned into electronic format as binary raster image files (TIFF and PDF format) at 300 pixels per inch. Resultant grain size (i.e. spatial resolution on the ground) of digital imagery was approximately 1 m^2, and the minimum mapping unit (i.e., the smallest patch of kelp canopy mapped) was approximately 5-6 meters in diameter. Each image was then individually registered to a geographic location (or, "georeferenced") using Arc View 3.2 Geographic Information System (GIS) software (Environmental Systems Research Institute 2002) in concert with the Image Analysis 1.1 extension (Environmental Systems Research Institute 2000). To accurately represent positions, distances, and shapes of features, all imagery was georeferenced to the Universal Transverse Mercator coordinate system, Zone 10 (Northern Hemisphere), World Geodetic System 1984 datum.

Survey imagery was georeferenced to the best available source data (i.e., highest spatial accuracy and image resolution). Source data (Digital Orthophoto Quadrangles, or "DOQs") were highly accurate (+/- 0.7m) for coastal areas from the Monterey Breakwater to approximately Cypress Point. DOQs were less accurate for coastal areas south of Carmel Highlands (+/-1.4 to 4.3 meters). Metadata for DOQs were unavailable for coastal areas from Cypress Point to Carmel Highlands, although spatial accuracy appeared to be approximately +/- 1.5m from comparisons with nearby DOQs that had appropriate metadata. Control points for georeferencing imagery were chosen at sea level or as close to sea level as possible; 5-32 control points were used per image (mean = 11 points/ image). Spatial accuracy generally decreased as a function of both distance from shore and coastal human populations due to lack of suitable landmarks; offshore rocks were used during georeferencing whenever possible.

Once spatial accuracy was acceptable (<10 meters Root Mean Square [RMS] error, when possible) for the first image from each of the 29 contiguous map series, each of the remaining maps in a given series was georeferenced to the first image in its respective series. All images were "re-sampled" (i.e. re-scaled to a common size after distortions due to the georeferencing process) to 1 m^2 using the affine transformation. Extraneous information not representing kelp canopy (e.g., shoreline, rocks) was removed from each image, and all images for each sampling date were combined together into one GIS layer and saved as vector and raster data. A total of 1,486 kelp maps from 58 aerial surveys were processed.

The spatial accuracy of the resulting maps was not tested formally. Most of the 29 map series within the study area appeared to be within technical specifications set by the United States Geological Survey (USGS) (anonymous 1999) at a scale of 1:12,000 (90% of points within +/- 9.85 meters of a landmark). However, compliance was largely due to a technicality in the mapping standards that limits of accuracy apply to positions of well-defined points only. Because the imagery of interest in this study (i.e. kelp canopy) was offshore, few well-defined landmarks existed. If the USGS technicality is ignored, 13 of 29 map series (45%) making up the study area were within accuracy standards, according to assessment of RMS error (Table 1). Twenty-two of the 29 map series (76%) were compliant with the relaxed accuracy standard of +/- 12.2 m for maps at a scale of 1:24,000. The set of maps that did not meet the standard for 1:24,000 maps were all confined to approximately 13 contiguous kilometers of coastline midway between Point Lobos and Point Sur (Fig. 1). This area had few landmarks for georeferencing and the source DOQ had relatively poor spatial accuracy (+/- 4.3m). Overall, despite spatial inaccuracies in some locations within the study area, horizontal accuracy was sufficient for purposes of this study. Informal assessments of positional accuracy were conducted by spot-checking the location of persistent, well-defined kelp canopies relative to bathymetric features mapped at high resolution (California Department of Fish and Game unpublished data), and correspondence between kelp canopy and bathymetry generally was in close agreement.

Areal estimates of kelp canopies were adjusted for differences in tide height during surveying. Although no metadata for survey flights were available, it was apparent from retrospective inspection of tide tables that aerial surveys were done during tidal stages ranging from approximately -1.5 feet to +3.5 feet relative to the Mean Lower Low Water datum. Because it is well known that the amount of canopy visible on the ocean surface may vary substantially according to tidal stage, I applied a conservative correction factor to account for differences in observed versus probable surface area. To my knowledge, no published relationship between time and canopy surface area previously existed, therefore I estimated a linear relationship of +/- 10% per 1 foot of tide height. Probable tide height at the time of survey was estimated by inspecting historical tide predictions for Monterey (Nautical Software Inc. 1995) relative to time of day for each survey date. Surveys were assumed to coincide with the lowest tide occurring between 2 hours after sunrise and 2 hours prior to sunset. While the assumptions of linearity and effect magnitude were untested, I determined that it was more valid to account for canopy differences resulting from tidal stage rather than ignore the issue.

Canopy Time Series Analysis

Canopy data from Zone B offered the optimal compromise between the spatial extent of the study area and time series length and resolution, therefore this zone was the "benchmark" against which subsequent smaller-scale analyses were related. The surface area of kelp canopy within this zone was calculated for each survey using GIS software, corrected for tidal height, and plotted against time. The time series was analyzed visually and summary statistics were compiled for timing of annual maximum and minimum canopy abundance.

To investigate the underlying "probabilistic" process influencing kelp canopies, the time series of canopy abundance within Zone B was analyzed for interannual trends, seasonal (i.e. periodic) trends, and noise in order to partition the major sources of variability into constituent components. First, the canopy time series was assessed for linear trends spanning multiple years. If any trend was found it was quantified and removed to satisfy the assumption of "stationarity" (i.e. constant mean and equal variances) required for time series analysis. Data were then linearly interpolated to intervals of thirty days in order to maximize statistical power, and then tested for periodicity and temporal autocorrelation via spectral analysis and correlograms, respectively. The sample size (n=50 surveys) was approximately the minimum recommended for time series analysis (reviewed in Legendre and Legendre 1998). Confidence intervals for determining statistical significance of correlograms were calculated according to Legendre and Legendre (1998).

The temporal spacing and extent of the canopy data dictated that the shortest and longest periods which could be detected statistically were equal to 60 days (i.e. twice the sampling interval; n = 25 months) and approximately 2 years (i.e. half of the series length; n=2), respectively. "Aliasing" effects (i.e. artificial signals due to actual frequencies in the canopy data higher than one per month) were possible as a result of the biweekly tidal rhythm, but were assumed to be negligible due to lack of a known biological mechanism that would operate on this timescale. All time series analyses were performed using JMP 5.0 statistical software (SAS Institute 2002).

The sinusoidal pattern of canopy abundance over time was assumed to be a response to "latent" forcing variable(s) of cyclic, exogenous physical factors (e.g., PAR, mean wave intensity). The obvious 12-month periodicity in the canopy time series was modeled by fitting a 4-parameter waveform to the non-interpolated data using the regression function:

$f = y0 + a * \sin (2 * Pi * x / b + c)$

where:

y0 = mean value of data (no units for proportions)

a = wave amplitude (no units for proportions)

x = Julian Day (predictor variable)

b = waveform period (days)

c = waveform position when x = 0 (radians)

The canopy time series was re-organized into a 12-month period by transforming survey dates to their respective Julian days (i.e. 1-365 day scale); Julian day was then used as the predictor variable. Canopy data were transformed to a proportion of the maximum abundance encountered in the time series to facilitate comparisons with future studies. Using Sigmaplot 6.0 graphing and curve-fitting software (SPSS 2000), the sine waveform function was fit iteratively to the canopy data until an optimal model was found. Multiple copies of the dataset were joined together for analysis (i.e. a so-called "toroidal" approach) in order to force the regression line to honor the same y-intercept value at 0 and 365 days. This approach artificially inflated the degrees of freedom, but results were unchanged according to sensitivity tests.

Assumptions of normality, equal variances, and independence of residuals were tested for compliance using the Kolmogorov-Smirnov test, Levene Median test, and Durbin-Watson test, respectively, in concert with plots of residuals versus expected values. The periodic component was quantified and extracted, leaving residual "noise." The time series analysis procedure was repeated on the residuals to assess second-order periodic components until none were statistically significant, then residuals were visually assessed for patterns superimposed upon random variability and measurement error (e.g., irregular and/or unpredictable variations due to transient exogenous perturbations such as wave events, or endogenous forcing such as "free oscillations").

Spatial Structure of Canopies

To complement the analysis of temporally explicit, spatially implicit patterns, I determined spatial structuring of kelp canopies using a reciprocal approach (i.e. spatially explicit, temporally implicit) over a similar spatial scale. To accomplish this, I constructed a variogram to assess the hypothesis that kelp canopies were spatially "patchy." A variogram was used in order to assess autocorrelation in the dataset by decomposing the spatial variability of the data into distance classes.

First, spatial data for each of the 36 canopy surveys between March 1986 to February 1989 were input into a GIS and merged into a composite image representing canopy "persistence" (*sensu* Bushing 1996, 1997). The temporal boundaries of data input to the persistence layer were set between March 1986 and February 1989 to maximize the number of complete kelp cycles (i.e. defined as minimum canopy to subsequent minimum canopy) over the greatest possible spatial extent (i.e. Zone A). For each 1m^2 grid cell in the composite image, canopy persistence was calculated by summing the number of surveys in which canopy was present. The persistence image was displayed in a GIS and color-coded according to persistence value, resulting in an image in which kelp beds that repeatedly occurred over time in the same place were clearly identifiable.

Next, a transect line was digitized using GIS through the mid-depth zones (ca. 13-17 m) of canopies spanning the length of the study area (ca. 62 km). Anisotropy was not assessed due to the narrow cross-shore distance of most kelp canopies relative to along-shore distance. Persistence values were extracted for each 1 m^2 cell intersecting the transect line and plotted against distance to assess the "proportional effect" (i.e. variability scaling as a function of the mean) (Isaaks and Srivastava 1989) and the assumption of "stationarity" (Legendre and Legendre 1998).

Using geostatistical software (Gamma Design Software 1998), an experimental variogram was calculated, then a "theoretical" variogram was fit to these data in order to model the underlying function. Five variogram models were evaluated for the best fit: spherical, exponential, Gaussian, linear, and "linear to sill." The range over which semivariance was calculated (i.e. the "Active Lag Distance") was set at 25% of the transect length to maximize statistical power, which declined as distance increased. The "Lag Class Distance Interval" (i.e. the bin size over which semivariance of pairs of points is averaged) was set to 100 meters as a compromise between spatial resolution and model generality. Typical "patch size" of spatial structures identified by variogram analysis was determined by multiplying the value of the range parameter by two.

Prior to variogram analysis, persistence values that were equal to zero were eliminated from the transect dataset to minimize the influence of biologically-unimportant "hole" effects in the variogram (recognized by oscillations about the variogram sill). These hole effects were interpreted to be manifestations of gaps between adjacent stands of kelp resulting from unsuitable conditions for kelp growth (e.g., sand channels). Specifically, hole effects were caused by correlations between pairs of persistence values being either in or out of phase with the abrupt boundaries between kelp beds; these effects were trivial and only served to reduce the coefficient of determination. Hole effects were not apparent when the distance interval between lag classes was increased (not shown), and the coefficient of determination likewise increased; however, increasing the lag distance interval correspondingly reduced the precision of correlation estimates at small spatial scales by increasing the range estimate, therefore it was not reported.

Spatiotemporal Variability of Kelp Canopies

To visualize how canopy abundance varied over time as a function of location, all available canopy data (i.e. Zones A-C) were standardized, contoured, and plotted (Golden Software Inc. 1999). Because the amount of available habitat area suitable for kelp growth per unit length of coastline was highly variable (a function of subtidal shelf width and suitable substrate), canopy data required standardization. To achieve this, the nearshore area within Zone A was subdivided into 235 "sites" with similar along-shore dimensions (265 m wide on average; SD = 49 m); the irregularity of the coastline prevented delineation of sites with strictly equal dimensions. Canopy abundance data for each site were then standardized relative to the proportion of maximum canopy abundance at that site from November 1985 to March 1989 (the date range for which canopy data were available for all 235 sites).

To assess temporal variability of canopies as a function of spatial scale, a precision curve was constructed for spatial "observation windows" of different sizes. These windows were created by sequentially aggregating the 203 contiguous sites within Zone B (e.g., window size #1 = 265 m, window size #2 = 530m ....window size #12 = 3,180m). Precision (i.e. standard error divided by the mean) was calculated for each window of a given size class using the standard error and mean abundance of standardized temporal data for each site, then precision values for all windows of a given class were averaged for that respective size class.

Timing of maximum and minimum canopy was summarized by site and month for the fundamental (i.e. smallest) observation windows. Tallies for minimum canopy were bound by the months of August to July because the temporal range of minimum canopy timing spanned calendar years. Data were not available for each month of each year due to vagaries of survey timing, so histograms should be interpreted with caution.

Canopy "Type" Classification

To assess whether kelp forests could be classified according to their temporal patterns of canopy abundance, kelp "beds" were subjectively delineated using the persistence GIS layer and classified via cluster analysis. Beds were defined as relatively distinct aggregations of kelp patches, and were chosen as the spatial unit because they were natural sampling units (cf. arbitrarily placed grids used in the previous sections). To delineate kelp beds, boundaries were digitized around kelp beds using GIS. Some beds were relatively continuous, therefore delineations were also made according to abrupt changes in coastal aspect (based on the assumption that wave exposure forces canopy dynamics, at least in part). Persistent patches of kelp canopy less than approximately 500 m in longest dimension were generally included as part of a larger bed nearby, if present; large, spatially contiguous areas of sparse canopy (e.g., north of Point Sur) were included as a single bed.

Because kelp beds ranged greatly in spatial extent, time series data for each bed were standardized relative to the proportion of maximum canopy observed in that bed from November 1985 - March 1989 (as previously described in the "Spatiotemporal Variability of Kelp Canopies" section above). Data were then standardized across sites *by date* to a mean of zero and unit variance, and a "bed x bed" matrix of Euclidean distances was calculated. A cluster analysis was then performed on the distance matrix using JMP 5.0 statistical software (SAS Institute 2002). "Outlier" kelp beds with highly anomalous temporal dynamics (e.g., including a preponderance of zeros) were removed from consideration prior to analysis in order to avoid distortion of clustering results

No particular linkage strategy is recommended above others for ecological data, therefore results from three appropriate clustering strategies (Unweighted-Pairwise-Group-Mean-Average (UPGMA), Ward's linkage, and Centroid linkage) were compared for the best "fit" to the original data. Fit was determined by degree of cophenetic correlation between the distance matrix to the cluster dendrogram output. Higher correlations indicated better representation of the input distance matrix. A dendrogram was constructed from the most appropriate cluster analysis, and clusters were ordered vertically by the values of the first principal component calculated from a "bed x bed" correlation matrix. A scree plot of the number of clusters versus Euclidean distance was inspected to determine the optimal number of clusters to retain for interpretation.

Results of cluster analysis could not be legitimately tested statistically (e.g., by ANOVA) "because the alternative hypothesis of the test would be constructed to fit the group structure computed from the very data...used for testing the null hypothesis" (Legendre and Legendre 1988). Instead, the clusters retained for interpretation were visually assessed in geographic space and plotted against time after averaging the relative abundance of canopies in constituent kelp beds.

Groupings of kelp beds resulting from cluster analysis were projected into geographic space to aid interpretation of results. To further aid interpretation of these clusters, groupings were displayed in concert with spectral wave data from the Monterey Bay buoy (36.75 North 122.42 West; National Oceanic and Atmospheric Administration unpublished data) to provide context for wave exposure. Unfortunately, the effects of wave exposure could not be tested directly without a quantitative measure of time-averaged "wave exposure" that accounted for the important mediating influences of refraction, diffraction, submarine slope, and local bathymetric/topographic peculiarities.

The time series of cluster groupings was plotted with respect to wave intensity and solar energy for environmental context. Wave intensity was modeled by calculating estimated horizontal orbital displacements (D_{Hmax} *sensu* Denny 1988) for the mid-depth range of kelp forests (i.e. 12 meters) using archived buoy data from the Monterey and Cape San Martin buoys (National Oceanographic and Oceanic Administration unpublished data). Incident solar radiation was predicted for latitude 36 N and longitude -122 W (Bird and Hulstrom 1981).

Canopy Time Series Modeling of Cluster Output

To determine whether the results of the clustering procedure could be used to refine the probabilistic process model of temporal canopy dynamics, kelp beds were grouped according to cluster, averaged for each survey date, and subjected to the curve-fitting procedure as described previously in the "Time Series" section. These analyses also served as an internal validation of results from cluster analysis.

RESULTS

Canopy Time Series Analysis

Once canopies were extracted from their spatial context (Fig. 2a-c) and quantified as an areal measurement (Fig. 3), it was obvious that kelp canopies followed a highly regular, seasonal pattern. Canopies attained maximum development between late July and September of each year and the maximum surface area observed ranged from 979 to 1,185 hectares (mean = 1117 hectares, coefficient of variation = 0.09) from 1986 through 1989. Minimum canopy abundance occurred between February and March each year and ranged from 103 to 221 hectares (mean = 155 hectares, coefficient of variation = 0.35).

No linear trends were apparent in the canopy time series among years (F = 0.52, df = 49, p = 0.47, $r^2 = 0.01$). The obvious 12-month cycle (Fig. 3) was the only periodic component detected by spectral analysis and correlogram assessment (Fisher's Kappa = 14.9, $p = 5.0 \times 10^{-9}$; Fig. 4). A 2-year cycle in minimum canopy abundance was suspected from visual inspection of canopy time series (Fig. 3), but statistical power to detect a 2-year period was negligible due to low sample size (n = 2). Canopy data were strongly autocorrelated, with highly significant values at lags 1, 5, and 6 months (Fig. 4). The highly significant positive correlation at lag 1 (r = 0.77) indicated substantial month to month dependence. The correlation at lag 12 (which would indicate an annual cycle) was not statistically significant, but this was not unexpected due to diminishing statistical power with increasing lag. Significant negative correlation at lags 5 and 6 were due to the cycle being maximally out of phase.

Regression results did not originally meet assumptions of normality or equal variances, therefore data were square-root transformed and analysis was repeated. The resulting model explained a striking proportion of the canopy variability ($r^2 = 0.78$, $F = 284$, $df = 239$, $p < 0.0001$; Fig. 5a, Table 2). Although the assumption of normality still was not met according to the conservative Kolmogorov-Smirnov test, inspection of residual plots against expected value indicated that assumptions were met satisfactorily.

Spectral analysis of residuals revealed no significant periodicity remaining in the time series (Fisher's Kappa = 4.7, $p=0.14$), further indicating that the regression successfully removed the 12-month cyclic trend. Data were autocorrelated at lag 1 ($r = 0.45$), revealing the "true" temporal autocorrelation inherent to canopies. Although no statistically significant periodicity was detected in the regression residuals, visual inspection of the residual time series (Fig. 5b) suggested the presence of an irregular, attenuating oscillation through approximately mid-1988. It was possible that this apparent pattern was a result of inaccurate model specification, but this seems unlikely given the excellent fit of the regression line. It was most likely that this pattern was the result of perturbations by large wave events, the effects of which were perpetuated in time by temporal autocorrelation of canopies.

Spatial Structure of Canopies

Kelp forests formed persistent canopies along much of the coastline within the study area (Fig. 6). In general, kelp canopies were less persistent and more infrequently distributed along the southern portion of the 62-kilometer transect line (i.e. persistence values were often zero). Therefore only persistence values from the northern 42 kilometers of the transect line were retained for variogram analysis in order to minimize analytical problems associated with non-stationarity and proportional effects. The variogram was best fit using an exponential model, but the fit of the model was quite poor (Fig. 7a). The poor fit was largely due to the abrupt increase in the variogram sill at approximately 4,250 meters, which suggested the presence of two, superimposed spatial structures.

The larger-scale spatial structure could not be re-analyzed independently of the smaller-scale structure nested within it. Therefore, I re-performed variogram analysis using an active lag distance of 4,250 meters in order to model the smaller-scale structure while isolating the effects of the larger-scale structure. The exponential model provided a good fit to the experimental variogram of the smaller-scale spatial structure ($r^2 = 0.88$; Fig. 7b), despite the lingering presence of trivial "hole" effects. The variogram model reached an asymptote (i.e. the sill parameter: Co + C) at a semivariance value of 58, which represented, in theory, the spatially-independent variance and the total sample variance. However, the sill value was less than the actual sample variance of 63 because the smaller-scale spatial structure was "nested" within a larger structure that had a greater sill value. Approximately 72% of the sample variance was spatially structured, as indicated by the parameter "C". The nugget variance parameter (Co) indicated that 28% of the variability in canopy persistence was unexplained (e.g., measurement and georeferencing error, random noise, historical influences, biological interactions).

The value of the range parameter (Ao) was 804 meters, which indicated: 1) the distance beyond which sampling units were no longer spatially correlated; and 2) the "patch size" of the smaller-scale spatial structure was approximately 1,600 meters in length. Error estimates were not calculated for parameter coefficients of variograms. However, for comparison, the theoretical model variogram with the second-best fit ($r^2 = 0.83$) yielded an estimate of 752 m for the range parameter, which indicated that the parameter value was robust. The apparent range value of the larger spatial structure was visually estimated to have a range of 4,250 meters (Fig. 7a), indicating a patch size equal to approximately 8,500 meters.

Spatiotemporal Variability of Kelp Canopies

Although temporal patterns of kelp canopies within the study area displayed remarkable consistency among years at the spatial scale of the study area, patterns of relative abundance exhibited substantial seasonal and interannual variability at local spatial scales (Fig. 8). The seasonal periodicity remained the dominant feature of the dataset, but subtle variability was evident at small scales, such as "hotspots" of elevated relative abundance that occurred in different places during different years (e.g., the southern half of the study area in 1986, the Carmel Bay area in 1987, and the exposed portion of the Monterey Peninsula during 1988).

In certain locations, kelp canopies persisted through some winters more than others (e.g., southern Monterey Bay, Carmel Bay), as shown by the narrower widths of the dark vertical bars in Fig. 7. Winter 1986/1987 was particularly mild, as shown by the relatively isolated patches of kelp canopy loss. Canopies were annihilated uniformly throughout the study area during the winters of 1987/1988 and 1989/1990 subsequent to powerful storms. However, data were available for only Zone C during the latter winter, and no surveys were done from May 8 through mid-September of that year. Nevertheless, canopies were still noticeably suppressed until at least May.

Canopies were especially depressed in the southern 25% of the study area during and after the winter of 1987/1988, and the northern half of the study area during winter 1985/1986 (except for the canopies in southern Monterey Bay, and those near the head of the Carmel Bay). Unique temporal dynamics were also observed at some locations, most noticeably at Stillwater Cove, where the canopy regularly developed, peaked, and declined earlier than in other areas. Canopy surveys were infrequent from May 1990 through the end of the study, so caution should be exercised when interpreting these interpolated data.

Maximum canopy occurred at least once during each calendar month except February when tallied using the smallest spatial observation window delineated for this study (i.e. mean = 265 meters of coastline; n = 235 subdivisions). However, maximum canopy most often occurred from July to October (Fig. 9a), although the histogram is somewhat misleading because no surveys were performed during August for two of the four years summarized. In comparison, minimum canopy occurred during every month of the year, with most occurrences from December - May (Fig. 9b). No data were available from August to October, 1985, but minimum canopy probably did not occur at many sites during those months. These results were in stark contrast to patterns observed at the spatial scale of the study area extent, albeit sample size was limited to the four years of the study at this spatial scale.

The size of the spatial window over which temporal patterns of canopy abundance were summarized was a critical determinant of the observed results. This scale-dependency was evident when the precision of mean canopy abundance over time was plotted as a function of observational window size (Fig. 10). Temporal patterns of canopy abundance were most variable when summarized at spatial scales of less than approximately 1,600 to 1,850 meters (i.e. equivalent to the distance at which the precision curve reached its asymptote). This result closely corresponded to the typical patch size of 1,600 meters estimated using variogram analysis (Fig. 7b). The consistency of results using these two different methods served as an internal verification that a universal pattern was present at this approximate spatial scale (although data were non-independent).

Canopy "Type" Classification

The GIS layer of kelp canopy persistence facilitated effective visualization of recurring kelp canopies throughout the study area, and 62 kelp beds were delineated (Fig. 6). Cluster analysis of these beds indicated a 3- and 7- cluster solution (Fig. 11), according to the relative magnitude of discontinuities observed in the scree plot (Fig. 11, below dendrogram). Only the results of the UPGMA method were reported because they exhibited a greater cophenetic correlation between the dendrogram output and the original distance matrix (Pearson's $r = 0.74$) than Ward's or Centroid linkage methods. Four "outlier" kelp beds were removed from consideration prior to analysis.

Surface canopies of these outlier beds were often non-existent, and when present, had unusual temporal dynamics. This was likely a result of unpredictability due, at least in part, to limited spatial extent (as suggested by Fig. 10). The 3-cluster solution was more robust than the 7-cluster solution, as indicated by near-perfect correlation among results of three major clustering algorithms (Ward's, UPGMA, and Centroid-linkage; not shown here). The 7-cluster solution did not correlate as well with the results from other algorithms, but was reported because it provided more detailed, biologically meaningful information than the 3-cluster solution, and corresponded well with ecological intuition and personal *in situ* experience within the kelp forests of this area.

Spectral wave information suggested a general relationship between patterns of cluster groupings and approximate wave exposure (Fig. 12). Wave energy typically enters the study area from 270º - 310º, and canopies in Cluster 2 were clearly located along coastline usually protected from the full force of incoming wave energy. Nearly half of the kelp forest habitat in this cluster was located in the relatively wave-protected part of southern Monterey Bay. The other major aggregation of canopies in Cluster 2 was located at the rear of Carmel Bay and at the head of the submarine canyon. Although the coastal orientation of Carmel Bay is approximately due west (the direction facing some of the largest incoming wave events), the canopies there are generally protected from the predominant northwest waves, and may experience similar levels of wave energy to southern Monterey Bay. Furthermore, the submarine canyon redirects incoming wave energy away from its head (Broenkow personal communication), where two of the kelp beds in Cluster 2 were located. The southernmost kelp bed in Cluster 2 was far removed from other kelp beds in its grouping, but was found in the only relatively protected location between Point Lobos and Cooper Point (i.e. in the lee of Point Sur, protected from northwesterly waves). This kelp bed was also inshore of a massive kelp forest/ reef system, which probably played a significant role in dampening incoming wave energy.

The Stillwater Cove kelp canopy (Cluster 3a) had unique temporal dynamics. This was not unexpected due to its location in a relatively enclosed embayment with atypical coastal orientation. Canopies in this area tended to develop and decline earlier than canopies elsewhere (Fig. 8, and the color map for Cluster 3a in Fig. 11).

Cluster 3b included four kelp beds that were closely related to Cluster 3a, and occurred in locations that generally appeared to be "semi-protected" from wave energy. Although the two southern kelp beds in this cluster occurred on the exposed coast, inspection of a high-resolution version of Fig. 6 revealed that these beds were highly convoluted and occurred near a large offshore pinnacle exposed at low tides. This evidence suggests that the seafloor in this area is probably characterized by high-relief bathymetry (e.g., "pinnacles"), which would provide the means for intercepting some of the substantial wave energy typical of this rugged section of coastline. The two northern beds in Cluster 3b were situated within relatively unique coastal locations. The bed found immediately adjacent to the Monterey Breakwater was probably the least wave-exposed kelp bed in the study area. The other kelp bed in this cluster, located on the north side of Point Lobos, also occupied a unique habitat: within an embayment facing due north.

Kelp beds in Cluster 3c were only found offshore of the exposed Monterey Peninsula coast. These beds probably experience different degrees of wave exposure than the kelp beds offshore of exposed coastline south of Point Lobos due to coastal aspect. Only 2 kelp beds made up Cluster 3d, and both of these were south of Point Sur in areas of relatively non-persistent kelp forests. Cluster 3e was the most populous grouping, comprising 26 kelp beds that mostly occupied exposed coastal areas south of Point Lobos. Many of these beds were spatially contiguous within superficially similar habitat (e.g., wave exposure, topography), indicating that canopies exhibited highly correlated temporal dynamics in response to similar environmental conditions. Two of the beds in this group occurred in the rear of Carmel Bay adjacent to "protected" beds.

Cluster 1 was the most enigmatic grouping. The beds in this group generally were characterized by exposed coastal orientations, non-persistent canopies, inshore distributions (i.e. relatively shallow water), and sandy beaches either directly inshore or nearby. The northernmost bed in this group occurred partly within the boundaries of high-resolution bathymetry maps, and inspection of depth data within this area confirmed that this bed occurred in relatively shallow water (approximately 10-12 meters depth at the seaward edge). Most of the beds in this cluster occurred in the southern part of the study area, especially offshore of the large, sandy beach north of Point Sur.

The surface area of canopies in kelp beds in Cluster 2 generally was an order of magnitude greater (in total) than beds in Cluster 3, which were approximately an order of magnitude greater than those in Cluster 1 (Fig. 13a). However, among-cluster

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No linear trends were apparent in the canopy time series among years ($F = 0.52$, $df = 49$, $p = 0.47$, $r^2 = 0.01$). The obvious 12-month cycle (Fig. 3) was the only periodic component detected by spectral analysis and correlogram assessment (Fisher's Kappa = 14.9, $p = 5.0\text{x}10^{-9}$; Fig. 4). A 2-year cycle in minimum canopy abundance was suspected from visual inspection of canopy time series (Fig. 3), but statistical power to detect a 2-year period was negligible due to low sample size ($n = 2$). Canopy data were strongly autocorrelated, with highly significant values at lags 1, 5, and 6 months (Fig. 4). The highly significant positive correlation at lag 1 ($r = 0.77$) indicated substantial month to month dependence. The correlation at lag 12 (which would indicate an annual cycle) was not statistically significant, but this was not unexpected due to diminishing statistical power with increasing lag. Significant negative correlation at lags 5 and 6 were due to the cycle being maximally out of phase.

Regression results did not originally meet assumptions of normality or equal variances, therefore data were square-root transformed and analysis was repeated. The resulting model explained a striking proportion of the canopy variability ($r^2 = 0.78$, F = 284, df = 239, $p < 0.0001$; Fig. 5a, Table 2). Although the assumption of normality still was not met according to the conservative Kolmogorov-Smirnov test, inspection of residual plots against expected value indicated that assumptions were met satisfactorily.

Spectral analysis of residuals revealed no significant periodicity remaining in the time series (Fisher's Kappa = 4.7, p=0.14), further indicating that the regression successfully removed the 12-month cyclic trend. Data were autocorrelated at lag 1 (r = 0.45), revealing the "true" temporal autocorrelation inherent to canopies. Although no statistically significant periodicity was detected in the regression residuals, visual inspection of the residual time series (Fig. 5b) suggested the presence of an irregular, attenuating oscillation through approximately mid-1988. It was possible that this apparent pattern was a result of inaccurate model specification, but this seems unlikely given the excellent fit of the regression line. It was most likely that this pattern was the result of perturbations by large wave events, the effects of which were perpetuated in time by temporal autocorrelation of canopies.

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The larger-scale spatial structure could not be re-analyzed independently of the smaller-scale structure nested within it. Therefore, I re-performed variogram analysis using an active lag distance of 4,250 meters in order to model the smaller-scale structure while isolating the effects of the larger-scale structure. The exponential model provided a good fit to the experimental variogram of the smaller-scale spatial structure ($r^2 = 0.88$; Fig. 7b), despite the lingering presence of trivial "hole" effects. The variogram model reached an asymptote (i.e. the sill parameter: Co + C) at a semivariance value of 58, which represented, in theory, the spatially-independent variance and the total sample variance. However, the sill value was less than the actual sample variance of 63 because the smaller-scale spatial structure was "nested" within a larger structure that had a greater sill value. Approximately 72% of the sample variance was spatially structured, as indicated by the parameter "C". The nugget variance parameter (Co) indicated that 28% of the variability in canopy persistence was unexplained (e.g., measurement and georeferencing error, random noise, historical influences, biological interactions).

The value of the range parameter (Ao) was 804 meters, which indicated: 1) the distance beyond which sampling units were no longer spatially correlated; and 2) the "patch size" of the smaller-scale spatial structure was approximately 1,600 meters in

The 4-parameter sine wave function again provided the best fit to the canopy abundance data (Fig. 14 a-c; Table 3). A suitable model that met statistical assumptions was not found for Cluster 1, despite attempted transformations of raw data (e.g., arcsine, square root, logarithmic). Poor results were expected for this cluster, however, due to both the irregular interannual fluctuations and abundance of zeros in the dataset. All assumptions for parametric statistics were violated, including serial correlation (Table 3), the latter appeared to be a consequence of the preponderance of consecutive zeros in the dataset during winter. Canopy data in Clusters 2 and 3 were fit well by the sine waveform regression ($r^2 = 0.67$ and $r^2 = 0.80$, respectively), although neither regression passed the conservative Kolmogorov-Smirnov test of normality. However, visual inspection of scatter-plots of regression residuals against expected value indicated that assumptions were met satisfactorily.

Although regression models could not be compared statistically for the same reasons as the cluster analysis results, inspection of the "a" and "y0" parameters indicated substantive differences in the mean canopy abundance (Cluster 2 > Cluster 3) and amplitude of the waveform (Cluster 3 > Cluster 2; Table 3). Decomposition of the periodic signals by cluster group did not enhance the percentage of overall variability explained as expected (weighted mean r^2 of 3 clusters = 0.77; $r^2 = 0.78$ for the original regression), but the variability of canopies in Cluster 2 was better explained ($r^2 = 0.80$). Residuals of regressions on Clusters 2 and 3 exhibited similar temporal patterns relative to residuals from the original regression, but had slightly higher first-order autocorrelation (r=0.56 and 0.49, respectively).

DISCUSSION

Temporal patterns of kelp canopy abundance were highly dependent upon the location and scale of observation. Abundance and timing of maximum and minimum canopy in the Monterey Bay area were generally consistent and predictable when quantified over spatial scales greater than approximately 1.6 kilometers. I attributed this consistency to: 1) the relatively large [spatial] observational window that served to average the influences of location and small-scale variability; 2) spatial autocorrelation; 3) strong physical forcing that resulted in strict canopy seasonality; and 4) month-to-month temporal autocorrelation. Deviations from these consistent temporal patterns qualitatively appeared to be driven largely by atypical wave events, and perhaps also the reverberating effects of the massive El Niño event in 1982-3. The latter deviation was evident only after removal of the seasonal trend, which tended to obscure subtle interannual variations in canopy abundance.

Canopy dynamics appeared increasingly stochastic when observed at spatial scales of less than about 1.6 km, which was approximately the same scale as the typical canopy "patch size" determined by variogram analysis. These results indicated that important physical and/or ecological phenomena were influencing canopies or the kelp plants that produced them at this scale (e.g. substrate characteristics, disturbance regime, so-called "contagious" processes of mortality, reproduction, dispersal, and recruitment). In turn, these small-scale processes were nested within larger-scale spatial processes (e.g., disturbance regime, upwelling, geology) suggested by different canopy "types" and variogram analysis (patch size of 8.5 kilometers). Furthermore, it was shown that canopies with different temporal dynamics (e.g., timing of minimum and maximum canopy, amplitude of seasonality) could be found in relatively close proximity (i.e. hundreds of meters).

The temporal patterns of canopy abundance that I observed were generally consistent with qualitative observations of maximum and minimum canopy timing and seasonality previously documented in central California (Miller and Geibel 1973, Gerard 1976, Cowen et al. 1982, and Harrold et al. 1988). My results were also consistent with the quantitative and semi-quantitative observations of Foster (1982), Kimura and Foster (1984), Reed and Foster (1984), and Graham et al. (1997), *when compared at similar spatial scales*. Of the quantitative studies, Graham et al. (1997) measured canopies at the smallest spatial scale (100 x 100 m), and correspondingly witnessed high interannual variability in maximum canopy abundance (> +100% to -50%) and timing of both maximum and minimum canopy (ca. March - October and November - April, respectively). They noted that the annual minimum canopy cover coincided with the first storms following summer, usually October to December, during which time kelp was often absent from their wave-exposed sites. Although the smallest sample unit size for which I quantified variability was substantially larger than that of Graham et al. (1997) (approximately 280 m alongshore x 200 m cross-shore, on average), I also observed maximum and minimum canopy over a long time period and substantial interannual variability, with canopy declining to zero at many locations during winter. This concordance of results was unsurprising given that my study used the same kelp canopy imagery as Graham et al. (1997).

Similar to Graham et al. (1997), Foster (1982) also observed high interannual variability (+200% to -80%) at his Stillwater Cove and Sandhill Bluff study sites when estimating canopy at a scale of ca. 500 x 500 m (actual dimensions un-reported). At Stillwater Cove, maximum canopy abundance occurred from early summer to fall (Foster 1982, Reed and Foster 1984). I found similar results, and also found that this kelp bed's canopy tended to peak earlier than most other canopies in the study area (Fig. 9 and Cluster 3a in Fig. 14).

My results and conclusions diverged from those of Foster (1982) and Graham et al. (1997) when canopy dynamics were considered over large spatial scales. Over large scales (i.e. > ~1.6 km), canopy cover was substantially less chaotic among- and within-years, and timing of both minimum and maximum was more consistent. For example, minimum canopy cover occurred during February or March, not immediately subsequent to the first storms after summer as reported by Graham et al. (1997). However, some of the differences among studies could have been attributable to differences in the time period analyzed. For example, Graham et al. (1997) reported results for 1990-1991, whereas I largely restricted analysis to the period of consistently collected data from 1985 - 1989.

In a study encompassing the same time period as Foster (1982), Kimura and Foster (1984) estimated canopy abundance at a scale of approximately 1,800 m alongshore x 600 m cross-shore (actual dimensions un-reported) for a kelp forest canopy offshore of Carmel Beach, adjacent to Foster's (1982) study site at Stillwater Cove. They reported highly regular seasonality, which was consistent with my findings in that canopy dynamics became more consistent when quantified at scales greater than approximately 1.5 km. Kimura and Foster's (1984) method of canopy measurement was semi-quantitative, however, therefore it was not possible to rigorously assess the degree of interannual variability in canopy abundance.

The non-linear nature of the relationship between canopy variability and sample unit size revealed the homogenizing effect of aggregating small-scale spatial heterogeneity (e.g., habitat complexity, "random" processes of disturbance, ecological interactions) in the presence of spatial autocorrelation (Levin 1989, Bellehumeur et al. 1997). Likely mechanisms responsible for the observed pattern of spatial autocorrelation (i.e. patch sizes of approximately 1.6 and 8.5 km) would presumably exhibit similar spatial structure as the pattern itself, but few process-oriented studies have rigorously spanned scales from meters to kilometers in kelp forest environments. However, several studies demonstrated empirically and theoretically that spore dispersal and recruitment of *Macrocystis* may commonly occur at the scale of meters to kilometers (Anderson and North 1966, Reed et al. 1988, 2004 and Gaylord et al. 2002). Further, Graham et al. (1997) concluded that sporophyte recruitment events were regulating *Macrocystis* population dynamics at their study sites in central California, which suggests that the spatial scales of dispersal and recruitment processes may be the driving factor of the observed pattern. Reproductive synchrony (Reed et al. 1997) at similar spatial scales would provide additional support.

Wave-induced disturbances also may occur at scales of meters to hundreds of kilometers due to the removal of individuals, entanglement, and spatial patterns of wave disturbance, respectively (e.g., Dayton et al. 1984, Seymour et al. 1989, Edwards 1999). Other potential mechanisms include geology, substrate, and time-averaged "wave exposure", but it seems unlikely that these potential causative factors would exhibit consistent spatial structuring at the scale of approximately 1.6 kilometers. It seems more likely that these factors drive autocorrelation at larger spatial scales (e.g., Edwards 2004), and could be responsible for the patch size of 8.5 km identified in this study.

Spatial patterns identified in my study were apparent in the results of several studies done within my study area. Nearby observations were predicted to be similar (i.e. correlated), and observations at greater distances less so. Visual examination of figures in Graham et al. (1997) suggested relatively high correlation of several dependent variables (i.e. density of *Macrocystis* canopy recruits, juveniles, adults, and surface canopy) between within-site "stations" positioned 100-300 meters apart for 2 of their 3 sites that were distributed over 8.5 km of Monterey Peninsula coastline. They had no explanation for the observed differences between the two stations at the other site, but speculated that subtle differences in wave exposure may have been responsible. Among-site correlations were weak, but correlations were confounded by differences in wave exposure among sites.

Similarly, Harrold et al. (1988) showed substantial among-site differences in adult *Macrocystis* densities over the same 8.5 km stretch of coastline, but comparisons were again confounded by differences in wave exposure. In contrast to Graham et al. (1997), Harrold et al. (1988) showed high within-site correlations of adult *Macrocystis* densities among transects at only one or two of their four sites. However, they sampled perpendicular to shore (i.e. "across" the variability) whereas Graham et al. (1997) sampled parallel to shore, and sample unit size was much smaller in the study by Harrold et al. (1988). Furthermore, an explicit goal of the study by Harrold et al. (1988) was to sample as many microhabitats as possible within a site, therefore it was likely that their results were attributable to small-scale habitat differences.

Cluster analysis of bed-specific canopy dynamics provided insight into the distribution of different kelp forest canopy types in the Monterey Bay area, and this technique appeared to be a useful classification tool. The cluster types and their locations were generally consistent with the expectation that canopy variability was correlated with the degree of wave exposure, although unfortunately this hypothesis could not be tested meaningfully without a quantitative metric. Cluster types and their spatial locations appeared to correspond relatively well to the kelp forest types proposed by Foster and Schiel (1988) and elaborated upon by Foster and Van Blaricom (2001), and *in situ* observations of algal communities in these areas since 1973 (e.g., Devinny and Kirkwood 1974, Foster 1982, Reed and Foster 1984, Kimura 1980, Kimura and Foster 1984, Harrold et al. 1988, Graham et al. 1997, Foster and Van Blaricom 2001). Cluster results did not corroborate the few studies prior to 1973 (Crandall 1912, Andrews 1945, McLean 1962) due to a major change in the regional distribution, abundance, and relative proportion of *Nereocystis* and *Macrocystis* forests beginning in the 1950s (reviewed in Miller and Geibel 1973). Interestingly, McLean (1962) noted that the only stands of *Macrocystis* were in parts of southern Monterey

Bay and Carmel Bay, and south of Point Sur. Although it is unclear whether or not he referred specifically to the *Macrocystis* bed in the lee of Point Sur, his description appeared to closely correspond to the locations where kelp beds in Cluster 2 were found.

Of Foster and Van Blaricom's (2001) four proposed types of kelp forests in central California, two, and possibly three, of these types were present in the study area. One of their types is found in wave-protected southern Monterey Bay, where kelp forests are characterized by persistent kelp canopies, relatively few understory kelps, and perennial red algae. Another type is associated with hard, high-relief substrate in wave-exposed areas south of Monterey Bay, characterized by a seasonally variable kelp canopy of *Macrocystis* or *Nereocystis* and abundant understory kelps and coralline algae. Their third type is similar to the latter, but with greater cover of sessile invertebrates. Depending on the interpretation of my cluster analysis, 3 or 7 types were identified; the 3-cluster solution corresponded most closely with Foster and Van Blaricom's (2001) type scheme. No single *in situ* study quantified community structure or habitat within each of these three clusters, but data were available from several individual studies to facilitate comparisons (e.g., Devinny and Kirkwood 1974, Kimura 1980, Harrold et al. 1988, and Foster and Van Blaricom 2001). However, conclusions based on this approach were potentially confounded by time.

Cluster 1 included canopies that were highly variable from year to year and were often eliminated entirely during the winter. These beds may have exhibited anomalous dynamics because: 1) they were occupied in whole or part by *Egregia* or

Nereocystis, a species with an annual life-history strategy which often occurs in habitats with increased water motion unsuitable for *Macrocystis* (Foster and Schiel 1985); 2) sand scour or burial was common; 3) recruitment limitation (Graham et al. 1997); or 4) habitats were sub-optimal due to high wave exposure (Graham 1997), or other factors. Kelp forests in this cluster occupied a very small percentage of the total canopy area, however, therefore it was unclear how important these areas were ecologically. However, Cluster 1 was more prevalent in the southern reaches of the study area, suggesting that this type may be more important south of the study area. This type did not have an analogue in Foster and Van Blaricom's (2001) classification scheme, and no *in situ* data were available to provide additional insight.

Foster and Van Blaricom's (2001) type 1 (as numbered by this study) corresponded with Cluster 2 in the present study, which occurred not only in southern Monterey Bay as they predicted, but also in protected parts of Carmel Bay and one bed south of Point Sur. These areas were all characterized by persistent kelp canopies with relatively high mean abundance (averaged over time) and low temporal variability. All three areas appeared to have low densities of understory kelps and low cover of sessile invertebrates (Devinny and Kirkwood 1974, Kimura 1980, Kimura and Foster 1984, Foster and Schiel 1985, and Foster and Van Blaricom 2001; but see Harrold et al. 1988). These studies also reported that cover of geniculate coralline algae and foliose red algae was generally high and intermediate, respectively, in both the Carmel Bay and Point Sur kelp forests, but the reverse appeared true for southern Monterey Bay. Overall, these areas appeared to be structured similarly with respect to algal and invertebrate communities, although species composition of foliose red algae and understory kelps varied somewhat among areas (e.g., *Laminaria setchellii* was observed in addition to *Pterygophora californica* at the Point Sur site).

Cluster 3 in my study appeared to represent Foster and Van Blaricom's (2001) type 2 (as numbered by this study). However, my study suggested that this general type may actually be partitioned into five groupings, albeit two of these groups were "singletons" comprised of only one or two kelp forests (Cluster 3a and 3b in Fig. 12). Cluster 3a represented Stillwater Cove, which Foster and Schiel (1988) specifically noted as exhibiting strong similarities in community structure with kelp forests along the Big Sur coast (i.e., south of Point Lobos). If this is the case, it would suggest that partitioning Cluster 3 into five discrete groupings would be excessive "splitting." However, Devinny and Kirkwood (1974) identified the Whaler's Cove kelp forest in southern Carmel Bay (included in Cluster 3b) as having a "transitional" algal community between protected and exposed types, which gave some support for the 7-cluster interpretation. Cluster 3b also included a seemingly anomalous kelp forest in the most wave-protected location in the study area; it was not clear why this canopy type was not grouped within Cluster 2, but factors other than wave exposure or canopy persistence may have been more important (e.g., increased siltation rates due to low water movement?).

Foster and Van Blaricom's (2001) Granite Creek site (immediately adjacent to the Granite Canyon Laboratory; Fig. 1) was dominated by *Nereocystis* and understory kelps. Canopy dynamics are known to be different between *Nereocystis* and

Macrocystis (Foster 1982, Foster and Schiel 1985), but the present study's classification method did not distinguish this kelp bed from others along the coast south of Point Lobos as expected. However, Foster and Schiel (1988) and Foster and Van Blaricom (2001) lumped seasonally variable *Nereocystis* and *Macrocystis* canopies into the same category (their type 2), which would similarly not have distinguished the Granite Creek kelp forest. An explanation for the differentiation between Cluster 3c and Cluster 3e was not obvious with respect to algal community characteristics described by Harrold et al. (1988) and Graham et al. (1997).

The classification method described in this study is a promising tool for distinguishing among kelp forest types at large spatial scales, but it obviously requires independent, *in situ* validation of ecological relevance, as Foster and Schiel (1988) and Foster and Van Blaricom (2001) suggested for their proposed divisions. The validity of the canopy types identified in this study was supported by consistently different patterns of abundance in the time series after aggregation by cluster type (Fig. 13). Type classification also yielded refinements to the probabilistic process models for Cluster 3, although total r^2 was not improved (Fig. 14 b-c, Tables 2 and 3). However, this supporting evidence should be considered a confirmatory internal validation.

Moreover, the results of the cluster analysis were sensitive to the choices made during analysis (e.g., distance matrix, two data standardizations, cluster linkage method). The resolution and extent of the time series was also important as it allowed classification based on interannual and seasonal differences in canopy dynamics. Results could have been misleading if annual replication was inadequate, as spatially and temporally variable disturbances (e.g., wave events) could have disproportionately affected canopies with fundamentally similar dynamics, potentially obscuring group membership.

The classification of kelp beds in this study resulted in distinct divisions between adjacent kelp beds that were surely an artificial partitioning of a more-or-less continuous variable, but the conceptual benefits of the model probably outweighed the relatively minor ecological simplifications. Nevertheless, this technique could prove useful to kelp forest ecology and resource managers if kelp forest community types could indeed be meaningfully classified according to their temporal dynamics. If validated, this scheme could be used to classify kelp forests at local scales within regions of central California as an ecologically meaningful alternative system to the California Department of Fish and Game's current administrative system. Furthermore, the results could be used to provide context for small-scale *in situ* studies (past and future), inform designation of appropriate experimental control sites or marine reserves, and to increase inference space (i.e. generality) if sampled randomly.

Conversely, the effects of the January 1990 wave event on the surface canopy were not subtle. This was apparently an extremely rare event probably unlike any since at least the 1950s when *Macrocystis* became widespread in the region (hindcasts reported in Seymour et al. 1989, National Oceanic and Atmospheric Administration unpublished data). Therefore the canopy abundance subsequent to the storm may have been one extreme in the continuum of possible realizations of minimum winter canopy abundance. Because of data gaps, it was unclear whether this storm subsequently affected maximum canopy in the following two years. Minimum canopy during 1990/1991 was not unusually low, but abundance was again low in December 1991, two to three months prior to expected minimum canopy. Actual minimum canopy abundance during winter 1991/1992 was probably even lower, indicating persistent storm effects. Graham et al. (1997) reported substantial mortality of adult *Macrocystis* resulting from the storm, but adult densities appeared to rebound to former levels within six months to one year at their two protected sites. The apparent synchronization of canopy dynamics following this wave event according to cluster type suggested that age structure may have been homogenized, as postulated by Seymour et al. (1989).

CONCLUSIONS

Description of a system is the fundamental step upon which the deduction of mechanistic processes is based. Numerous studies have quantified time series of kelp canopy abundance via canopy photos (e.g., North 1993, Tegner et al. 1996), but this study was unique in the description of both temporal *and* spatial patterns of kelp forest canopies. I have attempted to lay descriptive groundwork that will be helpful for generating hypotheses to explain underlying causes of variation, designing studies and monitoring programs (and statistical considerations), and putting past and future studies into spatial and temporal context. I identified several spatial and temporal patterns structuring kelp canopies, and possibly the kelp populations and communities with which they are associated. However, it was beyond the scope of this study to deduce the mechanisms for these patterns due to lack of available data (e.g., wave exposure), accessible spatial analytical techniques, and time. Process-oriented correlative and experimental work is left to subsequent investigations.

Large-scale, low-frequency processes (e.g., El Niños, major storms, global warming) are not amenable to manipulative experimentation, therefore it is imperative that lengthy time series be compiled to observe decoupled processes with sufficient replication to obtain meaningful results and conclusions. Statistical techniques for time series analysis typically require consistently-spaced replication with a sample size of at least 30-50 (reviewed in Legendre and Legendre 1998), a considerable investment in time, effort, dedication, and financial resources when canopy surveys must be replicated on an annual basis. Such a dataset is available for parts of southern California kelp canopies (e.g., Tegner et al. 1996), but not for central or northern California. As illustrated by the major change in the distribution and relative abundance of canopy-forming kelps in the Monterey Bay area during the previous 50 years, some of the most interesting processes occur over broad temporal and spatial scales. Remote sensing is an opportune, sustainable strategy to monitor such changes, ideally in conjunction with complementary *in situ* work.

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Appendix A

TABLES

Table 1. Statistics for spatial accuracy of kelp canopy maps, ordered by map series from north to south.

Map Series Number	Map Series Name	Mean RMS Error (m)	Minimum RMS Error (m)	Maximum RMS Error (m)	Number of maps in series
1	Monterey	7.8	6.5	9.4	58
2	Pacific Grove	8.7	6.8	12.5	58
3	Otter Point	8.9	6.2	11.4	58
4	Point Pinos	11.4	9.1	12.1	58
5	Point Joe	11.8	10.2	12.5	58
6	Bird Rock	7.7	5.5	9.8	58
7	Cypress Point	9.3	7.2	10.8	58
8	Sunset Point	5.6	4.1	7.1	58
9	Stillwater Cove	7.4	6.3	9.2	58
10	Carmel Beach	9.9	8.0	11.9	58
11	Carmel River	11.5	9.7	12.6	58
12	Point Lobos	12.2	10.3	12.7	58
13	Highlands	11.4	9.7	12.6	58
14	Yankee Point	13.7	12.2	15.1	48
15	Malpaso	13.6	12.2	14.6	48
16	Soberanes	33.2	31.9	34.8	48
17	Granite Canyon	12.8	10.6	14.0	48
18	Garrapata	14.5	12.5	15.9	48
19	Rocky Point	17.8	15.9	20.4	48
20	Bixby	16.2	14.4	17.4	48
21	Hurricane Point	7.5	5.3	9.1	48
22	Little Sur	12.0	10.2	13.8	48
23	unnamed	8.8	6.5	10.2	48
24	Point Sur	8.0	6.8	9.7	47
25	False Sur	10.6	8.7	12.3	40
26	unnamed	8.0	6.4	12.2	40
27	Big Sur	10.8	9.1	11.8	40
28	unnamed	7.4	6.0	8.8	40
29	Cooper Point	8.7	5.8	10.0	40

Table 2. Parameter estimates for waveform regression of kelp canopy abundance summed over entire study area.

Parameter	Coefficient	Standard Error	t	p
a	0.277	0.0095	29.2	<0.0001
b	364.5	1.3056	279.1	<0.0001
c	3.6157	0.0676	53.5	<0.0001
y0	0.6653	0.0066	100.9	<0.0001

Table 3. Regression results and parameter estimates for waveform regression model of kelp canopy abundance, grouped by cluster. Parameter y0 was reported in transformed units (values should be back-transformed for interpretation by squaring).

Cluster Number	Parameter	Coefficient	Standard Error	t	p
1	a	0.26	0.02	17.63	<0.0001
	b	364.11	2.68	135.99	<0.0001
	c	3.12	0.11	28.35	<0.0001
	y0	0.32	0.01	30.85	<0.0001
2	a	0.18	0.01	19.67	<0.0001
	b	363.88	2.44	148.88	<0.0001
	c	3.72	0.10	36.37	<0.0001
	y0	0.72	0.01	109.87	<0.0001
3	a	0.27	0.01	27.55	<0.0001
	b	364.26	1.73	211.17	<0.0001
	c	3.57	0.07	49.50	<0.0001
	y0	0.61	0.01	89.31	<0.0001

Appendix B

FIGURE LEGENDS

Figure 1. Locator map of study area relative to the state of California (inset). Zones A, B, and C were surveyed 41 times from November 1985 to March 1989; Zones B and C were surveyed an additional seven times through December 1989 (n = 48 surveys), and Zone C was surveyed another 10 times through December 1991 (n = 58 surveys).

Figure 2. Georeferenced canopy maps for each survey date. Asterisks indicate localities that were not surveyed. (a) November 1985 to October 1987 (Zones A-C); (b) November 1987 to December 1989 (Zones A-C); (c) February 1990 to December 1991 (Zone C only).

Figure 3. Time series of kelp canopy surface area for Zone B. Symbols and drop-lines identify individual surveys.

Figure 4. Autocorrelation plot of canopy data for Zone B. "Lag" is equivalent to the 30-day interval between successive data points, which is equivalent to "month" since data were equally spaced to 30-day intervals via linear interpolation.

Figure 5. (a) Relative abundance of kelp canopy within Zone B (labeled by year), and best-fit regression line with 95% confidence intervals (CIs) for regression and canopy data (back-transformed from square root). (b) Regression residuals back-transformed to original units for presentation.

Figure 6. Kelp canopy "persistence" from 1986 to 1989. The left panel is the northern half of the study area and the panel on the right is the southern half. For spatial reference, Soberanes Point is denoted in both panels. Borders around kelp forests are subjectively delineated kelp "beds" (see methods for Canopy "Type" Classification).

Figure 7. (a) Experimental and theoretical variogram depicting spatial structure of canopy persistence along a 42 km x 1 m transect. (b) Same as (a) but calculated over a 4,250 m active lag distance to isolate the smaller-scale spatial structure. Note that lower values of semivariance indicate greater spatial autocorrelation and horizontal dotted line denotes the sample variance.

Figure 8. Locator map and space-time contour plot of relative canopy abundance, standardized by subdivision to a proportion of the maximum value encountered during the period from November 1985 to March 1989. Tick marks on upper and lower axes denote timing of canopy surveys.

Figure 9. Frequency histograms of (a) peak and (b) minimum canopy timing. Only data from 1986 to 1989 were used for tallying peak canopy occurrences, and no data from Zone A were used from 1989 (only three surveys were available for that year in that area).

Figure 10. Measurement precision of kelp canopy variability in time as a function of spatial sample unit size (or, "observational window"). Lower values indicate "better" precision.

Figure 11. Results of cluster analysis for dissimilarity among discrete kelp beds within Zone A (assigned bed numbers not shown). Values in the color map are organized by bed number (rows) and survey date (columns); color intensity varies from red to blue according to magnitude of positive and negative standard deviation, respectively, from mean of column (i.e. date). Below dendrogram is a scree plot of Euclidean distance against the number of clusters. Discontinuities in the scree plot indicate the optimal number of clusters to be retained for interpretation.

Figure 12. Results of cluster analysis projected into geographic space. Inset: polar plot of mean daily wave intensity and directional data for Monterey Bay buoy from July 1991 (the first date directional data were available) to December 2002. Compass direction indicates direction from which waves came.

Figure 13. (a) Time series of absolute canopy abundance according to 3-cluster solution. Surface area was summed for canopies within each cluster. Blue vertical bars represent the divisions between the three sampling periods. (b) Time series of relative canopy abundance according to the 3-cluster solution. Values for kelp beds within each cluster grouping were averaged for each date. Error bars represent +/- 1 Standard Error. Sample size (i.e. number of beds) declined in successive periods. Pie charts indicate the number of kelp beds for which data were available for each sampling period, and the total "habitat area" for each cluster (i.e., defined as the total amount of surface area in which canopy was present at least once during the study). (c) Time series of horizontal orbital displacement (D_{Hmax}) and incoming solar radiation.

Figure 14. (a-c) Relative abundance of kelp canopy within Zone B (labeled by year) for each of three major clusters indicated by cluster analysis. Regression line is bounded by 95% confidence intervals for regression and data (back-transformed from square root).

Appendix C

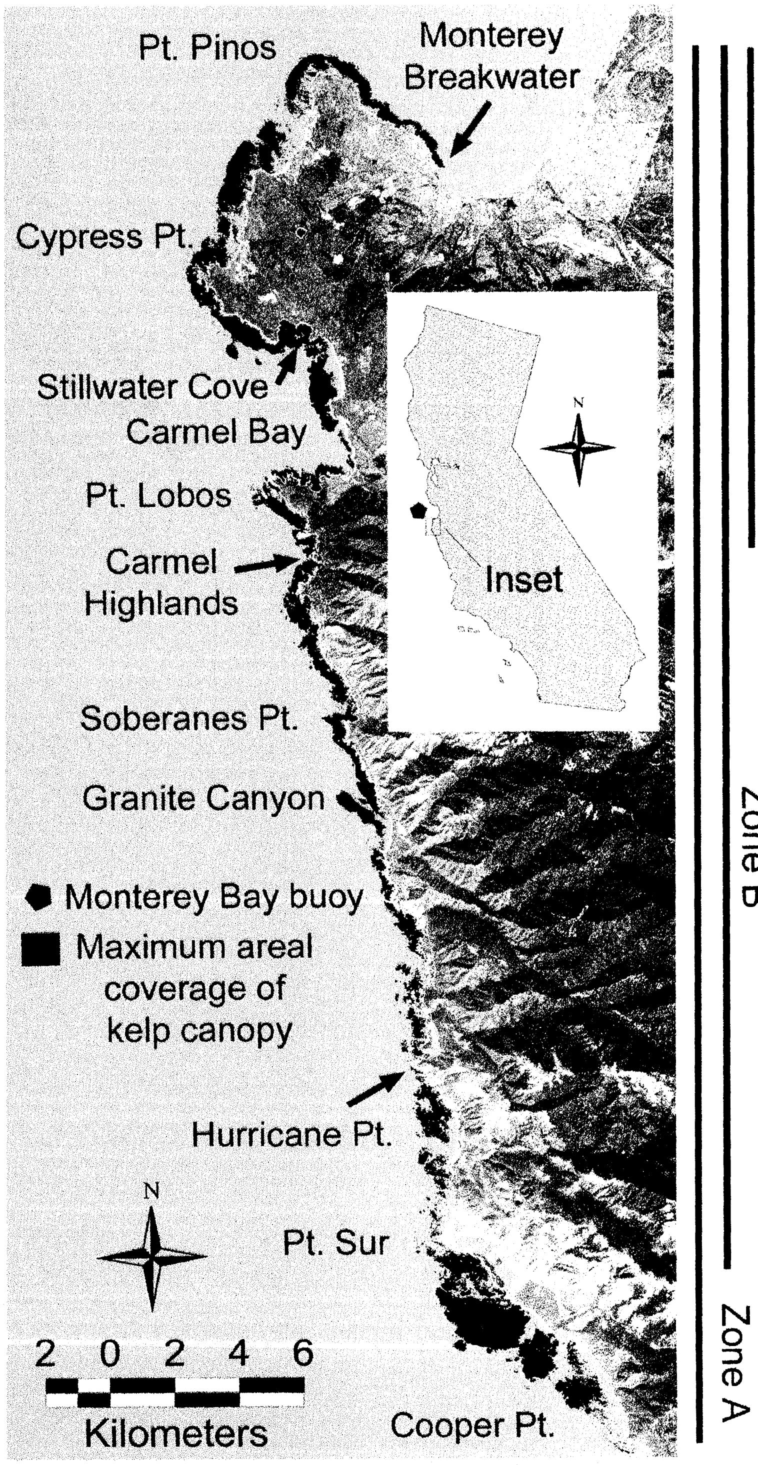


Fig. 1.

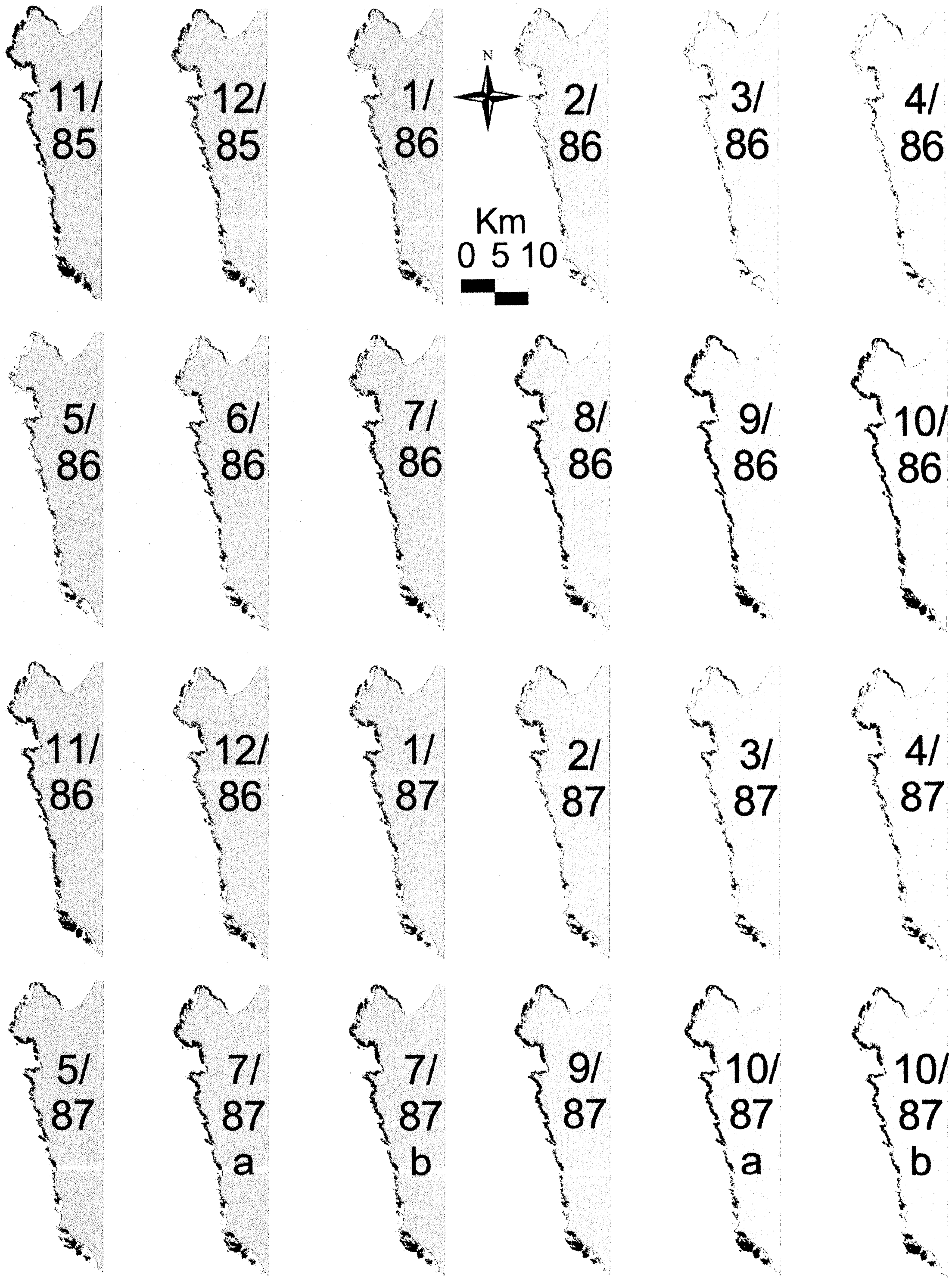

11/ 85
12/ 85
1/ 86
N
Km
0 5 10
2/ 86
3/ 86
4/ 86
5/ 86
6/ 86
7/ 86
8/ 86
9/ 86
10/ 86
11/ 86
12/ 86
1/ 87
2/ 87
3/ 87
4/ 87
5/ 87
7/ 87 a
7/ 87 b
9/ 87
10/ 87 a
10/ 87 b

Fig. 2. a)

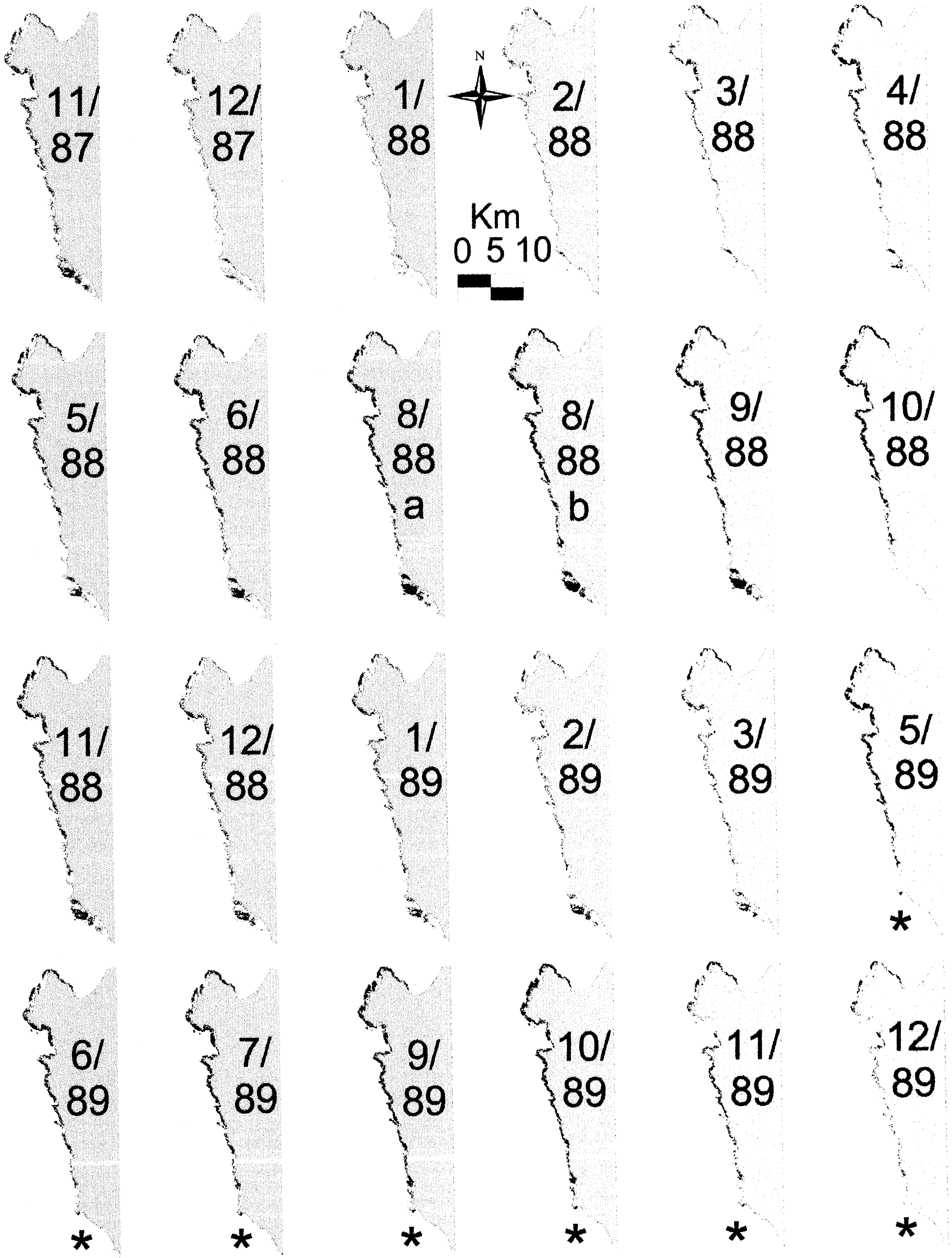

11/ 87
12/ 87
1/ 88
N
2/ 88
3/ 88
4/ 88
Km
0 5 10
5/ 88
6/ 88
8/ 88 a
8/ 88 b
9/ 88
10/ 88
11/ 88
12/ 88
1/ 89
2/ 89
3/ 89
5/ 89
*
6/ 89
*
7/ 89
*
9/ 89
*
10/ 89
*
11/ 89
*
12/ 89
*

Fig. 2. b)

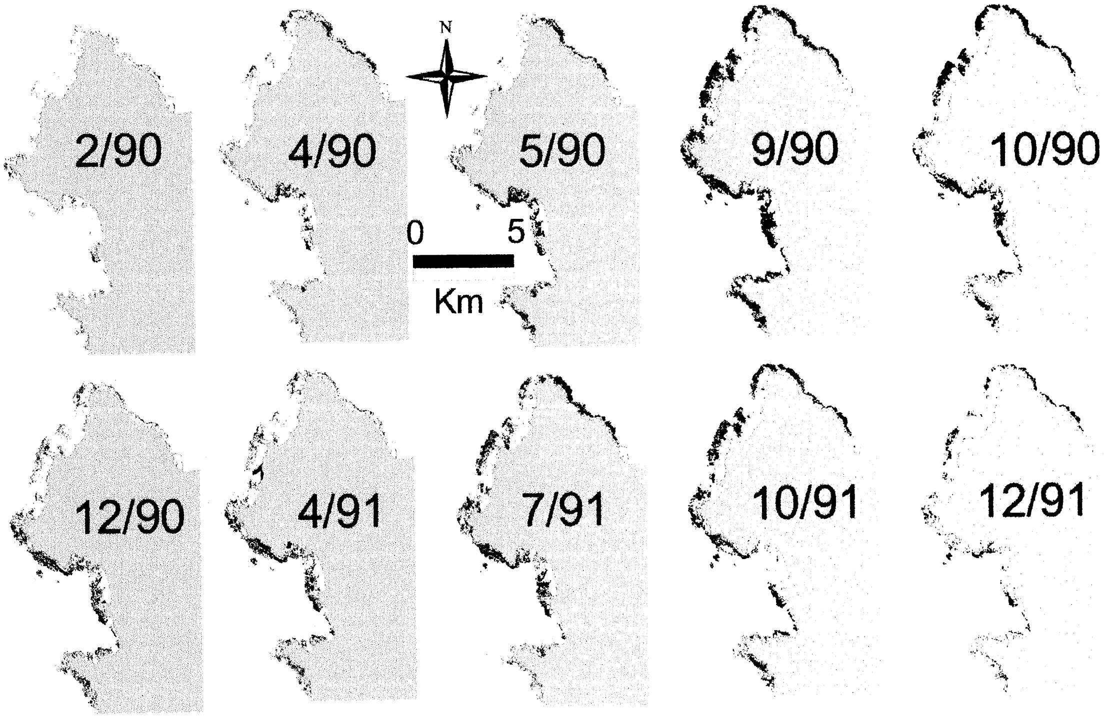


Fig. 2. c)

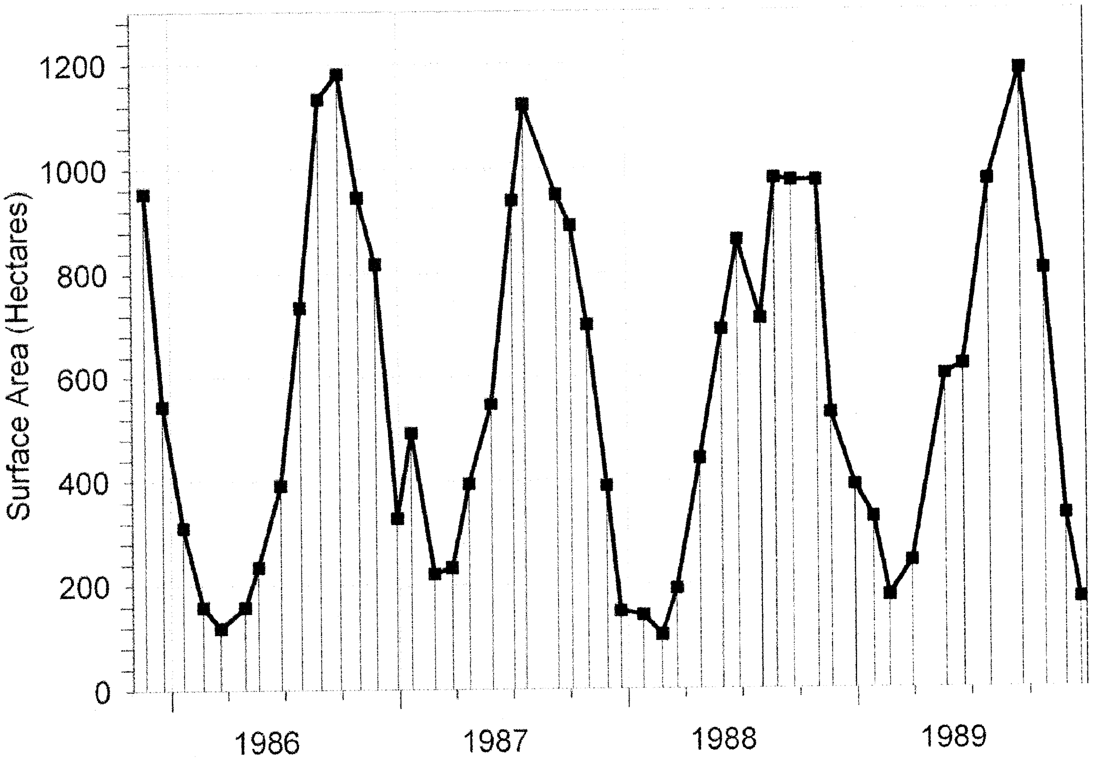
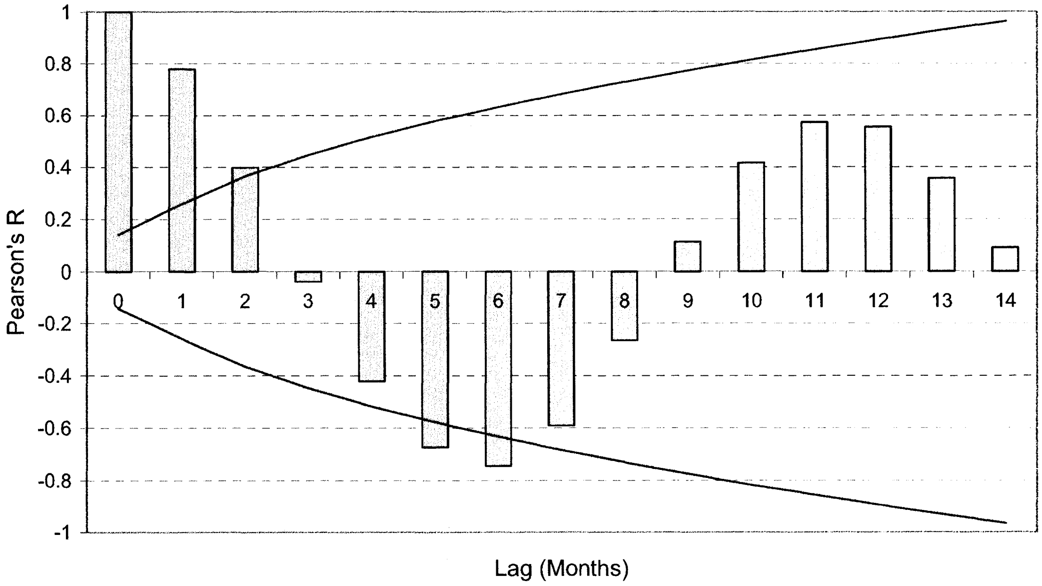

Surface Area (Hectares)
0
200
400
600
800
1000
1200
1986
1987
1988
1989

Fig. 3.



1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Pearson's R
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Lag (Months)

Fig. 4.

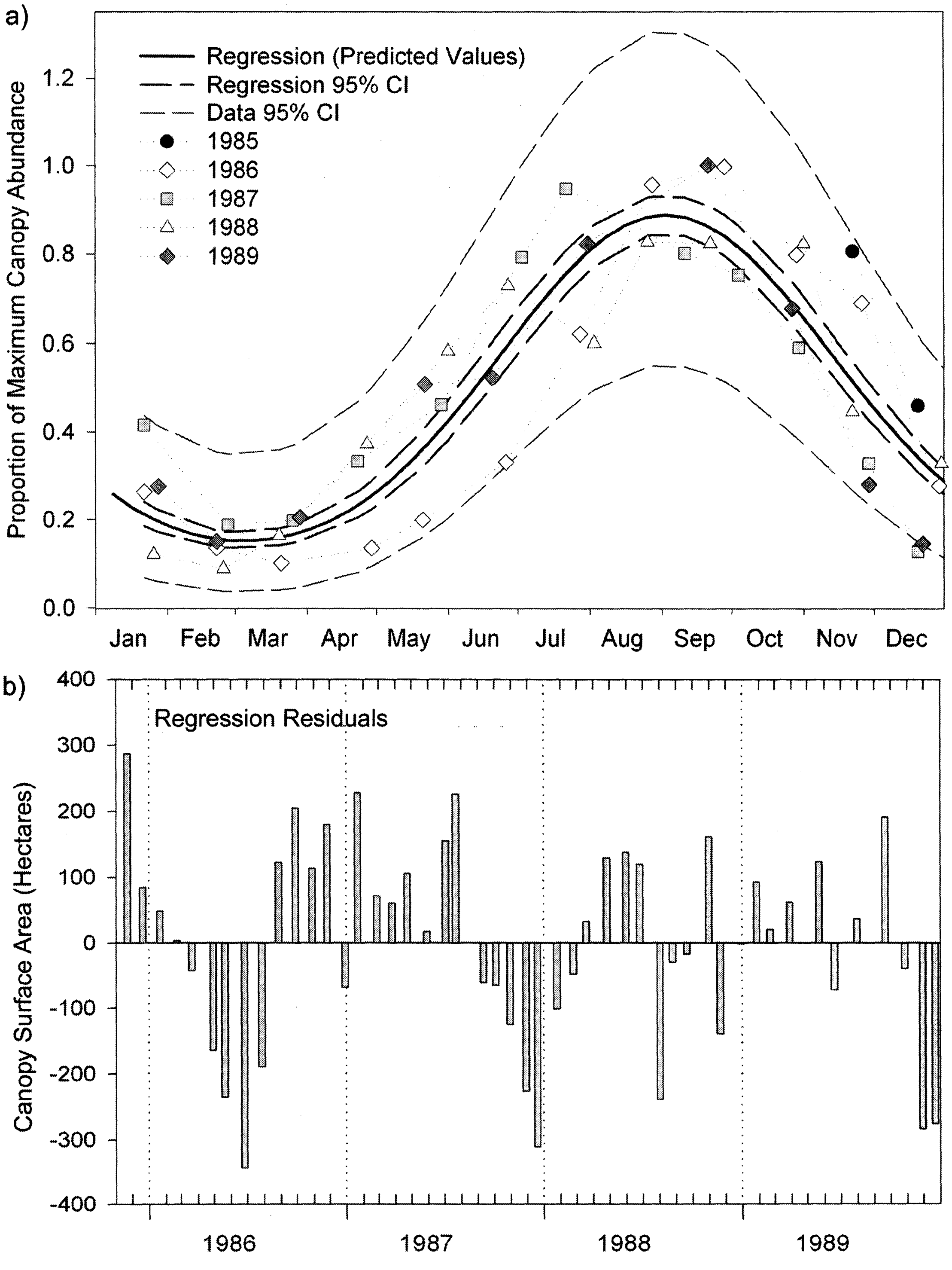

a)
Regression (Predicted Values)
Regression 95% CI
Data 95% CI
1985
1986
1987
1988
1989
Proportion of Maximum Canopy Abundance
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
b)
Regression Residuals
Canopy Surface Area (Hectares)
400
300
200
100
0
-100
-200
-300
-400
1986
1987
1988
1989

Fig. 5.

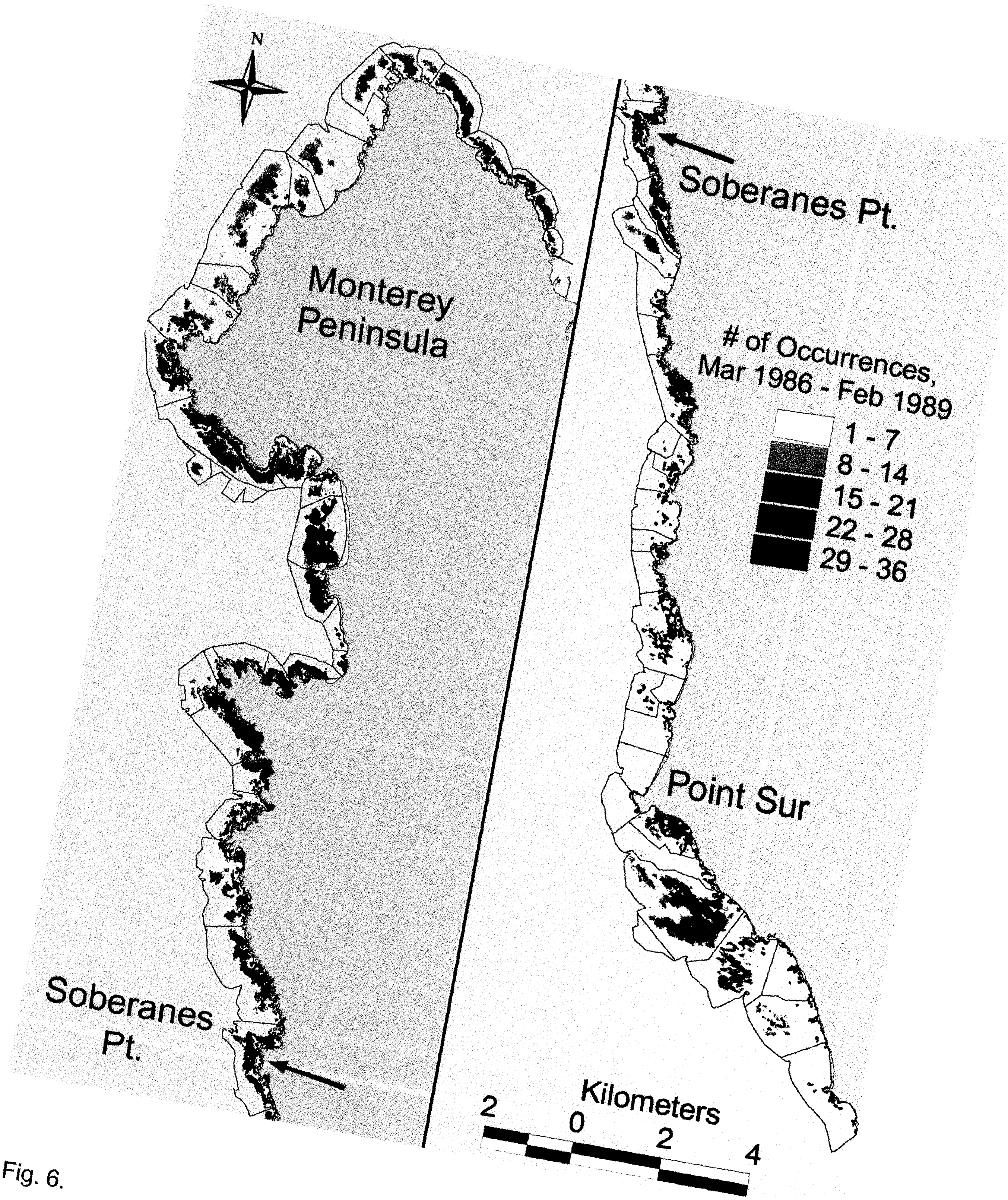

N
Monterey Peninsula
Soberanes Pt.
Soberanes Pt.
Point Sur
# of Occurrences, Mar 1986 - Feb 1989
1 - 7
8 - 14
15 - 21
22 - 28
29 - 36
Kilometers
2
0
2
4

Fig. 6.

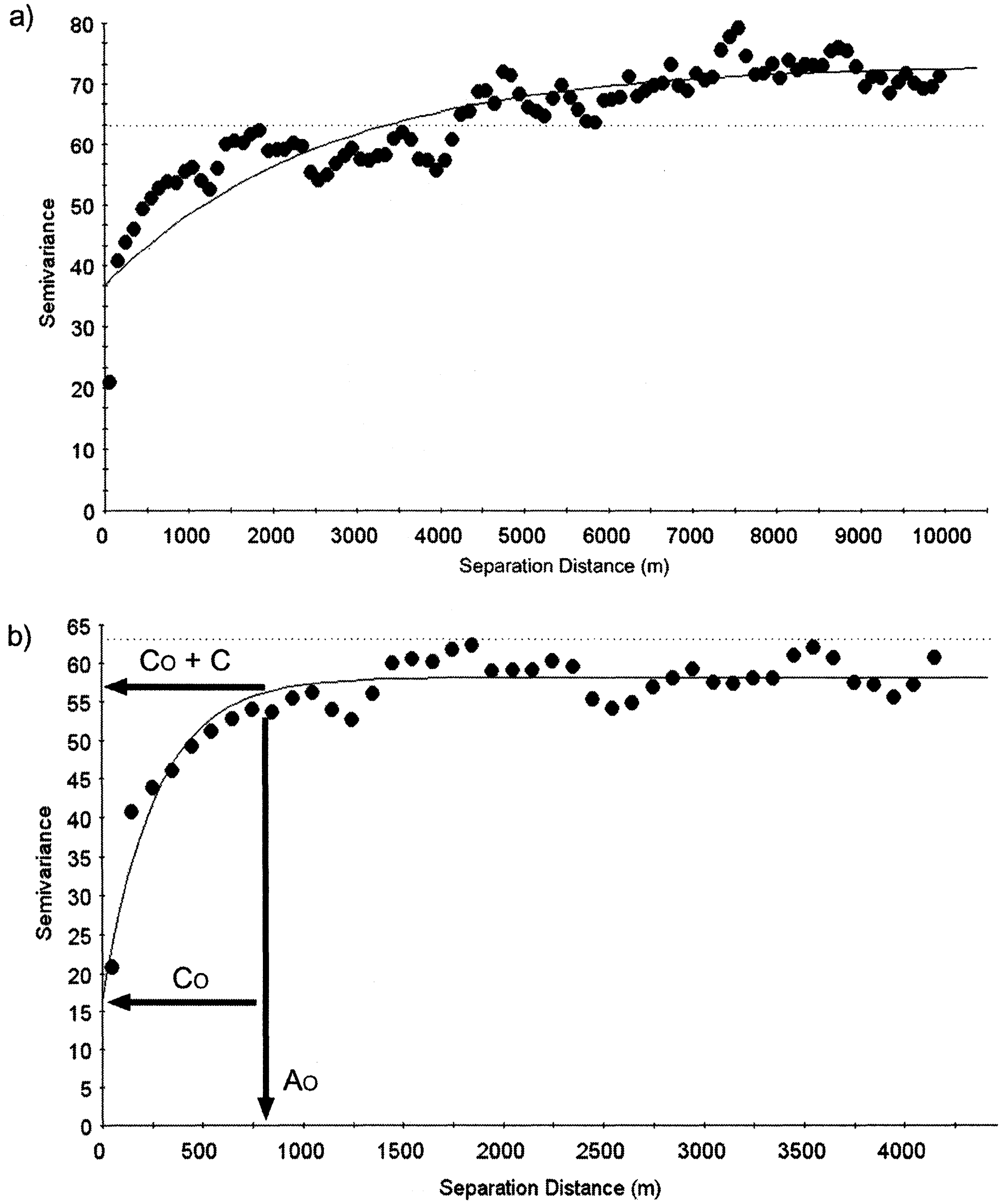

a)
Semivariance
0
10
20
30
40
50
60
70
80
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
Separation Distance (m)
b)
Semivariance
0
5
10
15
20
25
30
35
40
45
50
55
60
65
Co + C
Co
Ao
0
500
1000
1500
2000
2500
3000
3500
4000
Separation Distance (m)

Fig. 7.

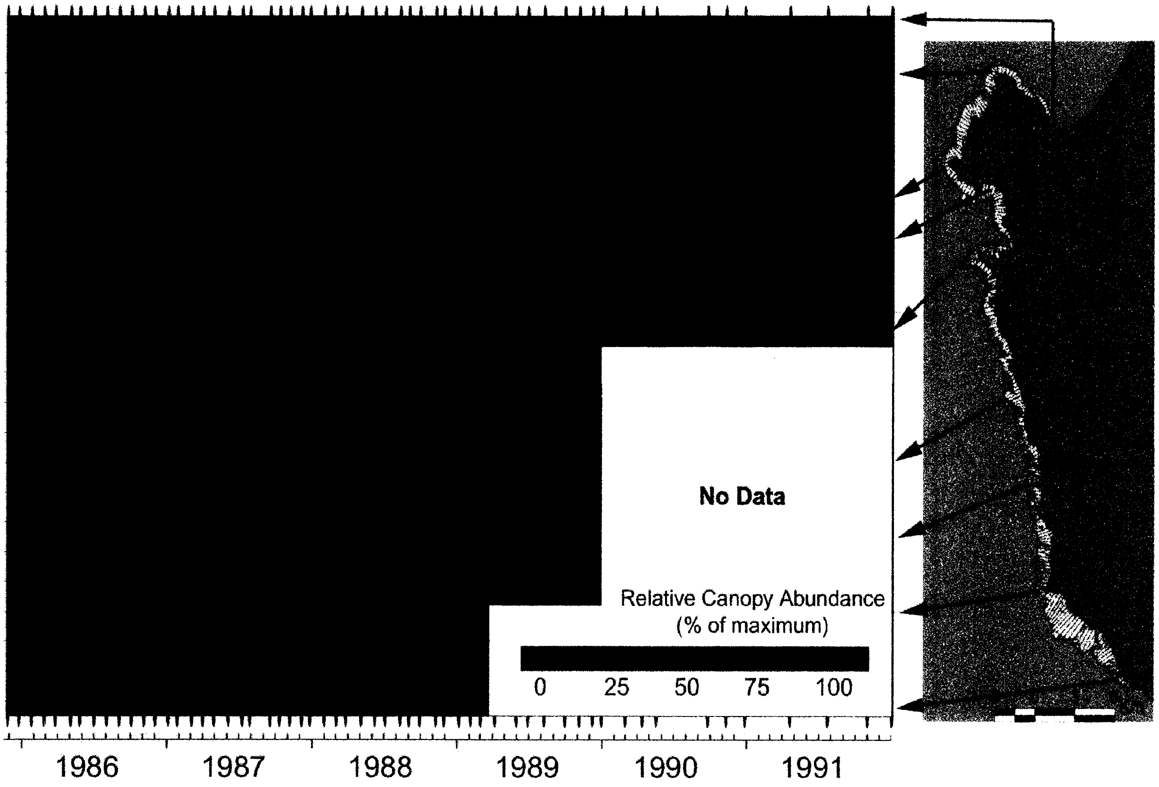
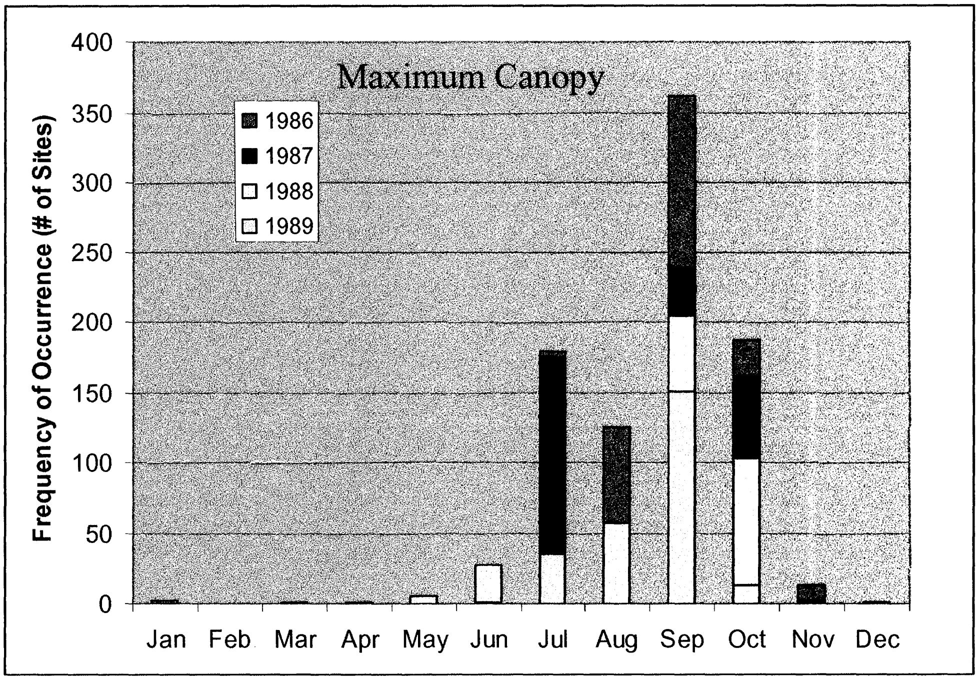

No Data
Relative Canopy Abundance
(% of maximum)
0
25
50
75
100
1986
1987
1988
1989
1990
1991

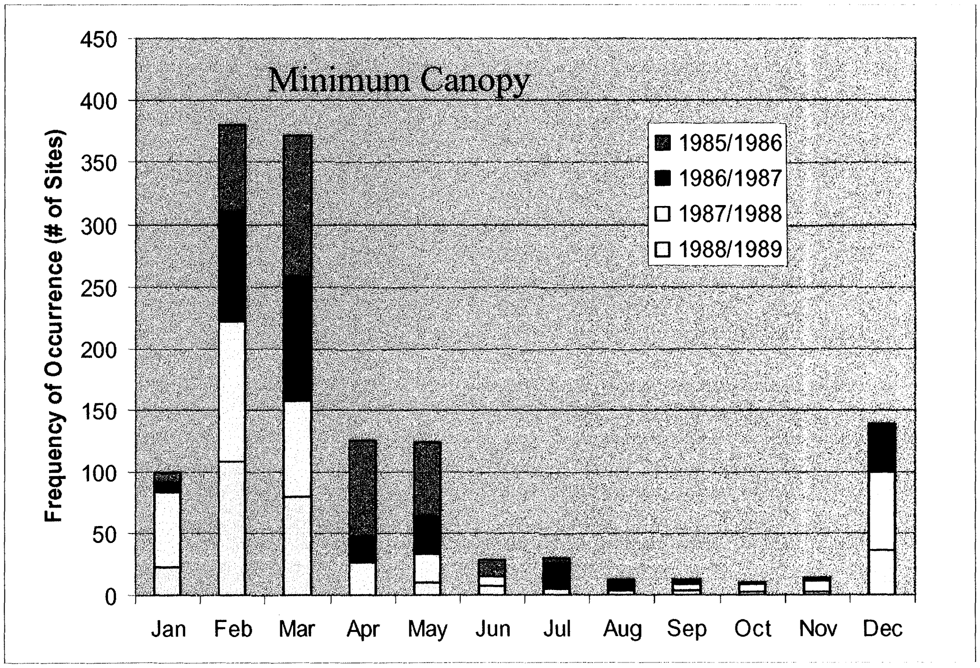
Fig. 8.

a.



Maximum Canopy
1986
1987
1988
1989
Frequency of Occurrence (# of Sites)
400
350
300
250
200
150
100
50
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

b.



Minimum Canopy
1985/1986
1986/1987
1987/1988
1988/1989
Frequency of Occurrence (# of Sites)
450
400
350
300
250
200
150
100
50
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig. 9.

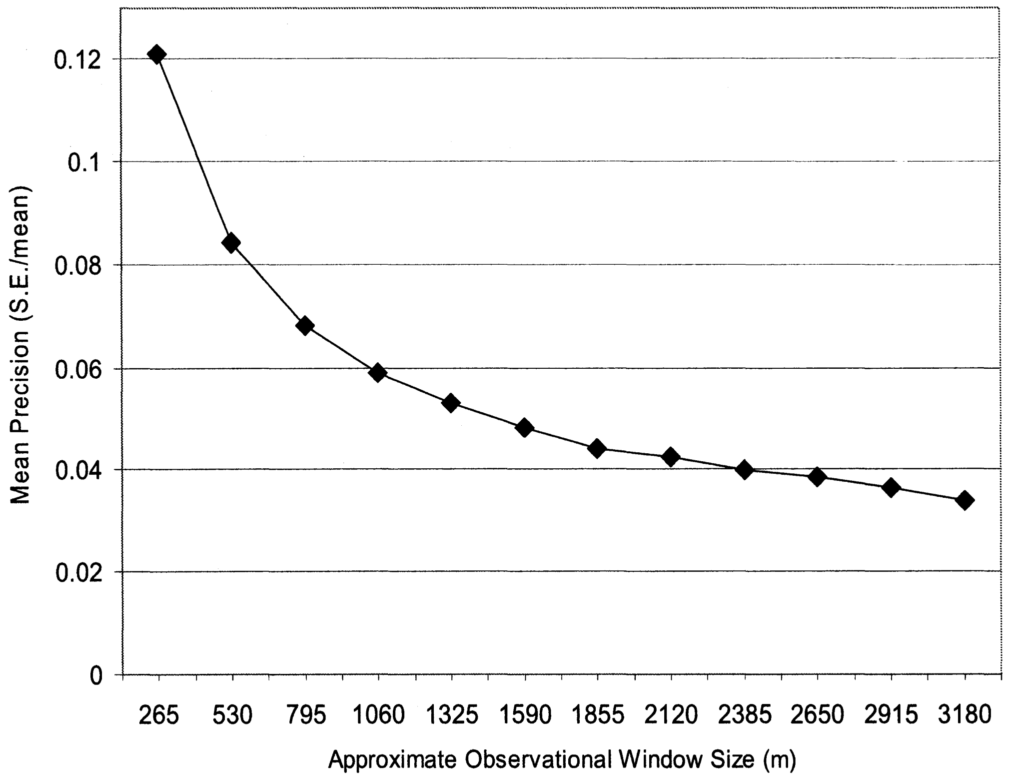

Mean Precision (S.E./mean)
0.12
0.1
0.08
0.06
0.04
0.02
0
265
530
795
1060
1325
1590
1855
2120
2385
2650
2915
3180
Approximate Observational Window Size (m)

Fig. 10.

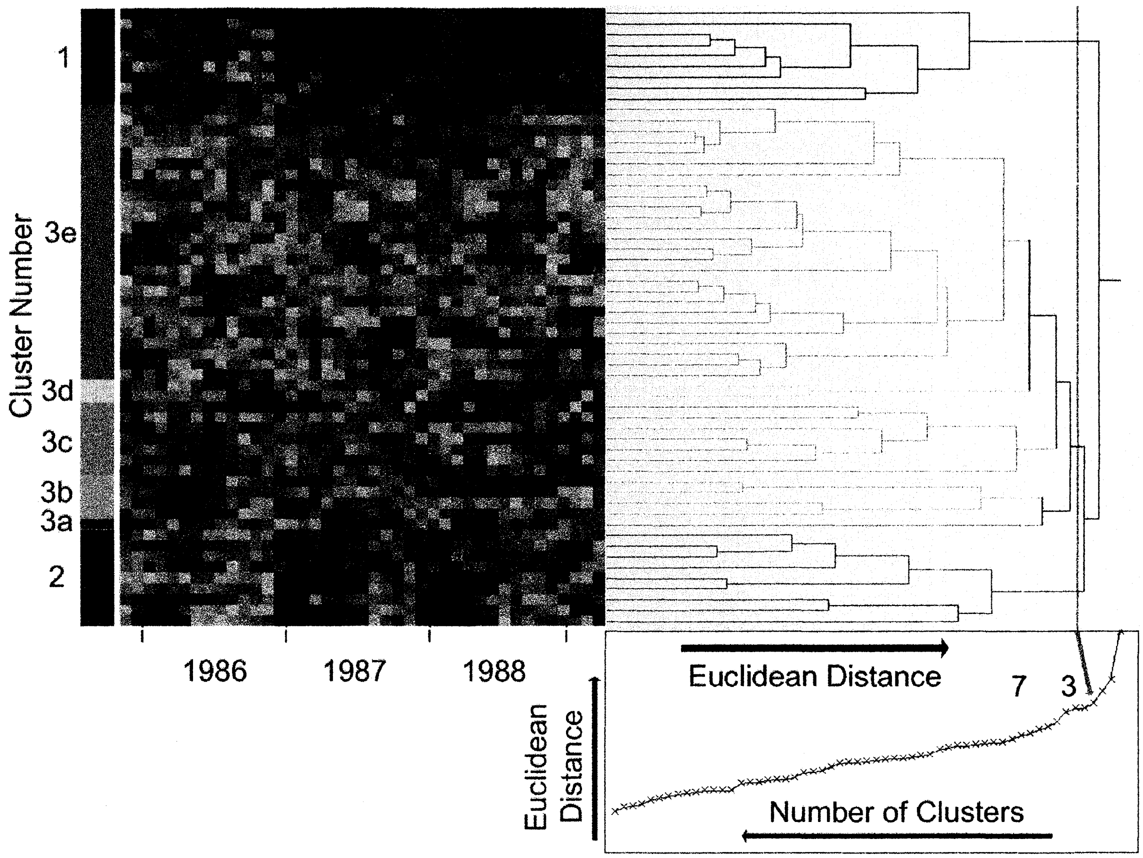

Cluster Number
1
3e
3d
3c
3b
3a
2
1986
1987
1988
Euclidean Distance
7
3
Euclidean Distance
Number of Clusters

Fig. 11.

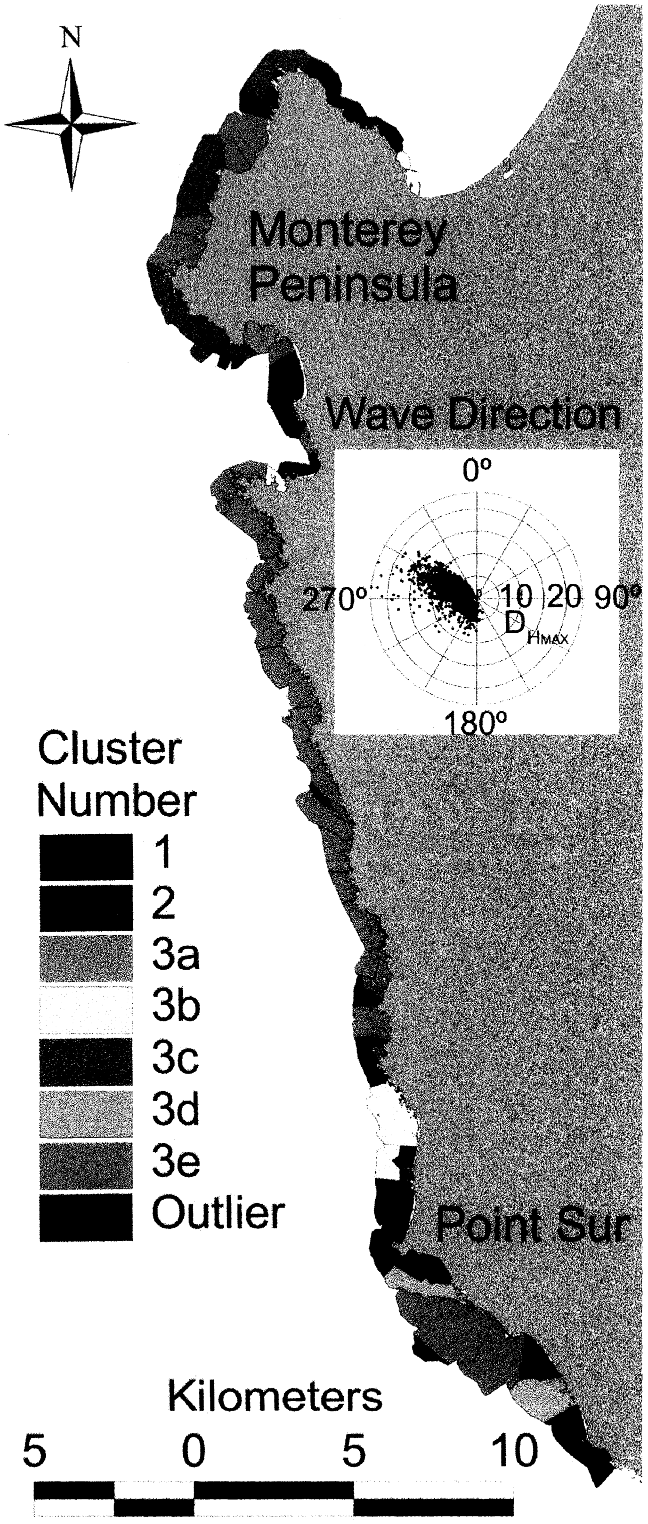

N
Monterey Peninsula
Wave Direction
0°
270°
10 20 90°
D HMAX
180°
Cluster Number
1
2
3a
3b
3c
3d
3e
Outlier
Point Sur
Kilometers
5 0 5 10

Fig. 12.

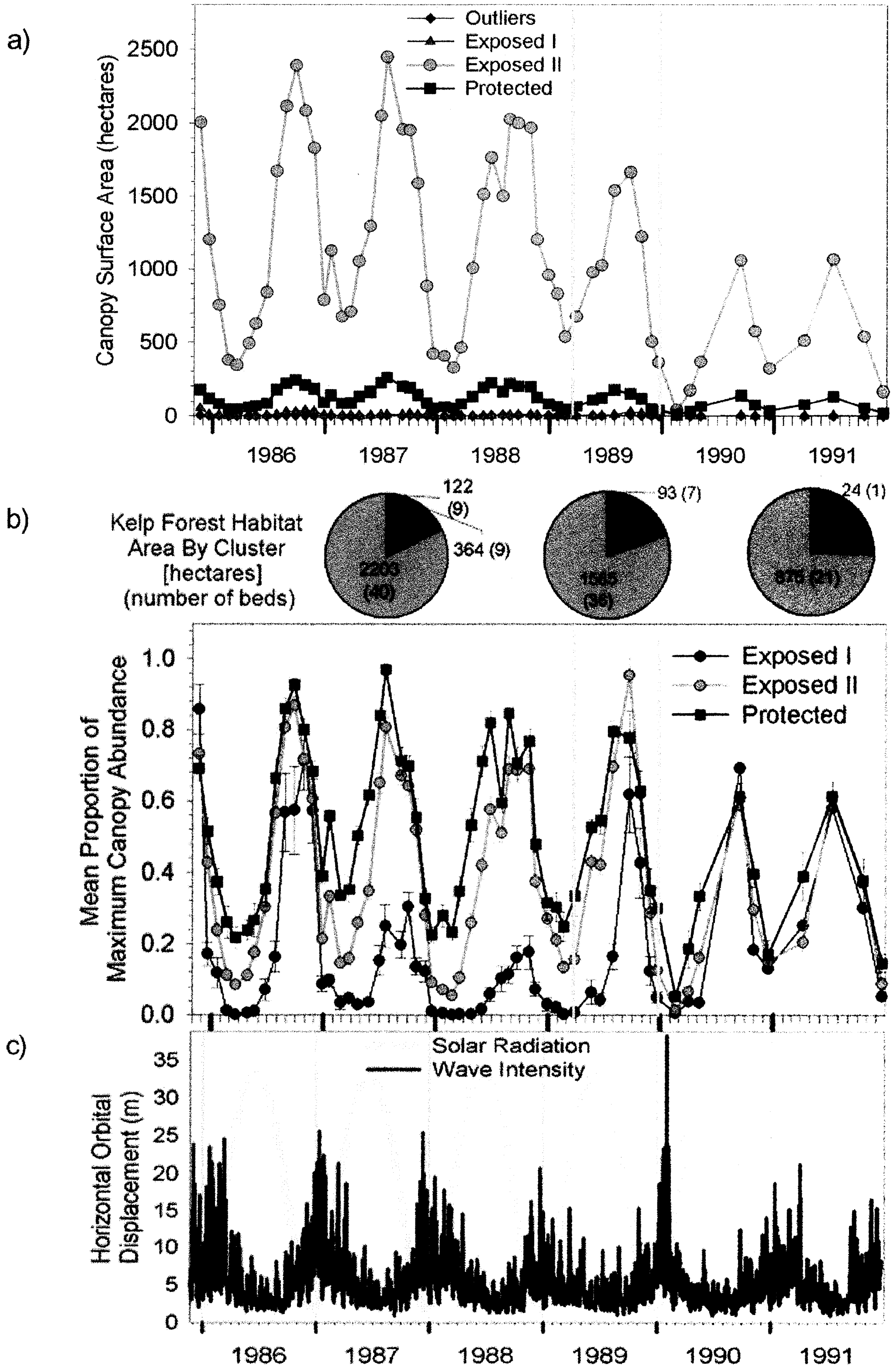

a)
Outliers
Exposed I
Exposed II
Protected
Canopy Surface Area (hectares)
2500
2000
1500
1000
500
0
1986
1987
1988
1989
1990
1991
b)
Kelp Forest Habitat Area By Cluster [hectares] (number of beds)
122 (9)
364 (9)
2203 (40)
93 (7)
1565 (36)
24 (1)
875 (21)
Mean Proportion of Maximum Canopy Abundance
1.0
0.8
0.6
0.4
0.2
0.0
Exposed I
Exposed II
Protected
c)
Solar Radiation
Wave Intensity
Horizontal Orbital Displacement (m)
35
30
25
20
15
10
5
0
1986
1987
1988
1989
1990
1991

Fig. 13.

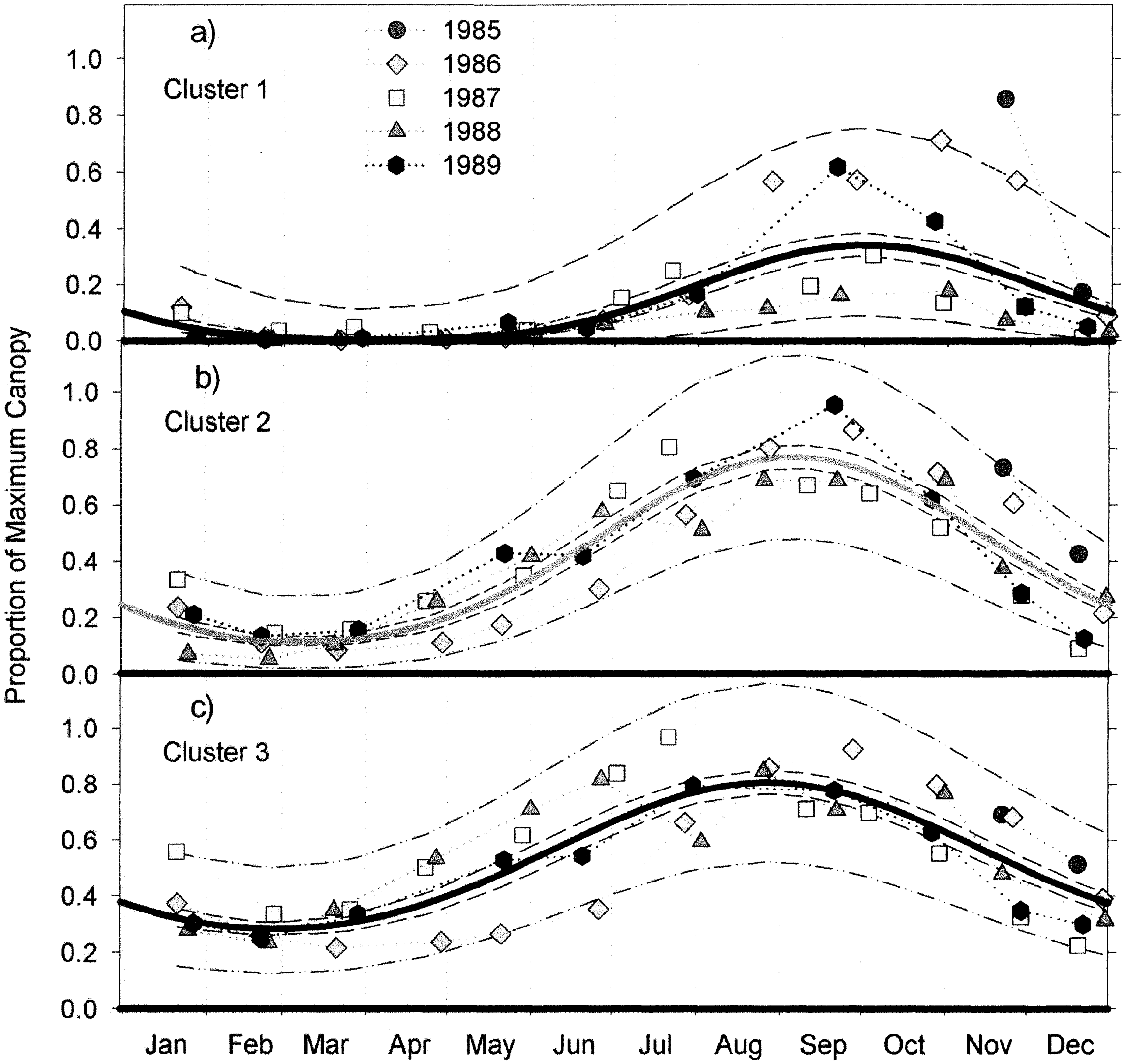

a)
Cluster 1
b)
Cluster 2
c)
Cluster 3
1985
1986
1987
1988
1989
Proportion of Maximum Canopy
0.0
0.2
0.4
0.6
0.8
1.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig. 14.